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U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Science Center

NOAA Technical Memorandum NMFS

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Preface

The main purpose of technical recovery planning for Pacific salmon and steelhead is to produce biologically based viability criteria for listed Evolutionarily Significant Units (ESUs) that will be considered in setting recovery goals. These viability criteria, and the analyses from which they stem, must refer to specific populations and population groups (i.e., populations or groups of populations within a ESU). The purpose of this report is to describe the historical population structure of coho salmon in the Southern Oregon/Northern California Coast (SONCC) ESU in order to guide viability analyses, and to provide a historical context for other parties interested in recovering coho salmon in the geographic region.

We collected and examined available information relevant to the question of population structure of coho salmon in the SONCC ESU, and we present that information here. Readers interested in the conclusions can refer to the abstract, Table 1, and Figure 9.

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Abstract

This report describes the historical population structure of coho salmon in the Southern Oregon/Northern California (SONCC) Evolutionarily Significant Unit (ESU) that includes coastal watersheds from Elk River (Oregon) in the north to Mattole River (California) in the south. Developing an understanding of historical population structure of populations within an ESU is a prerequisite in recovery planning that ultimately results in the development of biological viability criteria. These viability criteria, and the analyses from which they stem, must refer to specific populations and population groups (i.e., populations or groups of populations within a ESU). Types of information we considered in this report included historical distribution, geographic isolation, dispersal rates, genetic data, life history information, population dynamics, and environmental and ecological diversity. Our analysis of historical population structure was strongly constrained by the lack of data available for consideration; however our approach was intentionally consistent with the approaches taken by Technical Recovery Teams (TRTs) working in more data-rich areas of California and the Pacific Northwest (Currens et al. 2002; Lawson et al. 2006). Because of this lack of data, our determination of historical population structure of SONCC Coho Salmon ESU was based primarily on a simple conceptual model of spatially dependent demographics of 50 populations considered to be historically present. Readers interested in the conclusions and specific population designations can refer to Table 1 (page 26), and Figures 8 and 9 (pages 40 and 46).

In general, the historical population structure of coho salmon in the SONCC ESU was characterized by small-to-moderate-sized coastal basins where high quality habitat is in the lower portions of the basin and by three large basins where high quality habitat was located in the lower portions, middle portions of the basins provided little habitat, and the largest amount of habitat was located in the upper portions of the sub-basins. Nineteen populations that were determined to have minimal demographic influence from adjacent populations and were viable-in-isolation were classified as Functionally Independent populations. Twelve populations that appeared to have been viable-in-isolation but were demographically influenced by adjacent populations were classified as Potentially Independent populations. Small populations of coho salmon that do not have a high likelihood of sustaining themselves over a 100-year time period in isolation and receive sufficient immigration to alter their dynamics and extinction risk were classified as Dependent (17 populations). Two populations were determined to be Ephemeral (Hubbard and Euchre creeks). Ephemeral populations do not have a high likelihood of sustaining themselves over a 100-year time period in isolation, and do not receive sufficient immigration to affect this likelihood. In addition, the habitat supporting an Ephemeral population is expected to be occupied only rarely.

In anticipation of developing of viability criteria at the population scale and integration of population information into viability criteria at the ESU scale, we identify groups of populations that span the diversity and distribution that currently exists or historically existed within the ESU. We refer to these groups as ‘diversity strata’ to reflect our primary focus on the issue of diversity, broadly defined, as the basis for delineating these groups. The TRT organized the independent and dependent populations of coho salmon in the SONCC ESU into diversity strata largely based on the geographical arrangement of the populations and basin-scale environmental and ecological characteristics.

The TRT recognizes that future information and data collection, when available, may provide support for reconsidering our approach, assumptions, and results. In our analyses, much of the uncertainty stemmed from the lack of appropriate data, particularly historical information on distribution, abundance, and dispersal rates. Moreover, recent data are sparse and provided a limited basis for inferring historical population structure.

Acknowledgements

This effort to identify historical populations of Southern Oregon and Northern California Coasts coho salmon was conducted by the SONCC Workgroup of the Oregon and Northern California Coast Technical Recovery Team. The Workgroup consisted of scientist from NOAA National Marine Fisheries Service-Southwest Fisheries Science Center, USGS California Cooperative Fish Research Unit, the Yurok Tribe, the Hoopa Valley Tribe, USDA Forest Service-Pacific Southwest Research Station, USDA Forest Service-Smith River National Recreation Area, and the California Department of Fish and Game. In developing this report, the Workgroup relied on published literature, information reports, and unpublished reports and data made available by state, tribal, and federal agencies.

Throughout the preparation of this report, the Workgroup and the ONCC TRT were provided with information from numerous scientists and fishery managers. Specifically we would like to acknowledge the thoughtful and insightful reviews by the Oregon Department of Fish and Wildlife and the California Department of Fish and Game. Others we would like to acknowledge for meeting with the Workgroup or providing information include Julie Firman (ODFW), Jon Grunbaum (USFS), Bill Jong (CDFG), Scott McBain (McBain and Trush, Inc.), Al Olsen (USFS), Larry Preston (CDFG), Stewart Reid (Western Fishes), Seth Ricker (CDFG), Jeff Rodgers (ODFW), Tom Satterthwaite (ODFW), Tom Shaw (USFWS), Russ Stauff (ODFW), and Jerry Vogt (ODFW). Members of other TRTs throughout California and the Pacific Northwest that provided guidance and feedback throughout this project included Drs. Brian Spence, Steve Lindley, and D. Boughton.

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The Oregon and Northern California Coast Technical Recovery Team consisted of Dr. Walt Duffy, USGS California Cooperative Fish Research Unit; Dave Hillemeir, Yurok Tribe Fishery Biologist; George Kautsky, Hoopa Valley Tribe Fishery Biologist; Dr. Thomas Lisle, USDA Forest Service, Pacific Southwest Research Station; Mike McCain, USDA Forest Service, Smith River National Recreation Area; Mike Rode, California Department of Fish and Game; Dr. Thomas Wainwrigth, NOAA NMFS Northwest Fisheries Science Center; Thomas Nickelson, Oregon Department of Fish and Wildlife; Charles Huntington, Clearwater Biostudies, Inc.; Dr. Gordon Reeves, USDA Forest Service, Pacific Northwest Research Station. The Technical Recovery Team was co-chaired by Dr. Peter Lawson, NOAA NMFS Northwest Fisheries Science Center, and Dr. Thomas Williams, NOAA NMFS Southwest Fisheries Science Center. Recovery Coordinators were Greg Bryant (NOAA NMFS Southwest Regional Office) and Rosemary Furfey (NOAA NMFS Northwest Regional Office).

The SONCC Workgroup consisted of Dr. T. Williams, Dr. W. Duffy, D. Hillemeir, G. Kautsky, Dr. T. Lisle, M. McCain, M. Rode, and Dr. P. Lawson.

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1. Introduction

1.1. Background

The NOAA's National Marine Fisheries Service (NMFS) is responsible for evaluating the status and developing recovery plans for Pacific salmonid species listed under the U. S. Endangered Species Act (ESA). A major goal of the Technical Recovery Team (TRT) for the Oregon and Northern California Coasts Recovery Domain is to develop biological viability criteria for coho salmon (*Oncorhynchus kisutch*) in the Oregon Coast (OC) and Southern Oregon/Northern California Coast (SONCC) Evolutionarily Significant Units (ESUs), listed as threatened under the ESA[1]. This document represents this effort for the SONCC ESU that includes coastal watersheds from Elk River (Oregon) in the north to Mattole River (California) in the south[2] (Figure 1).

The SONCC Coho Salmon ESU was listed as Threatened under the U.S. ESA in 1997 (Federal Register 62:24588-24609). As part of the recovery planning process, the NMFS brought together a group of scientists to serve as a TRT with a goal of providing a scientific context for identifying necessary actions to help the ESU recover. The TRT tasks were to: (1) identify biological viability criteria for populations and the ESU that would lead to recovery and delisting of the ESU; (2) characterize associations between coho salmon abundance and habitat; (3) identify factors of population declines within the ESU; and (4) identify research, evaluation, and monitoring needs.

An ESU is composed of a number of populations with varying features and dynamics. An understanding of the biological organization of populations within an ESU and the temporal and spatial scales relevant to this organization is critical to developing meaningful biological viability criteria. For salmonids, this can range from dependent populations, to independent populations, to population groups, and finally the ESU

[1] As of January 2006, the NMFS determined the Oregon Coast Coho Salmon Evolutionarily Significant Unit does not warrant listing as an endangered or threatened species under the ESA (Federal Register 71:3033-3048).
[2] The Oregon and Northern California Recovery Domain overlaps with the North-Central California Coast Recovery Domain in the area between Redwood Creek (Humboldt County) and the Mattole River. In this region, the TRT for the Oregon and Northern California Coast Recovery Domain is responsible for developing viability criteria for coho salmon and the TRT for the North-Central California Coast Recovery Domain is responsible for Chinook salmon and steelhead.

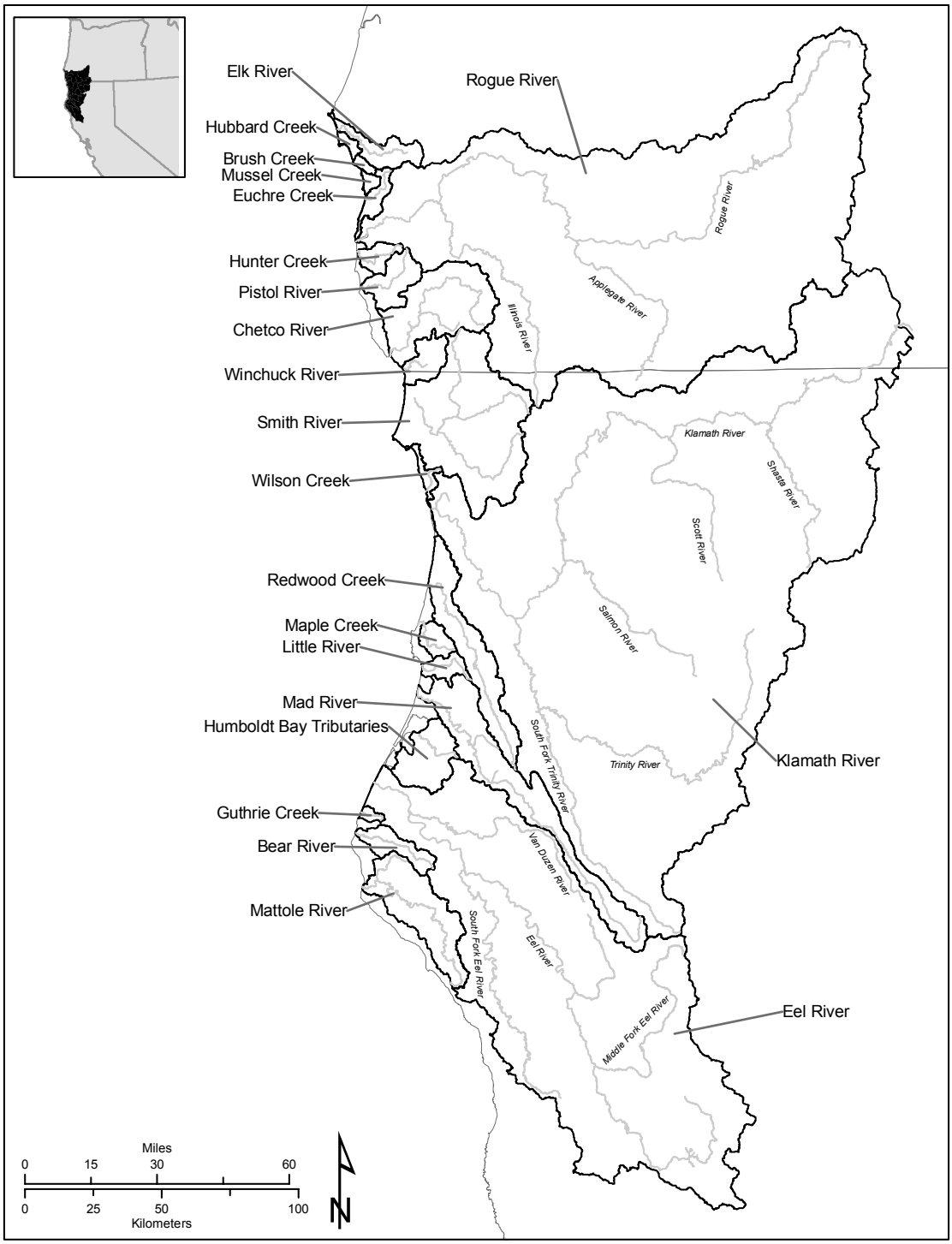


Figure 1. The Southern Oregon/Northern California Coasts Coho Salmon ESU.

(Bjorkstedt et al. 2005; Lawson et al. 2006). This definition of biological organization or biological structure was the first step taken by the TRT because it is critical to understanding the population characteristics that contribute to the viability of populations and thus their contribution to the persistence of the ESU. In the Viable Salmonid Populations document, the NMFS developed the concept of "independent" populations and the characteristics of such populations that indicate viability (McElhany et al. 2000). Those characteristics include abundance, productivity, diversity, and spatial structure.

This document outlines the conceptual approach used to identify the historical population structure within the SONCC Coho Salmon ESU. We apply this approach to delineate historical population structure based on available information and to identify the types of data necessary to refine the historical population structure we propose. Our focus on the historical population structure of the ESU is based on the concept that the historical structure and dynamics of the ESU represent viable conditions. The historical conditions may not be the benchmark for ESU viability, but the further conditions diverge from historical conditions, the less likely the ESU would be viable. The approach used here draws heavily on McElhany et al. (2000), the work of the Oregon Coast Workgroup of the ONCC (Lawson et al. 2006), the work of the North-Central California Coast TRT (Bjorkstedt et al. 2005), and the Central Valley TRT (Lindley et al. 2004).

1.2. The Geographic Setting and General Ecology of SONCC Coho Salmon

The geographic setting of the SONCC Coho Salmon ESU includes three large basins and numerous smaller basins across a diverse landscape. The Rogue River and Klamath River extend beyond the Coast Range and include the Cascade Mountains. The Eel River basin also extends well inland, including inland portions at relatively high elevation and portions that experience dryer and warmer summer temperature. The numerous moderate and smaller coastal basins in the ESU experience relatively wet, cool, and temperate conditions that is in contrast to interior sub-basins of the Rogue, Klamath, and Eel basins, which exhibit a range of conditions including snowmelt-driven hydrographs, hot dry summers, and cold winters. The lower portions of these large basins are more similar to the smaller coastal basins in terms of environmental conditions than they are to their interior sub-basins.

In general, coho salmon within the SONCC ESU exhibit a three-year life cycle. Entry of adults into natal streams and rivers in the ESU usually occurs from mid-November to January, coincident with the onset of rain-induced freshets in the fall or early winter. Spawning typically takes place in small-to-moderate-sized coastal streams or tributaries to larger rivers and usually occurs within a few days to a few weeks of freshwater entry. Depending upon water temperature, eggs incubate for approximately 8 – 12 weeks before hatching, after which alevins or "sac-fry" continue to reside in the gravel for an additional 2 – 8 weeks (Sandercock 1991). Fry emerge in early spring.

Most juveniles undergo smolt transformation and begin their seaward migration one year after emergence from the redd. In more northern latitudes, a significant proportion of juveniles may spend a second (or even third) full year in freshwater (Sandercock 1991). This life history pattern has recently been documented in the California portion of the SONCC Coho Salmon ESU (Bell et al. 2001). In the SONCC Coho Salmon ESU, smolt outmigration occurs in spring, generally peaking in April or May (Weitkamp et al. 1995). The ocean phase of coho salmon typically lasts about 18 months; however, often a proportion of male fish return after only six months at sea as precocious males ("jacks") that are substantially smaller than adults returning after a full year-and-a-half at sea. The proportion of precocious males in the escapement population can be highly variable (Sandercock 1991). Female "jills" do occur, but are much less common than jacks. Thus, the typical life-span of almost all coho salmon is three years, the exceptions being 2-year old jacks and occasional 4-year old adults of both sexes. The relatively rigid life history exhibited by females, which limits demographic interactions among brood years, makes coho salmon somewhat more vulnerable to environmental perturbations than other salmonid species with a broader array of life-history types. The occurrence of jacks, on the other hand, can allow for genetic exchange among brood years within a population (i.e., brood years within a population are more similar to each other than they are to other populations).

2. Conceptual Approach for Identifying Historical Populations

2.1. Evaluation of Historical Population Structure Within an ESU

Technical aspects of recovery planning focus primarily on two levels of biological structure: the ESU and the populations that make up the ESU. The appropriate scales at which these units are viewed or delineated are not explicitly defined, although it is clear that the scales relevant to population structure are shorter and smaller than those for ESU structure. Specifically, rates of exchange among distinct units at these two levels of biological structure are expected to differ because dispersal among populations within an ESU is expected to greatly exceed rates of exchange between ESUs. This has important implications for divergence at different biological scales (Moritz 1994; Moritz et al. 1995). ESUs are defined by deep evolutionary divergence and represent major independent lineages within a species, within which variation and structure change on time scales of tens to hundreds of generations. In contrast, populations are units within which individuals and subpopulations typically interact most strongly at time scales of days to a few generations. Our approach was based on a conceptual model of population dynamics for this ESU and on existing literature regarding the functioning of complex populations in general and salmon populations in particular (Rieman and Dunham 2000).

With these considerations, the TRT adopted a conceptual approach to identifying and classifying historical populations that explicitly recognized the links between spatial and temporal scale, the spatial arrangement of basins, and biological structure. We developed this framework in concert with the Oregon Coast Workgroup of the ONCC TRT and the TRT of the North-Central California Coast Recovery Domain. This approach differs from those used elsewhere in the Pacific Northwest because of the linear nature of the coastline throughout Oregon and northern California. In addition, watersheds throughout the SONCC ESU vary widely in size. In contrast, other Recovery Domains in the Pacific Northwest span radially structured landscapes with less variation in basin size, such as the Puget Sound or interior basins of the Columbia River. Such differences have important implications for the potential dynamics of an ESU and its constituent populations (Fagan 2002) that we attempt to

accommodate in our analyses. These differences in the spatial arrangement and size of basins result in different intra- and inter-basin movement of fish and, therefore, different population structures and population dynamics. While the role of the larger basins (i.e., Rogue, Klamath, and Eel rivers) may be obvious, the role that the smaller basins play in the dynamics of the ESU was also recognized by the TRT.

2.1.1. Definition of a Population

The starting point for this approach is a definition of "population" that we base on the definition offered by McElhany et al. (2000) as an extension of Ricker's (1972) definition of "stock": A population is a group of fish of the same species that spawns in a particular locality at a particular season and does not interbreed substantially with fish from any other group. Local populations (i.e., stocks) of Pacific salmon and trout (*Oncorhynchus* spp.) are reproductively isolated in space and time and have evolved in response to both regional and local environmental conditions. In extending Ricker's stock concept, McElhany et al. (2000) sought a definition that would support the delineation of "independent" populations[3], which by virtue of being independent units, offer a means of simplifying the complex issue of assessing ESU structure and risk (Esler 2000).

In general, we follow the broad concepts outlined by McElhany et al. (2000). However, a simple dichotomy between "independent" and "non-independent" populations does not adequately capture the complex population structure and relative nature of population independence in the ESU under consideration. Therefore, we extend the concepts in McElhany et al. (2000) to develop a population classification scheme that reflects the properties of individual populations and the interactions among populations. In particular, we require a population definition that is relevant to our geographical setting and that accommodates watersheds of different sizes, without compromising the definition of a population as a discrete biological unit.

[3] An "independent" population is "any collection of one or more local breeding units whose population dynamics or extinction risk over a 100-year time period is not substantially altered by exchanges of individuals with other populations (McElhany et al. 2000)."

2.1.2. Rules for Identifying Populations: Concepts and Application

Basins across the SONCC ESU vary greatly in size, large basins may have multiple populations, and very small basins (e.g., < 4 km of stream) probably did not historically support viable populations but are not necessarily a part of a larger population. To capture the full range of coho salmon habitat in the SONCC ESU, we adopted two rules. Our first rule was that each basin would naturally form a separate demographic unit (e.g., population). Since there is a strong tendency for coho salmon to return to their natal stream to spawn (Quinn 1993), the resulting population structure is largely determined by the spatial arrangement of their natal streams, including the structure of freshwater spawning and rearing habitats and migration pathways that allow dispersal among these habitats. Therefore, we defined historical populations based on points of saltwater entry.

Our second rule was that spawning groups within a large basin may comprise multiple populations if sufficient barriers to effective migration exist. We assume that migration (straying) within a basin is far more likely than straying among basins with different ocean-entry points. However, within large basins substantial gaps in the distribution of suitable spawning and rearing habitats and watershed-scale heterogeneity in environmental conditions can limit effective migration and therefore result in discrete populations. In the case of different ocean entry points, the rate of straying is largely a function of distance between the stream mouths and depends on the strength of an individuals' homing behavior. In the case of gaps in available habitat, environmental heterogeneity must be sufficient to create substantially different environmental cues that affect the homing response or present different selective regimes and, thus, foster population divergence. This divergence is demonstrated by substantial variation in life history traits, genetic composition, or phenotypic characteristics among putative populations.

2.1.3. A Model for Evaluating the Population Structure of an ESU

The conceptual approach we use breaks the original concepts developed by McElany et al. (2000) down into two characteristics of a population — viability and independence — and is described in more detail by Bjorkstedt et al. (2005). We began by developing for each

population (1) an estimate of (or proxy for) "viability-in-isolation", which is based on the probability of extinction for a population in complete isolation from all other populations, and (2) an estimate of self-recruitment to be used as a measure of the degree to which each population's dynamics are determined internally. Viability-in-isolation is a function of numerous population characteristics that for the most part can generally be reduced to carrying capacity, intrinsic productivity or mean population growth rate, and (temporal) variance in population growth rate (McElhany et al. 2000; Lande et al. 2003). For consistency with other TRTs and the conservation biology literature, we used a time frame of 100 years for evaluating viability, and considered a population that, in isolation from all other populations, has a low (<5%) probability of extinction over 100 years to be "viable-in-isolation", in contrast to those that are not viable (see McElhany et al. (2000) for discussion of 100-year time scale). Self-recruitment is a function of the size of the population and the number of immigrants to the population, which itself is a function of the size of each population that is a source of immigrants and the rate at which individuals from each donor population disperse to the recipient population. In the case of anadromous salmonids, "self-recruitment" is the proportion of a population's spawning run that is of native origin.

"Self-recruitment" and "viability-in-isolation" represent two axes along which we can set thresholds to distinguish "viable" from "non-viable" populations on one axes, and "independent" from "dependent" on the other, resulting in four types of historical populations (Figure 2):

- *Functionally Independent Populations* — populations with a high likelihood of persisting over 100-year time scales, and that conform to the definition of independence offered by McElhany et al. (2000): an independent population is one "whose population dynamics or extinction risk over a 100-year time period is not substantially altered by exchanges of individuals with other populations."

- *Potentially Independent Populations* — populations with a high likelihood of persisting in isolation over 100-year time scales, but are too strongly influenced by immigration from other populations to exhibit independent dynamics.

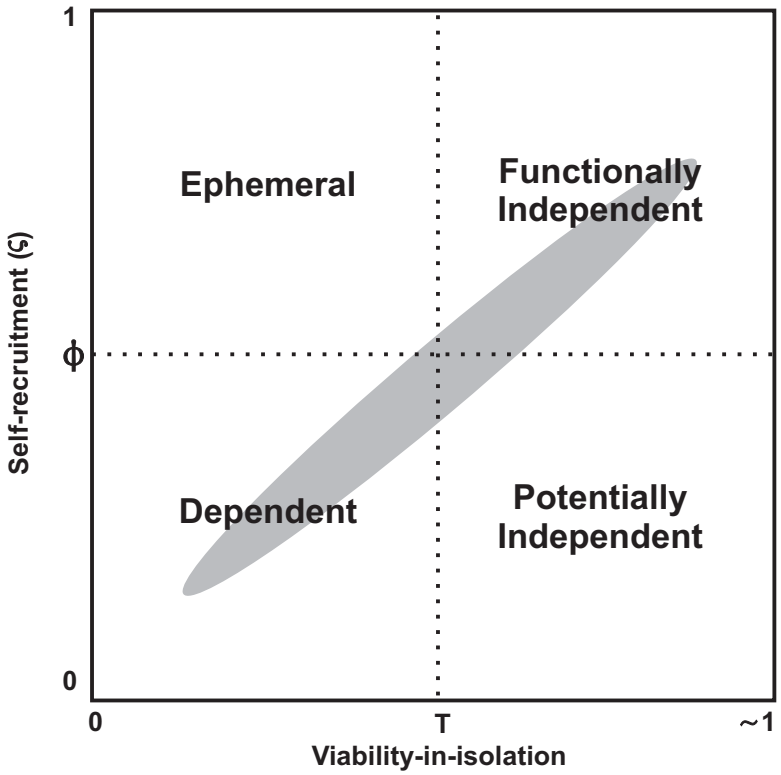


Figure 2. Schematic of population types as a function of viability-in-isolation and self-recruitment. Note that these two parameters are not independent, resulting in a diagonal distribution of populations between the dependent and functionally independent quadrants (shaded oval). Critical values for viability-in-isolation (T) and self-recruitment (Φ) are described in text.

- *Dependent Populations* — populations that do not have a high likelihood of sustaining themselves over a 100-year time period in isolation, yet receive sufficient immigration to alter their dynamics and extinction risk.

- *Ephemeral Populations* — populations that do not have a high likelihood of sustaining themselves over a 100-year time period in isolation, and do not receive sufficient immigration to affect this likelihood. Habitats that support such populations are expected to be occupied only rarely.

Note that self-recruitment and viability-in-isolation are not independent parameters (Figure 2), but are linked through a common dependence on population size. Large populations are more likely to be both viable-in-isolation and exhibit dynamics only weakly affected by immigration, and small populations are likely not to be viable-in-isolation but more strongly influenced by immigration.

For our purposes, populations that are viable-in-isolation are independent populations, either functionally or potentially. The boundary between independent and dependent populations is determined by the abundance (or habitat capacity), below which there is a low likelihood of a population persisting without migrants from other populations. Ideally, estimates from robust population viability analysis (one capable of estimating and excluding the influence of immigration) would be used to arrange populations along the viability-in-isolation axis. Unfortunately, estimates of absolute extinction probabilities are very sensitive to model parameters and structure. Moreover, these data (e.g., population size, dispersal rates, life-stage specific survival rates, fecundity) are not available for populations of coho salmon in the SONCC ESU.

Recognizing these limitations, we instead focused on developing proxy measures of viability-in-isolation for each population. The relation between population size and extinction rate is well known from theoretical and empirical studies (Lande et al. 2003), and the development of relevant metrics for population size is somewhat more tractable than for other

factors that affect population viability (e.g., measures of density dependence, resilience, intrinsic productivity, or variance in productivity). We therefore focused on measures of historical habitat carrying capacity, a robust predictor of population size, as a metric of population viability.

Independent populations, populations that were viable-in-isolation, were determined to be either Functionally Independent or Potentially Independent based on their historical interaction with other populations. Populations that have high levels of self-recruitment on average provide more individuals to other populations than they receive, and have demographics that are not greatly influenced by other populations. Therefore, as for viability-in-isolation, our calculation of self-recruitment for populations within an ESU amounts to ranking populations according to the likelihood that each will exhibit independent dynamics.

The connectivity-viability framework (Bjorkstedt et al. 2005) is reduced to a model for ranking the status of populations within the ESU, given we cannot develop absolute measures of viability-in-isolation and self-recruitment. The position of individual populations in viability-independence space, however, is not static over time. A population's status at any point in time is a function of its abundance and that of its neighbors. Therefore, the position of a population in viability-independence space predicted by the connectivity-viability model should be envisioned as a central point, a long-term mean about which the population's true state fluctuates through time. A population that on average acts as a Potentially Independent population can act as a Functionally Independent population if larger adjacent populations are diminished or extirpated.

Dependent populations and Potentially Independent populations contribute to other populations through straying. Dependent Populations and the watersheds that support them serve at least two roles within an ESU. First, although they are not themselves dominant sources of dispersers within the ESU, dependent populations increase connectivity within an ESU by allowing dispersal among independent populations to occur in incremental steps. Second, in the case of catastrophic disturbance, nearby Dependent populations can support normally independent populations by providing a small, nearby source of colonists.

3. Methods and Results

The approach we used to identify and classify populations was consistent with approaches used by other TRTs developing technical recovery plans for coho salmon (Bjorkstedt et al. 2005; Lawson et al. 2006) and is based on our desire to have an approach with three characteristics: consistency, reproducibility, and transparency (Lawson et al. 2006). We believe the rule-based approach we employ fulfills these requirements. It can be applied in a consistent manner across the ESU and the methods are relatively simple with a logical connection between the available data and the conclusions. In addition, we believe that another group of scientists could apply similar methods to these data and reach similar results. Information about historical distribution and population structure are limited, therefore the TRT examined characteristics of current populations and their habitat to assist in identifying selective and isolating factors that could result in demographic independence among coho salmon populations in the SONCC ESU. Factors examined included (1) historical distribution, (2) geographical isolation, (3) biological characteristics, and (4) environmental and ecological diversity.

3.1.1. Identifying the Historical Distribution of Populations

Because our focus is on the historical population structure, the TRT needed to identify the historical distribution of coho salmon in the SONCC ESU. In general, we used the results from a Geographic Information Systems (GIS) model to predict the intrinsic potential (IP) of coho salmon rearing habitat in watersheds throughout the range of SONCC coho salmon (Burnett et al. 2003). The IP model was also used as a proxy for population size (described below). A detailed description of the model is provided in Appendix A, Agrawal et al. (2005), and Burnett et al. (2003).

The IP model we implemented predicts the distribution of "intrinsic potential" (IP) for habitat suitable for rearing juvenile coho salmon. In brief, the model predicts the potential for a stream reach to exhibit habitat characteristics suitable for this specific life history stage as a function of the underlying geomorphic and hydrologic characteristics of the landscape. A stream reach is a section of stream or river approximately 50 to 200 m in length, and is

generally defined with respect to geomorphological features by the DEM model (United States Geological Survey 2002). In general, we use mean gradient, mean annual discharge, and valley constraint[4] of stream reaches as the basis for our analysis. These characteristics are selected on the basis of being effectively constant features of the landscape that directly control the processes that create, alter, and maintain essential features of salmon habitat.

Specifically, IP is calculated as the geometric mean of suitability scores, which range from 0-1 and describe the potential that a stream reach with a specific value for a given characteristic will exhibit suitable habitat. These scores are generated by mapping the values for each of the three habitat characteristics onto suitability curves (Burnett et al. 2003; Agrawal et al. 2005)[5]. The IP model itself has the structure of a limiting factors analysis, in that a low suitability score for a single habitat characteristic can greatly reduce (or eliminate) the potential for suitable habitat. We used this approach to generate predictions of IP for habitat of coho salmon using approaches developed by (Burnett et al. 2003). We excluded areas above migration barriers in two ways. First, areas upstream of documented natural barriers were excluded. For California streams we used the California Coastal Conservancy's Fish Passage Assessment Database (The Coastal Conservancy 2004), for Oregon streams we used the USGS Forest and Rangeland Ecosystems Science Center's barrier database (Greswell et al. 1999). Second, the IP model had a gradient threshold that excluded any reach that exceeded 7% gradient and all stream reaches upstream of that reach.

In addition, in the upper Trinity River (United States Fish and Wildlife Service and California Department of Fish and Game 1956) and in the upper Klamath River (Hamilton et al. 2005) we had supporting historical literature that described the historical upstream distribution in these specific basins. In general, the extent of historical distribution of SONCC coho salmon is similar to the present distribution throughout most basins within the ESU (the major exceptions being the Klamath River upstream of Iron Gate Dam, the Trinity River

[4] Valley constraint is defined as the ratio of the width of the valley floor (floodplain) and the width of the active stream channel.

[5] In general, the form of these functional relations is not well known, except perhaps at the extremes where the likelihood of suitable habitat is very high or very low. The suitability curves used here (and elsewhere (Lawson et al. 2006)) were developed under a fuzzy logic framework wherein the marginal effect of a habitat characteristic is assumed to decline monotonically (linearly) over the range of values intermediate to conditions that do not limit the potential for suitable habitat to occur and conditions that totally prevent the occurrence of suitable habitat (Burnett et al. 2003).

upstream of Lewiston Dam, and portions of the upper Rogue River). However, throughout the ESU anthropogenic factors (e.g., habitat loss, migration barriers and impediments, harvest, hatchery operations) significantly influence the current population structure. Although the current distribution may not differ greatly, these anthropogenic factors have reduced the capacity of many areas that historically were the most productive (e.g., lowland habitat) and therefore have modified the interaction among populations (Beechie et al. 1994).

3.1.2. Geographical Isolation

Geographical information allows inference regarding the distribution and discreteness of spawning groups of anadromous salmonids. Fish species typically consist of many geographically localized populations and, to varying degrees, reproductively isolated populations (Taylor 1991). This is particularly true for local populations of Pacific salmon and trout that tend to become distinct from other local populations because of their high fidelity for returning to their natal stream for spawning. Throughout the life cycle, anadromous salmonids occupy a wide range of habitats, all of which are important to population viability. However, because the hierarchical nature of population structure of anadromous salmonids results from homing to natal streams (National Research Council 1996), it makes sense to focus our attention at the scales and habitats that underlie this structure. This homing behavior results in local breeding populations in different portions of a stream, basin, or region, and allows for the evolution of adaptations to local environmental conditions determined by the interaction of physical processes and characteristics of watersheds (e.g., topography, hydrology) and salmonid life history. Thus, spawning habitats provide a useful focus for examining population structure. Comprehensive, detailed information on the current and historical distribution of spawning and rearing areas was generally unavailable for portions of the SONCC Coho Salmon ESU. What data were available were often little more than presence-absence data for a watershed, rather than appropriately designed surveys and monitoring that would more accurately describe coho salmon distribution throughout the ESU. Therefore, the IP model was used to develop a historical picture of the distribution and amount of coho salmon habitat in the SONCC ESU.

3.1.3. Biological Characteristics

Biological characteristics were examined to determine if patterns in these various measures might indicate how historical populations were structured. Many of these characteristics (e.g., life history, population dynamics) have both a genetic and environmental basis. Populations that exhibit similar characteristics result from either shared genetic heritage or similar responses to shared environmental conditions.

Dispersal rates — Estimates of dispersal rates among populations and the reproductive success of immigrants to a population are useful for developing parameters and testing the assumptions of models such as the connectivity-viability model, and generally for gaining insight into connectivity within an ESU or population. Few direct estimates of rates of dispersal among populations are available for coho salmon in the SONCC ESU and other adjacent regions (Shapovalov and Taft 1954; McElhany et al. 2000), which limits the utility of such information for evaluating population structure within the SONCC ESU, except as they inform models of population connectivity such as the connectivity-viability model described above. These data provide only general guidance for selecting dispersal parameters in modeling exercises. Indirect estimates of migration derived from genetic data require ancillary information on populations' sizes to be converted to dispersal rates for meaningful use in a model. Direct measures of dispersal as well as indirect, genetic signatures of dispersal can be strongly influenced by the introduction of hatchery fish, because, depending on hatchery practices, introduced fish may stray at rates higher than naturally born fish (Pascual et al. 1995). Therefore, any available estimates, especially if developed for hatchery fish or a population strongly influenced by hatchery fish, must be considered cautiously.

Genetic data — Information on genetic population structure can be used to describe how genetic variation is distributed among and within populations, or to gain insight into the adaptive significance of genetic variation in populations. Data suitable for examining adaptive genetic differences are not common, and such differences are difficult to document. However, demonstration of such differences, whether based on molecular genetics or quantitative traits, provides strong evidence for discrete populations. Genetic information derived from analysis of estimates of allele frequencies at neutral markers is far more common and can be used to

develop inferences regarding reproductive isolation and rates of exchange among spawning groups (Waples 1998).

The TRT reviewed several genetic analyses based on neutral molecular markers that included samples from the SONCC ESU. Unfortunately, these studies did not include within-basin samples, thus providing little information on population structure within the larger basins in the SONCC ESU (i.e., Rogue, Klamath, and Eel rivers).

In general, the available genetic analyses showed an isolation-by-distance relationship and general concordance between geographic and population genetic structure and supports the use of geographic structure as a template for interpreting population structure throughout coastal basins in California and southern Oregon (see review by Bjorkstedt et al. (2005)). In the initial coast-wide status review (Weitkamp et al. 1995) the genetic data available for southern Oregon coast and Northern California region were, for the most part, based on allozyme analyses and typically indicated little evidence for concordance between geographic and genetic structure along the coast except at the larger spatial scales represented by the SONCC ESU and CCC ESU. More recently, work at the NMFS Fisheries Ecology Division provided additional genetic data based on 18 microsatellite loci (L. Gilbert-Hovath et al., Southwest Fisheries Science Center, Fisheries Ecology Division Santa Cruz, Calfiornia, unpublished data). Although most of the sites were from the CCC Coho Salmon ESU, several samples from locations within the SONCC Coho Salmon ESU were included in their analysis. Results from their analyses included: (1) all of the exact tests for population differentiation proved significant, providing evidence of substantial genetic structure among the samples included, (2) phylogenetic trees clearly distinguished the CCC ESU from the SONCC ESU, and (3) there was significant isolation-by-distance that indicated that dispersal was a driving force underlying population structure (Bjorkstedt et al. 2005).

Life history — Life history and phenotypic traits can reflect local adaptation (Waples 1991). However, interpretation of these traits is difficult because their expression is a result of environmental and genetic factors (Barlow 1961; Leary et al. 1985; Funk et al. 2005). Identification of populations based on phenotypic variation must consider that differences observed may be environmentally induced rather than genetically based (Swain and Foote 1999). As mentioned previously regarding adaptive genetic variability, documenting the

adaptive nature and heritability of phenotypic variability is difficult. Without such evidence, such information must be considered cautiously, as phenotypic variability induced entirely by differences in environmental conditions is not informative with respect to population structure. Nevertheless, phenotypic variability provides a potential proxy for genetic information as well as evidence of variation in selective environments experienced by salmon.

Comprehensive Status Review Updates were completed for all listed ESUs (Good et al. 2005). In preparing these updates, the NMFS scientists compiled, summarized, and analyzed all available data relevant to ESU status, and where possible focused analysis and interpretation at the population level. Life history data sets were very limited and were not available at an appropriate scale (e.g., within population descriptions but not among population descriptions and comparisons) to be useful by the TRT for identifying populations.

Population dynamics—An understanding of population dynamics can be useful in understanding the interactions among populations. Analysis of correlations in long-term abundance data from adjacent populations may indicate demographic independence. A lack of correlation in abundance between two populations in close geographic proximity provides evidence that they are not demographically coupled. However, correlation in environmental conditions that influence population dynamics can confound such analyses. Therefore, as for analyses of genetic information, correlation analyses are best treated as one-way tests, and cases where positive correlation exists require more work to rule out confounding influences before being taken as evidence for substantial exchange among spawning groups.

We know of few time series amenable to this sort of analysis in the SONCC Coho Salmon ESU. Data that are not useful for the present purpose are not explicitly examined in this report, although they have been considered elsewhere as part of the ESU status reviews (Good et al. 2005).

Summary of Biological Characteristics

Little of the biological characteristics examined provided information useful for developing and understanding the historical population structure of SONCC coho salmon populations. The genetic data provides support for an isolation-by-distance view of population structure, although at this time finer resolution of population structure from genetic data are

not available. Information on dispersal rates, life history and phenotypic traits, and population dynamics are not generally available for SONCC coho salmon. Where they are available, they are not often collected at a large enough spatial scale useful for distinguishing populations. In addition, the lack of time series and the tendency of many of the characteristics to be highly variable (e.g., run timing, jacking rate, etc.) and often attributable to environmental variation limit their use for distinguishing populations.

3.1.4. Environmental and Ecological Diversity

Environmental and ecological characteristics, both biotic and abiotic, comprise the selective environment in which salmon exist. We examine diversity associated with spatial variation in these characteristics, because such diversity can contribute to viability at both the population and ESU level (McElhany et al. 2000). Such variation often underlies biological structure and can contribute to population structure. These characteristics include such physical characteristics as temperature, precipitation, stream flow, and peak flow timing, as well as biological attributes at local and regional scales (e.g., ecoregions). The existence of distinctive habitat features provides opportunities for unique adaptations in the local population (Waples 1991). For information on variability in the environment to be useful in determining population independence there must be supporting biological information linking the habitat differences to adaptations (Swain and Foote 1999). Also, we expect spawning groups that experience different selective regimes (i.e., environmental conditions), if sufficiently isolated to meet the definition of independence, will exhibit phenotypic divergence.

The potential for environmental and ecological heterogeneity to drive local adaptation is strongly dependent on dispersal rates among populations (i.e., stray rates), the degree to which selective regimes differ, and the intensity of the selection on populations. Although spatial variation in environmental conditions can serve as an indicator of variation in selective regimes, inferences regarding population structure are sensitive to assumptions about dispersal rates and about the strength of divergent selection associated with this variation in environmental conditions. For these reasons, information on variability in environmental conditions is not likely to be independently informative with respect to population delineation

among otherwise indistinguishable groups of salmon.

We developed a multivariate analysis of environmental and ecological characteristics for watersheds in the SONCC Coho Salmon ESU to serve two purposes. First, the analysis helps us to identify differences in ecological and environmental characteristics among coastal basins and therefore may indicate differences in selective regimes that result in population divergence. Second, the analysis allows us to identify differences in ecological and environmental characteristics within large basins, which are useful in considering whether sub-basins within large basins might support separate populations. An additional use of these data is to identify groups of watersheds that share similar characteristics; the analysis supports our efforts to define diversity strata as a basis for future development of ESU viability criteria.

To conduct the analysis, we assembled a broad suite of environmental data in a GIS, extracted specific metrics for watersheds throughout the SONCC ESU, and applied Principal Components Analysis (PCA) and cluster analysis to the scaled and centered data to discern regional groups of watersheds with similar environmental characteristics. A total of 17 characters were used to characterize each basin or sub-basin (Appendix Tables B1 and B2). A broader suite of data than reviewed here was considered in preliminary analyses, but a number of variables were dropped due to correlation with variables retained for the final analysis.

Because we are interested in group structure as well as factors that differentiate watersheds, we used a clustering algorithm based on the average (Euclidean) distance among members of adjacent clusters rather than a nearest-neighbor analysis. Appendix Table B2 lists the data types retained for analysis, and the loadings for each on the first three principal component vectors (see also Plates 1 – 8). The first three principal components explained 73% of the variance in the environmental data set. Displaying watersheds in 3-D space defined by the first three components (Figures 3 and 4) suggests a set of groupings, as well as highlighting important differences among sub-basins of the Rogue, Klamath, and Eel rivers and Humboldt Bay tributaries. Cluster analysis (Figure 5) reveals similar groupings. Particularly clear are the differences in the coastal basins and interior basins of the Rogue, Klamath, and Eel rivers. In addition, the coastal basins of the southern Oregon Coast and those in northern California cluster separately in the dendrogram (Figure 5).

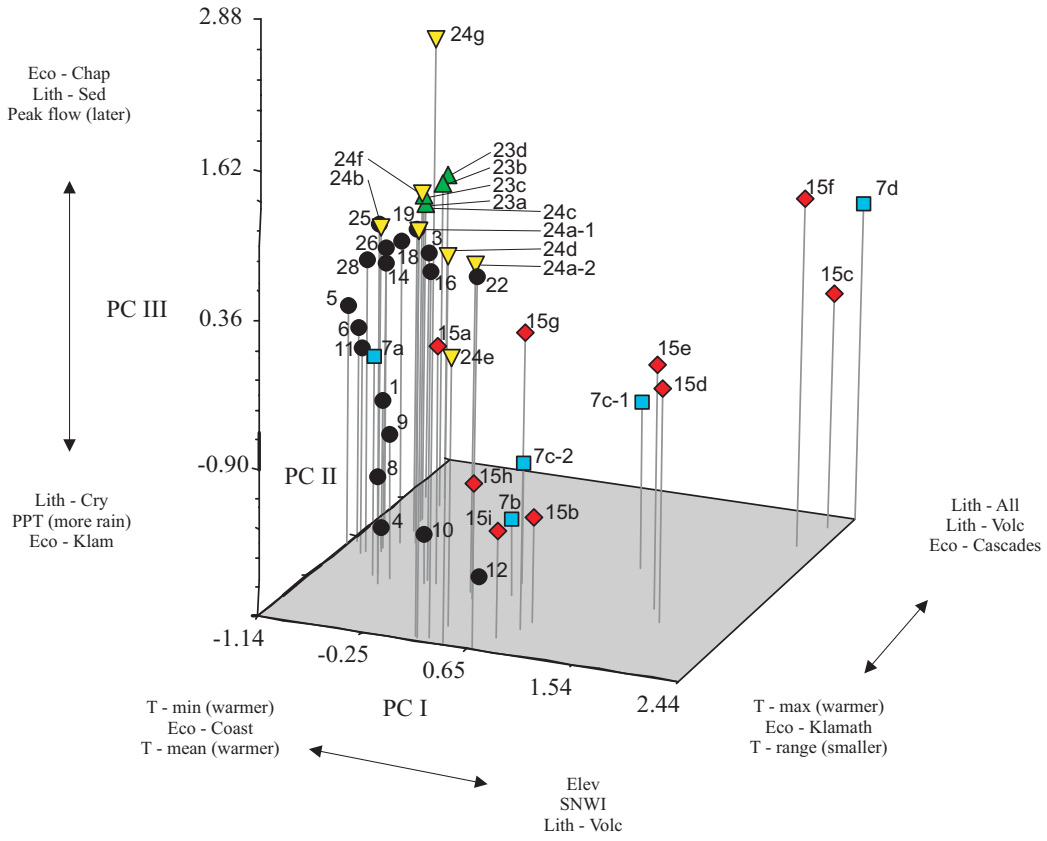


Figure 3. Plot of first three principal components, based on environmental variables, showing the position of selected watersheds. Watershed numbers correspond to those listed in Table 1. The sub-basins of the three large basins and the Humboldt Bay tributaries are identified by unique symbols and colors colors (Rogue River 7 – blue square ■; Klamath River 15 – red diamond ◆; Humboldt Bay tributaries 23 – green triangle ▲; Eel River 24 – yellow triangle ▼).

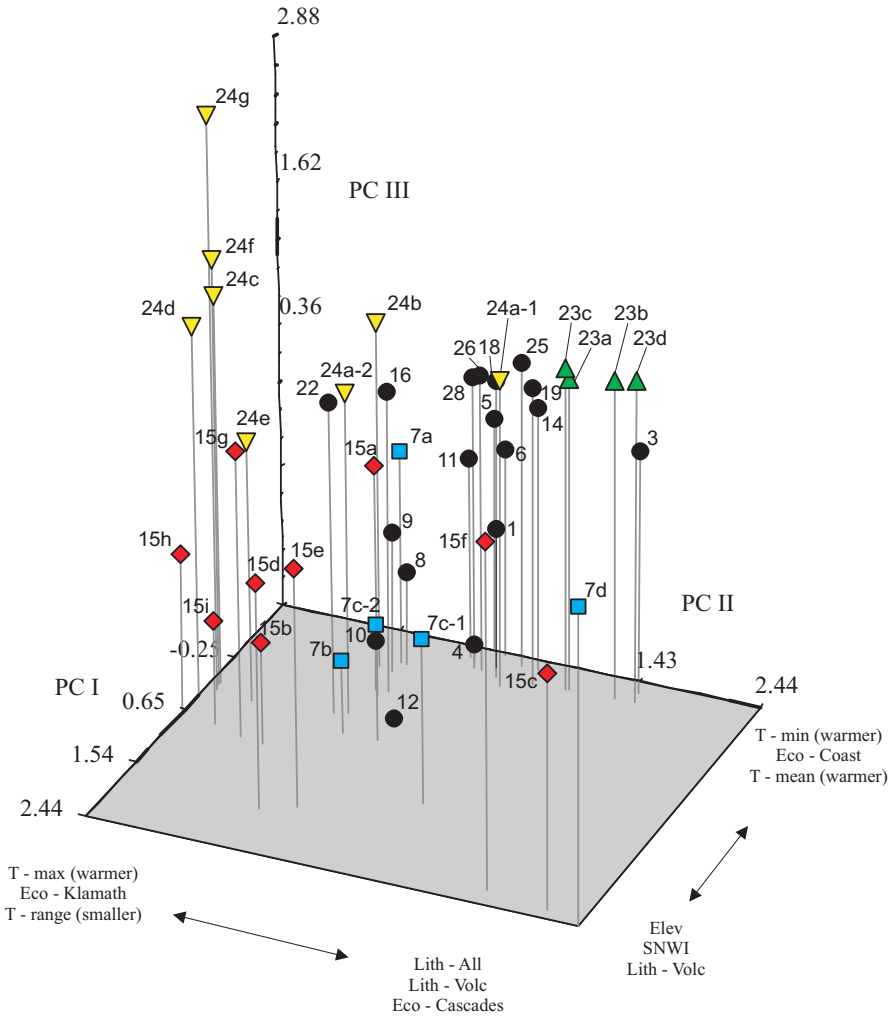


Figure 4. Plot of first three principal components, based on environmental variables, showing the position of selected watersheds (rotated perspective of Figure 3). Watershed numbers correspond to those listed in Table 1. The sub-basins of the three large basins and the Humboldt Bay tributaries are identified by unique symbols and colors colors (Rogue River 7 – blue square ■; Klamath River 15 – red diamond ◆; Humboldt Bay tributaries 23 – green triangle ▲; Eel River 24 – yellow triangle ▼).

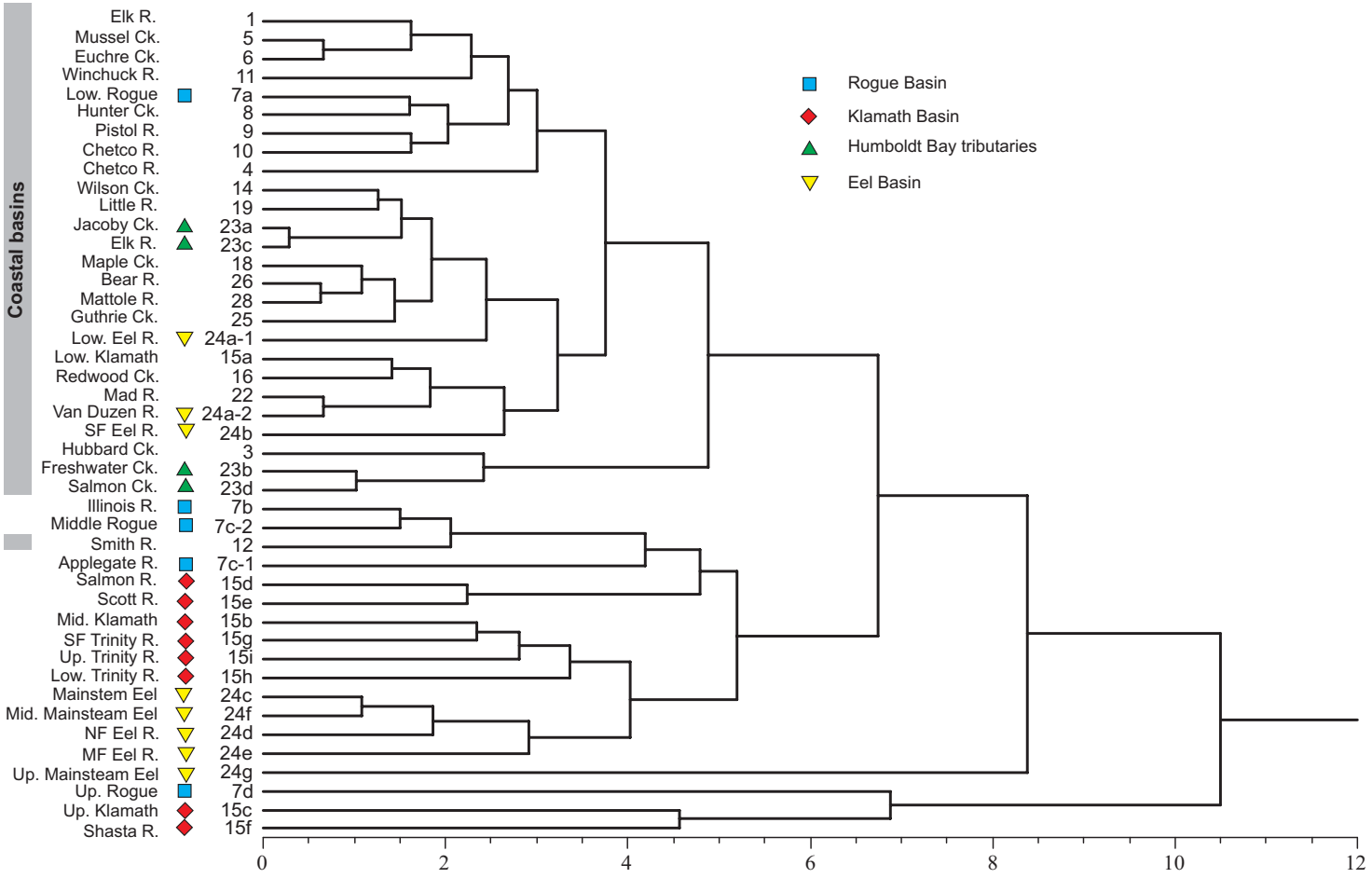


Figure 5. Dendrogram based on weighted pair-group method, arithmetic average (WPGMA) of Euclidian distances applied to scaled and centered environmental data for watersheds in the Southern Oregon/Northern California Coasts Coho Salmon ESU. Watershed numbers correspond to those listed in Table 1.

The regional groups identified include:

Interior sub-basins — This group includes the middle and upper portions of the three large basins in the SONCC ESU (Rogue, Klamath, and Eel rivers). Within the interior sub-basins, the upper portions are characterized by higher mean elevations, stream flows heavily influenced by snowmelt, wide seasonal fluctuations in air temperature, and cooler minimum air temperatures compared to coastal basins. The middle portions of these large river systems have sub-basins that are characterized by warmer maximum air temperatures, less seasonal fluctuations in air temperature than upper sub-basins, warmer minimum air temperatures, and little influence of snowmelt.

Coastal basins — These areas are characterized by warmer winter air temperatures, low elevations, warmer mean air temperatures, less seasonal fluctuations in air temperature, and located within the coastal ecoregion. Included in this group are the lower portions of the Rogue, Klamath, and Eel rivers, and Van Duzen River that were similar based on the environmental variables in the analysis.

Summary of environmental and ecological diversity

An examination of a wide range of environmental and ecological characteristics of the SONCC Coho Salmon ESU indicates differences across the landscape, although generally at such a broad spatial scale so as to be limited in its use to distinguish among populations. The exceptions were within the larger basins (i.e., Rogue, Klamath, and Eel basins) where the range of environmental conditions were greatest, specifically at the scale of major sub-basins, and were especially useful when considering population structure within the larger basins (see Section 3.2.2).

3.2. Methods for Population Identification and Classification

Our approach for defining population units and population structure was conducted in two steps. The first was to identify the population units and the geographic area in which they occur. The second was to classify each of the population units as either Functionally

Independent, Potentially Independent, Dependent, or Ephemeral populations based, on our conceptual model.

3.2.1. Population Identification Method

As previously described, the TRT used two rules for identifying populations: the first identifies all basins that include one or more populations. Populations throughout the SONCC Coho Salmon ESU were divided at saltwater entry points. For each direct ocean tributary, the populations that spawn within a specific freshwater basin were considered a population unit. For our purposes, estuaries were considered part of the freshwater system, so that multiple streams entering a common estuary were considered a single population (i.e., Humboldt Bay tributaries).

For the SONCC Coho Salmon ESU, application of isolation by ocean-entry results in a large set of demographic units for consideration. To keep the number of units at a number that could be reasonably evaluated, we used a size criterion that limits the set of demographic units to be considered. This size threshold was based on an examination of the results of GIS modeling (IP) of potential occurrence of coho salmon rearing habitat within each watershed of the ESU. We included all direct watersheds to the Pacific Ocean with $\geq$ 3.4 IP km in the connectivity-in-viability analysis. This yielded 33 watersheds for consideration (Table 1). We separated these watersheds into two sets: (1) those with $<$ 5 IP km[6] juvenile coho salmon rearing habitat, which were not considered by name in our analyses, and (2) those watersheds with $\geq$ 5 IP km, which were assigned specific identifiers.

The second rule is directed at large basins that may contain more than one population unit. For two or more populations to be considered as separate population units within a basin there must be sufficient gaps in available habitat and environmental heterogeneity must be sufficient to create substantially different environmental cues that affect the homing response or present different selective regimes and, thus, foster population divergence.

In Table 1 we identify major sub-basins within the Rogue River, Klamath River, and Eel River basins for later consideration. We examined environmental variability in these sub-

[6] IP km are units of intrinsic potential integrated over stream distance, and are used here as a measure of habitat size and a proxy for capacity (abundance).

basins and throughout the ESU for consideration of the biological significance of environmental heterogeneity and gaps in suitable habitat.

3.2.2. Population Identification Results

Having included watersheds that share a migration corridor, estuary, and common ocean-entry point as separate units in the multivariate analysis, we are able to examine whether watersheds differ sufficiently to warrant considering populations at a finer scale. Three cases exist where this was warranted: Rogue River, Klamath River, and Eel River. The locations of the sub-basin divisions are given in Table 2. In addition to the analyses of environmental variability, the TRT examined results from the IP modeling to assess the distribution (e.g., contiguous versus isolated) of habitat among sub-basins that might lead to population structuring.

Rogue River — Our multivariate analysis suggested substantial environmental variability within the Rogue River basin that resulted in delineation of four populations: upper Rogue, middle Rogue/Applegate River, Illinois River, and lower Rogue River. The upper Rogue River (7d), upstream of Evans Creek (inclusive) is at relatively high elevations, has substantial snowmelt that results in a later peak flow than other sub-basins, and the lithology and ecoregions of this area are much different from those found elsewhere in the Rogue River basin. The Applegate River (7c-1) and the middle Rogue River (7c-2), from the confluence of the Illinois River (non-inclusive) upstream to Evans Creek, exhibit very similar environmental characteristics providing little support for differentiating populations between these sub-basins. In addition, IP results show a rather contiguous distribution of habitat between these regions. The lower Rogue River (7a), from the mouth upstream to the Illinois River confluence, is more similar to smaller coastal basins than the other sub-basins of the Rogue

Table 1. Independent and dependent populations of coho salmon in the Southern Oregon/Northern California Coasts Coho Salmon ESU, including integrated intrinsic potential (IP) values with 21.5 °C air temperature mask (locations where IP was reduced by temperature mask have pre-mask values in parentheses) and self-recruitment values. Population types include Functionally Independent (FI), Potentially Independent (PI), Dependent (D), and Ephemeral (E) populations. Basins with integrated IP < 3.4 km with temperature mask were excluded from analyses. Basins in italics contained an integrated IP TM value < 5 km and are not included by name or number in subsequent analyses, but were incorporated into self-recruitment analysis. Self-recruitment values for the Rogue, Klamath, and Eel rivers are based on the available habitat in the lower portions of each basin (see text for details).

Basin	ID	IP (km)	Self-recruitment	Population type		
				FI	PI	D
Elk River	1	62.64	0.99	X		
Mill Creek	2	7.25	0.91			X
Hubbard Creek	3	17.94	0.96			E[a]
Brush Creek	4	5.68	0.82			X
Mussel Creek	5	6.06	0.81			X
Euchre Creek	6	32.31	0.97			E[a]
Greggs Creek		3.40	0.67			X
Rogue River		2344.58 (2547.01)				
Lower Rogue River	7a	80.88	0.98		X	
Illinois River	7b	589.69		X		
Middle Rogue and Applegate rivers	7c	758.58 (760.67)		X		
Upper Rogue River	7d	915.43 (1115.77)		X		
Hunter Creek	8	14.63	0.89			X
Myers Creek		3.45	0.62			X
Pistol River	9	30.23	0.88			X
Chetco River	10	135.19	0.96	X		
Winchuck River	11	56.50	0.91		X	
Smith River	12	385.71	0.99	X		
Elk Creek	13	17.38	0.65			X
Wilson Creek	14	18.80	0.76			X
Klamath-Trinity		2247.74 (3048.37)				
Lower Klamath River	15a	204.69	0.99	X		
Middle Klamath River	15b	113.49 (178.59)			X	
Upper Klamath River	15c	424.71		X		
Salmon River	15d	114.80 (145.90)			X	
Scott River	15e	440.87		X		
Shasta River	15f	531.01 (606.86)		X		
South Fork Trinity River	15g	241.83 (342.47)		X		
Lower Trinity River	15h	112.01 (170.49)			X	
Upper Trinity River	15i	64.33 (533.79)		X		

Basin	ID	IP (km)	Self-recruitment	Population type FI	PI	D
Fern Canyon		3.66	0.36			X
Redwood Creek	16	151.02	0.98	X		
McDonald Creek	17	5.44	0.63			X
Maple Creek/Big Lagoon	18	41.30	0.90		X	
Little River	19	34.20	0.88		X	
Strawberry Creek	20	5.71	0.72			X
Norton/Widow White Creek	21	8.54	0.83			X
Mad River	22	152.87	0.97	X		
Humboldt Bay tributaries	23	190.91	0.95	X		
Eel River - Full		1459.81 (1773.37)				
Lower Eel and Van Duzen rivers	24a	393.52	0.99	X		
South Fork Eel River	24b	481.11		X		
Mainstem Eel River	24c	143.90 (156.73)			X	
North Fork Eel River	24d	53.97 (83.54)			X	
Middle Fork Eel River	24e	77.70 (252.77)			X	
Middle Mainstem Eel River	24f	255.50 (281.31)		X		
Upper Mainstem Eel River	24g	54.11 (124.39)			X	
Fleener Creek		3.87	0.48			X
Guthrie Creek	25	14.16	0.79			X
Bear River	26	47.84	0.93		X	
Singley Creek		3.40	0.46			X
McNutt Gulch	27	5.90	0.60			X
Mattole River	28	249.79	0.99	X		

[a] – Hubbard and Euchre creeks were designated as Ephemeral populations.

Table 2. Population unit boundaries of sub-basins in the Rogue, Klamath, and Eel rivers for SONCC Coho Salmon ESU.

Basin	ID	Population Unit	Boundaries
Rogue	7a	Lower Rogue River	Mouth of Rogue upstream to confluence of Illinois
	7b	Illinois River	
	7c	Middle Rogue River	Confluence of Illinois River upstream to confluence of Evans Creek (non-inclusive); includes Applegate River.
	7d	Upper Rogue River	Evans Creek (inclusive) upstream to IP limit.
Klamath	15a	Lower Klamath River	Mouth of Klamath upstream to confluence with Trinity River.
	15b	Middle Klamath River	Confluence of Trinity River upstream to Portuguese Creek (inclusive in Middle Klamath); Seiad and Grider creeks in Upper Klamath basin.
	15c	Upper Klamath River	Portuguese Creek (non-inclusive) upstream to Spencer Creek (inclusive).
	15d	Salmon River	
	15e	Scott River	
	15f	Shasta River	
	15g	S. Fk. Trinity River	Confluence of Trinity River is lower boundary.
	15h	Lower Trinity River	Confluence of Klamath River upstream to confluence with North Fork Trinity River (non-inclusive).
	15i	Upper Trinity River	Confluence of North Fork Trinity River (inclusive) upstream to Ramshorn Creek (inclusive).
Eel	24a	Lower Eel/Van Duzen River	Mouth of Eel River upstream to confluence with South Fork Eel River.
	24b	South Fork Eel River	
	24c	Mainstem Eel River	Confluence of South Fork Eel River upstream to confluence with Middle Fork Eel River.
	24d	North Fork Eel River	
	24e	Middle Fork Eel River	
	24f	Middle Mainstem Eel River	Confluence of Middle Fork Eel River upstream to Tomki Creek (inclusive), upstream in Outlet Creek and tributaries to IP limit.
	24g	Upper Mainstem Eel River	Eel River upstream of confluence of Tomki Creek (non-inclusive) to IP limit.

River basin, particularly in terms of precipitation patterns and timing of peak flows. Besides exhibiting differences in environmental conditions, the IP model indicates that the primary habitat for coho salmon is in the upper portions of the Illinois River (7b) basin, which is disconnected from the rest of the sub-basins and mainstem Rogue River.

Klamath River — Our analysis suggested substantial environmental variability within the Klamath River basin that resulted in nine populations: lower Klamath River, middle Klamath River, Salmon River, Scott River, Shasta River, lower Trinity River, upper Trinity River, and South Fork Trinity River. The lower Klamath River (15a), from the mouth of the Klamath River upstream to the confluence of the Trinity River is more similar to smaller coastal basins than the other sub-basins of the Klamath River basin, particularly in terms of precipitation patterns and timing of peak flows. The middle Klamath River (15b) extends upstream to Portuguese Creek (inclusive) and is substantially different from the Klamath River upstream and downstream and adjacent sub-basins (Salmon and Scott rivers), particularly in precipitation and flow patterns, and the various temperature measures used. The upper Klamath River (15c), upstream of Portuguese Creek, includes Seiad and Grider creeks and extends upstream to Spencer Creek (inclusive), the reported historical upstream extend of coho salmon in the basin (Hamilton et al. 2005). The upper Klamath River exhibits different flow patterns than the middle Klamath River and adjacent sub-basin (Shasta River) in addition to differences in temperature, ecoregion, and lithology found downstream and in the Shasta River. Precipitation rapidly declines at the transition between the middle and upper portions of the Klamath River, coinciding with the more constrained stream channel in the upper Klamath River. The Shasta (15f), Scott (15e), and Salmon (15d) rivers along with the Upper Klamath River exhibit substantial differences in environmental characteristics compared to other portions of the greater Klamath Basin (Figures 3 and 4). Among these four areas, the Shasta and Scott river basins differ in terms of their lithology, the timing of peak flow, and the influence of springs and snowmelt. This influence of springs is rather unique to the Shasta and Scott rivers compared to other basins in the SONCC Coho Salmon ESU. Our analysis suggested substantial environmental variability within the Trinity River. The influence of snowmelt and the timing of peak flow differed among the three proposed regions. The upper

Trinity River (15i), including the North Fork Trinity River, exhibits a snowmelt hydrograph whereas the Trinity River and its tributaries downstream of the North Fork Trinity River do not. Rain-on-snow events in the upper Trinity River result in different consequences than in the lower Trinity River. In addition, there is a substantial change in the channel morphology in the area near the confluence of the North Fork Trinity River. The upper Trinity River also experiences a larger range in air temperatures than the lower Trinity River (15h) and there exist differences in the underlying lithology among these regions in the Trinity River. The lower Trinity River extends from the confluence of the Klamath River upstream to, but not including, the North Fork Trinity River. The Upper Trinity River extends upstream from the North Fork Trinity River to Ramshorn Creek (inclusive), the reported historical upstream extend of coho salmon in the basin (United States Fish and Wildlife Service and California Department of Fish and Game 1956). The South Fork Trinity River (15g) extends upstream from the confluence with the Trinity River to the extent indicated by the IP model (see IP results). The IP model indicates that most coho salmon habitat is located in the upper portions of the watershed, primarily in Hayfork Creek, relatively disconnected from that in the lower Trinity River.

Humboldt Bay — The four main tributaries to Humboldt Bay (Jacoby Creek [23a], Freshwater Creek [23b], Elk River [23c], and Salmon Creek [23d]) all exhibit very similar environmental characteristics (Figures 3 and 4). There is little support for proposing an environmental hypothesis for population structure among these basins.

Eel River — The Eel River basin includes four major sub-basins (the Van Duzen River and the South Fork, North Fork and Middle Fork of the Eel River) and numerous smaller mainstem tributaries that drain a basin that spans a variety of ecosystems. Our analysis highlights substantial environmental variability within the Eel River basin. To account for this variability, we partitioned the Eel River into seven regions (three of the four major tributaries and four major sections of the mainstem; the Van Duzen River and lower mainstem Eel River were grouped as a single unit) for inclusion in the analysis. The South Fork Eel River (24b), the Van Duzen River (24a-2), and the lower portions of the Eel River (24a-1) downstream of

the confluence with the South Fork), in particular, differ substantially from the other parts of the Eel River basin, and exhibit environmental characteristics similar to smaller and intermediate-sized coastal watersheds in the SONCC Coho Salmon ESU. The IP model predicts a rather contiguous distribution of habitat between the lower Eel River and the Van Duzen River, but the more suitable IP habitat in the South Fork Eel River is discontinuous with that in the lower Eel River with some of the better habitat predicted to have been present in the upper portions of the South Fork Eel River. The other major tributaries to the Eel River, the North Fork (24d) and Middle Fork (24f) of the Eel River, along with the mainstem Eel River (24c), middle mainstem (24f), and upper mainsteam Eel River (24g), are affiliated with the larger interior sub-basins in the Rogue River basin and Klamath River basin in terms of the environmental characters examined, although these Eel River regions show a strong affinity for each other in the cluster analysis (Figure 5). Within this group of interior Eel River regions, there is substantial environmental variability. One can look to the historical distribution of other species of salmonids, such as various life history forms of Chinook salmon and steelhead, to gain insight into variation in environmental conditions within the Eel River basin. For example, strong anecdotal evidence suggests that spring-run Chinook salmon occupied the North Fork and Middle Fork of the Eel River (Keter 1995), and summer steelhead historically occupied the North Fork and Middle Fork of the Eel River as well as the Van Duzen River and Larabee Creek (an intermediate-sized tributary that lies next to the Van Duzen River on the north side of the mainstem Eel River); all of these basins share the characteristic of draining relatively high elevations and substantial spring snowmelt. As a contrasting example, only winter steelhead and fall-run Chinook salmon occupy the lower, warmer South Fork Eel River.

3.3. Population Classification

Historical populations were classified into four types based on the viability-in-isolation and degree of isolation (self-recruitment). The types of populations are Functionally Independent, Potentially Independent, Dependent, and Ephemeral. Two of the 33 population units included in our analysis were classified as Ephemeral (Hubbard and Euchre creeks). In the absence of estimates of population viability and historical population capacity, historical

habitat capacity was used as a proxy. This historical habitat capacity was based on a landscape-based model (IP; Appendix A, (Agrawal et al. 2005)). Along the Oregon Coast, appropriate data were available to compare historical abundance of adult coho salmon based on in-river catches with adult abundance estimates based partially on the IP model (Lawson et al. 2006). The results from the Oregon Coast indicate that IP performed very well as a proxy for capacity of a basin when compared to historical catch data. Throughout most of the SONCC Coho Salmon ESU, data are lacking to perform such an analysis, particularly the habitat-specific smolt production estimates that are available from the Oregon Coast.

The distance between ocean entry points of basins was used as a measure of population isolation. Insight gained from the analyses of genetic data from coastal populations of coho salmon along the Oregon and northern California coasts generally support this assumption of the geographic model for historical population (i.e., isolation by distance). Therefore, we use the connectivity-viability to synthesize information on the relative size of historical populations of coho salmon and their distribution along the coast. Below, we develop the inputs for the connectivity-viability model for coho salmon populations in the SONCC Coho Salmon ESU and review results.

3.3.1. Population Classification Methods

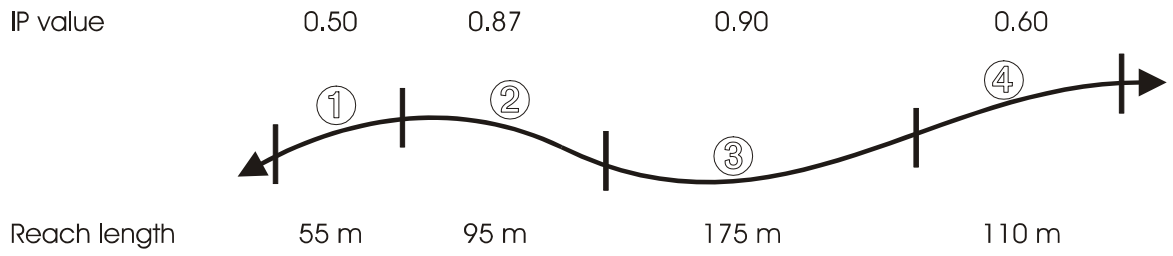
Historical population size — We use predictions from the IP model, excluding areas with mean August temperatures exceeding 21.5ºC, as the basis for our habitat-based population proxy (Appendix A), and assume that carrying capacity of coho salmon populations is linearly proportional to the length of accessible habitat within a watershed weighted by the intrinsic potential for habitat suitable for juvenile rearing (IP km). IP km calculated for areas not excluded by a temperature mask of mean August temperature ≥21.5ºC were used as a proxy for population size in the analysis[7] (Plates 9 and 10). The abundance estimates developed by Lawson et al. (2006) were highly correlated ($r^2 \approx 0.90$) with IP km (T. Nickelson, personal communication). The IP km values used and reported for a population are an integrated value.

[7] Results from the connectivity-viability analysis for the SONCC Coho Salmon were not highly sensitive to small changes in the mean August temperature selected to exclude areas from our habitat-based population proxy.

Within a population's habitat area, each reach is weighted by (i.e., multiplied by) its IP value, and these are summed throughout the area for a population total (Figure 6).

The temperature mask developed for our analysis was very general since it had to be applied to a wide and diverse geographical area. Recent work by Welsh et al. (2001) and Madej et al. (2006) illustrate more detailed, site-specific approaches that might be considered during recovery planning to target specific streams and water temperature issues. Of particular note in the work by Welsh et al. (2001) and Madej et al. (2006) is the suggestion that thermal restriction may have reduced available rearing habitat from historical levels. Madej et al. (2006) estimated that thermal restriction may have reduced the historical distribution of juvenile coho salmon habitat by 75% in Redwood Creek ,suggesting that watershed disturbance can impose a temperature barrier where none existed historically. Madej et al. (2006) also found that water temperatures in Redwood Creek reached their maximum in the middle basin and become cooler farther downstream; Madej et al. (2006) suggest that perhaps "coastal fog, old-growth redwood trees in the riparian zone, and an abundance of cool-water tributaries and seeps" contribute to the cooling trend in the lower basin.

Isolation/self-recruitment — The classification of populations that we used was based on the historical capacity of a population and the level of self-recruitment (i.e., proportion of native spawners), based on geographic distance between ocean entry points and the relative sizes (capacity) of the populations. Few data exist for dispersal rates of coho salmon, therefore the model uses a relatively simple approach that is a function of the distance among ocean entry points. Distances between each pair of ocean entry points were calculated with GIS and represented the distance as the fish swims (i.e., not straight line distances). Tributaries of Humboldt Bay were considered a single basin (i.e., a single population). The historical capacity based on the IP model was used as a proxy for abundance for each population. In the connectivity-viability model, the proportion of native spawners was assumed to be a constant 95% of the potential returning adults to a basin, the remaining 5% dispersed to adjacent ocean-entry points along the coast with an exponential decline with distance. To account for



No.	Reach length (m)	IP value	Integrated IP (IP m)
1	55	0.50	27.5
2	95	0.87	82.65
3	175	0.90	157.50
4	110	0.60	66.00
Total	435	-	333.65

Figure 6. Calculation of integrated intrinsic potential (IP) from reach specific IP values.

migrants across the ESU boundaries, the Sixes River to the north and Usal Creek to the south were included in the analysis.

3.3.2. Population Classification Results

The results of this analysis based on historical watershed capacity (proxy for abundance) and location of the watershed in the ESU, shows a distribution ranging from small, dependent populations to large, independent populations (Figure 7). The connectivity-viability model estimates the level of self-recruitment for each stream. Streams with a higher level of self-recruitment (proportion of native spawners) are more isolated. In order to assign the relative roles of populations in the ESU, we developed criteria for assigning roles (e.g., Functionally Independent) to each population. Although to some extent these criteria were artificial and arbitrary, they were based on our understanding of the techniques used and population dynamics of salmonid populations in the context of self-recruitment and historical capacity.

The criterion used to identify Functionally Independent populations was relatively straightforward because the structure of the model used a 95% fidelity rate. Populations that on average received at least 95% native return were net donors, whereas populations that received less than 95% native return were net receivers, and therefore not Functionally Independent. The horizontal line in Figure 7 depicts this criterion.

We used a threshold value of 34 IP km to differentiate among populations likely to have been viable-in-isolation from those that are not. This threshold is based on simulation analyses developed by Nickelson and Lawson (1998), and has been selected for consistency with the TRTs responsible for the Oregon Coast Coho Salmon ESU (Lawson et al. 2006) and Central California Coast Coho Salmon ESU (Bjorkstedt et al. 2005). Briefly, Lawson et al. (2006) used the stochastic life-cycle model of Nickelson and Lawson (1998), which itself is based on an extensive empirical data set for Oregon Coast coho salmon, to develop predictions of extinction risk for a population of coho salmon as a function of the amount of "high quality" habitat available to the population. "High quality" habitat is defined as habitat where populations will replace themselves when at full seeding and marine survival is 3% (Nickelson 2001). The model provides quantitative predictions of extinction probabilities, but

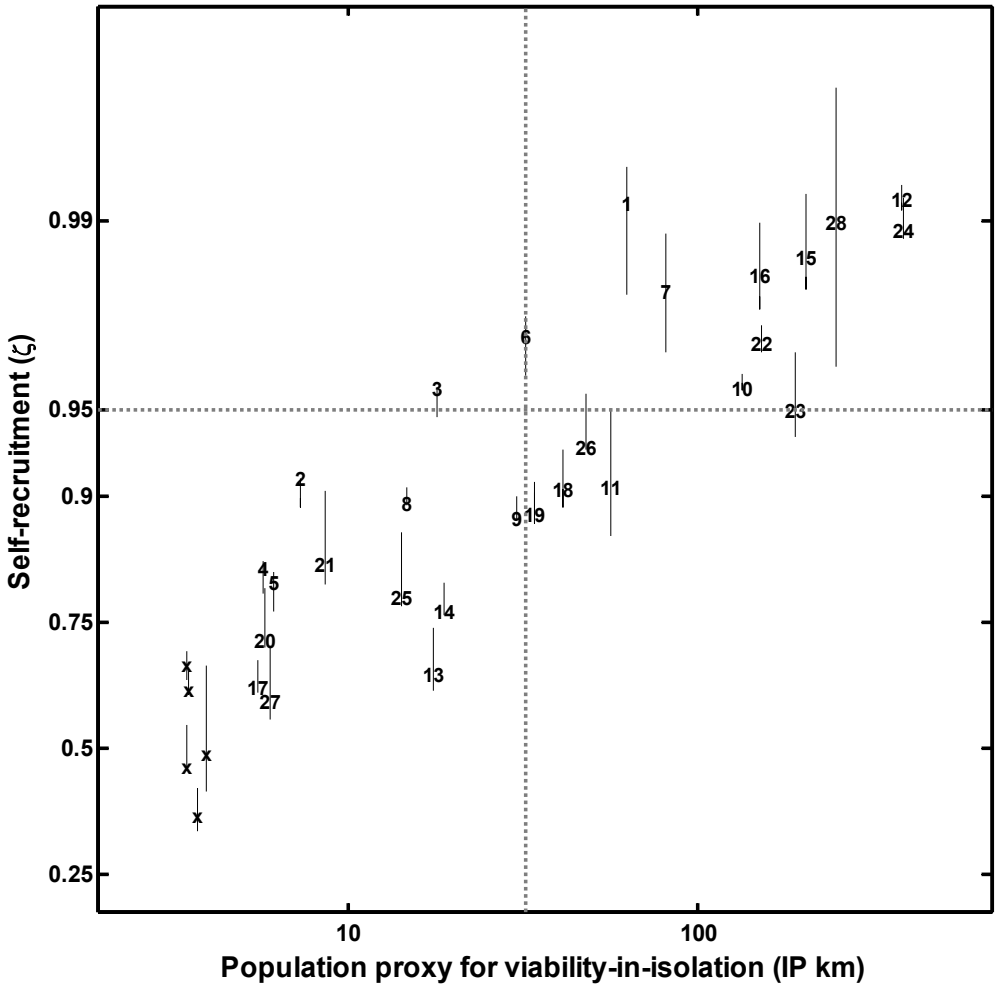


Figure 7. Structure of SONCC Coho Salmon ESU based on predictions of viability-in-isolation analysis based on predictions from the IP model, excluding areas where mean August air temperature exceeded 21.5 °C, and self-recruitment. Populations are identified by numbers corresponding to those listed in Table 1. Solid vertical lines indicate the range of self-recruitment observed for dispersal functions defined by exponential decay over distance with decay parameters ranging from –0.01 km^{-1} to –0.1 km^{-1}; identification numbers indicate self-recruitment for δ = -0.05 km^{-1}. Horizontal gray dotted line demarcates source populations (populations above the line for which self-recruitment exceeds fidelity) from sink or pseudo-sink populations (populations below the line for which fidelity exceeds self-recruitment). Vertical gray dotted line indicates threshold for viability-in-isolation at 34 IP km (see text for details).

these probabilities are sensitive to many of the model parameters (e.g., freshwater production, marine survival, density dependence). In contrast, a more qualitative result of their model was that as habitat quantity decreases, extinction probability increased exponentially. In their model, extinction probabilities consistently begin to rise sharply as available high quality habitat decreased below 24 km of high quality habitat. Since we use IP km (i.e., integrated IP km), not stream length of high quality habitat, we examined the results of (Nickelson 2001) and found that on average 34 IP km was equal to 24 km of high quality habitat used in the Oregon streams Nickelson investigated. Therefore, we use 34 IP km as our threshold for independent populations. This is not to say that populations occupying watersheds with less than 34 IP km will not necessarily go extinct within 100 years if isolated from immigration. Rather, we expect that extinction rates for such populations will be sufficiently high for extinctions to be an important element of the population's dynamics over time scales on the order of hundreds of years.

From the modeling work and empirical data from Oregon, 24 km of habitat (34 IP km for our purposes) was predicted to produce 15,000 spawners at 10% marine survival (Nickelson and Lawson 1998). It was at this value where the probability of extinction increased rapidly and therefore the TRTs for both the Oregon Coast Coho Salmon ESU and the SONCC Coho Salmon ESU set the vertical line to distinguish between viable-in-isolation (i.e., persistent) and non-viable populations (Figure 7). Although 15,000 spawning coho salmon sounds like a relatively high threshold for historical viability-in-isolation, this was calculated to be a maximum assuming 10% marine survival (Lawson et al. 2006). In years with 1% marine survival, such populations would have fewer than 1,500 spawners. In general, these estimates assume the best possible production, a condition that most likely occurred rarely (Nickelson and Lawson 1998; Lawson et al. 2006).

We included all direct tributaries to the Pacific Ocean with 3.4 IP km in the connectivity-viability analysis for the SONCC Coho Salmon ESU, and treated the Humboldt Bay tributaries as a single population with a proxy size based on IP predictions. Assuming that all populations within Humboldt Bay error in returning to the bay at the same rate, treating the tributaries as a composite population has no effect on dispersal to nearby populations. In addition, the IP km from the lower regions of the three large basins (i.e., Rogue, Klamath, and

Eel rivers) were used to represent the basin in the analysis given the discontinuous distribution of habitat in these large basins. In the lower Rogue River and lower Klamath River, the suitable habitat is concentrated in the most downstream portions of these lower regions. In the Eel River, the IP km used in the connectivity-viability analysis was the total for the lower Eel River and Van Duzen River for similar reasons. These lower portions of the large basins are more similar to other coastal basins than to other portions within the basin in terms of the environmental variables examined.

Population designation was based on where each population was located in the viability-independence space, with the range of self-recruitment observed for various dispersal distances (Figure 7; the solid vertical lines above and below each population number in Figure 7 represent the results of a range of dispersal distances, i.e., varying dispersal kernels in the model) providing some insight into the sensitivity of the assumptions of the analysis. Populations with a self-recruitment value greater than or equal to 0.95 and having at least 34 km of integrated IP were designated as Functionally Independent, populations with at least 34 km of integrated IP but a self-recruitment value less than 0.95 were designated as Potentially Independent. All other populations were designated Dependent populations except for Euchre Creek that was designated as an Ephemeral population. For instance, Bear River was designated as a Potentially Independent population, although depending on the dispersal value used, it could be considered a Functionally Independent population. This results from the size and location of the Bear River between the large Eel River and also the relatively large Mattole River. Other populations where a difference in the dispersal kernel would result in a change in designation are the Humboldt Bay tributaries (23) and the Winchuck River (11). The Humboldt Bay tributaries, like the Bear River, are impacted by the Eel River. Humboldt Bay's designation is sensitive to the value of the dispersal kernel, although less so than the Bear River. The designation of the Winchuck River is only slightly sensitive to the value of the dispersal kernel. The Winchuck River being impacted by its size and location relative to the Smith River and Chetco River. Few populations had IP values close to the 34 IP km value used to determine viability-in-isolation. Euchre Creek (6) had 32.31 IP km, and a self-recruitment value of 0.97, resulting in it being designated as an Ephemeral population. This is due to its location, relative to nearby populations, and its relative size compared to adjacent

populations. In general, we anticipate that Ephemeral populations will function within the ESU in a manner similar to Dependent populations, although habitat where Ephemeral populations are found will be unoccupied more frequently. Pistol River (9) with 30.23 IP km had the highest value of IP of the Dependent Populations. Little River (19) with 34.20 IP km had the lowest value of IP of the Potentially Independent populations.

Table 1 and Figure 8 summarize our conclusions regarding the historical population structure of coho salmon within the SONCC Coho Salmon ESU. These conclusions are based on analysis of self-recruitment to putative populations for coastal basins (viability-in-isolation) and for interior sub-basins, the distribution of coho habitat based on the IP model and variability in environmental and ecological characteristics of the sub-basins. The genetic data available for coastal populations of coho salmon supports our use of an "isolation-by-distance" dispersal assumption, and with the exception of the Winchuck River, Humboldt Bay tributaries, and Bear River, the designation of Functionally or Potentially Independent was consistent for the range of dispersal kernels used in our analysis. Our greatest uncertainty in population designation was with Euchre Creek, Pistol River, Little River. Bear River was heavily influenced (i.e., receives strays from the Eel River) by our treatment of the Eel River in the viability-in-isolation analysis. Little River just met our 34 IP km threshold for independence. Conversely, Euchre Creek and Pistol River fell just below our 34 IP km threshold for independence.

The TRT did not consider the connectivity-viability model appropriate for use within the Rogue, Klamath, and Eel basins of the SONCC Coho Salmon ESU. The primary reasons were that they are more radially distributed than the ocean-entry points of coastal basins and that the fidelity rate within these large basins would be different and more variable than that for ocean-entry points. Based on the TRT's analysis of environmental and ecological diversity, these large basins were divided into major sub-basins. In addition to the analysis of environmental and ecological diversity, the TRT examined results from the IP modeling to assess the distribution (e.g., contiguous versus isolated) of habitat among sub-basins that might lead to population structuring. Once these populations units were delineated, the TRT then assessed the amount of IP km to determine the role these population units played within the ESU. In general, the amount of IP km in the major sub-basins is where the majority of the

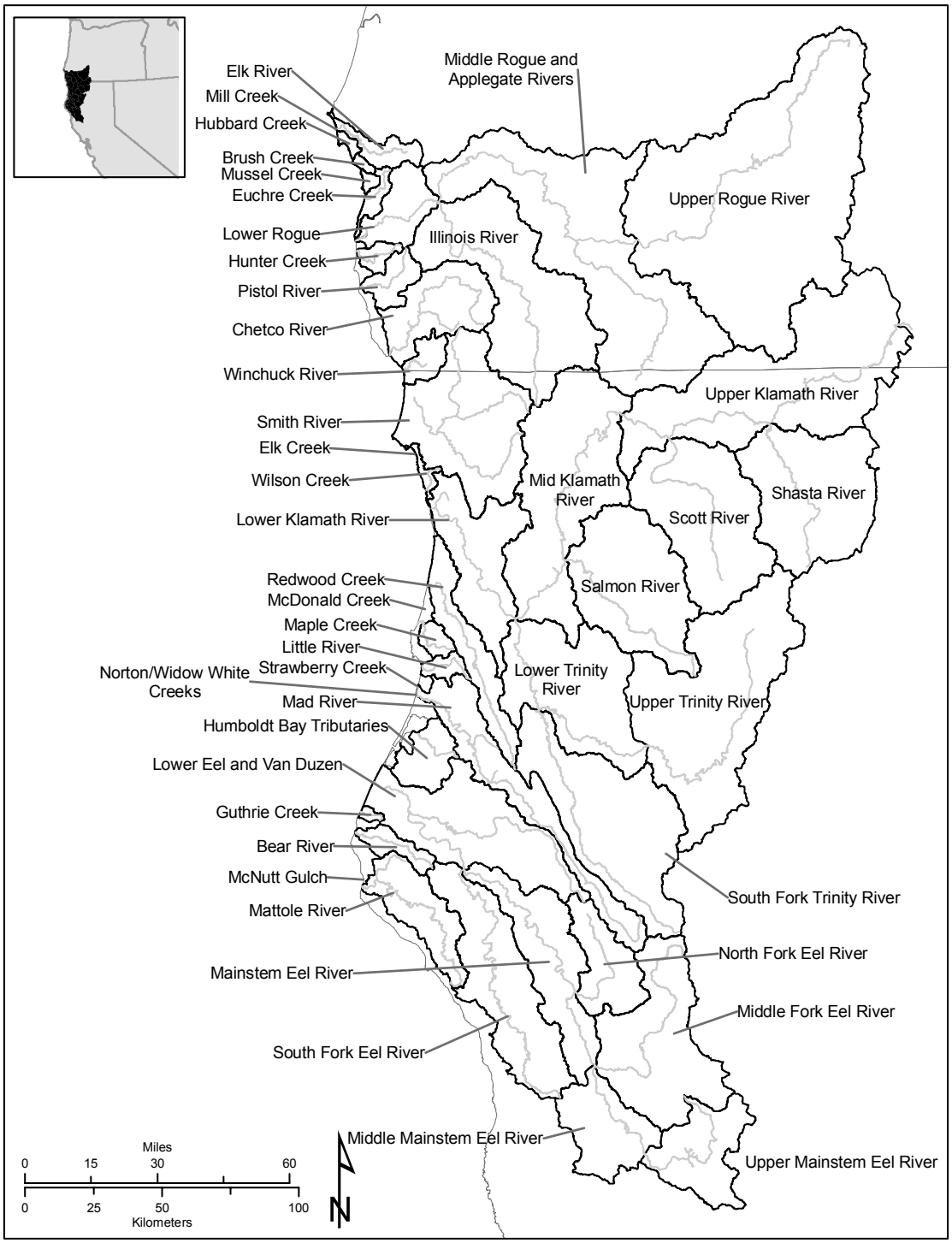


Figure 8. Historical population structure of coho salmon in the SONCC Coho Salmon ESU.

IP km for the ESU resides. All of the sub-basins identified had more than 34 IP km and were therefore designated as independent populations, but given the TRT's concern of greater straying within these major basins, it was determined that the larger sub-basins (e.g., IP km > 200) were acting as Functionally Independent populations and the smaller sub-basins acted as Potentially Independent populations within the ESU. Therefore, sub-basins determined to be Functionally Independent had IP km values that ranged from 205 (Lower Klamath River) to 915 (Upper Rogue River); the one exception was the Upper Trinity River with an IP value of 64 km. The TRT was uncertain about historical conditions in this area; the snowmelt driven hydrograph and lower gradient valley made it suitable in terms of the IP model, but the temperature mask excluded much of the area. We are uncertain if our IP temperature mask appropriately modeled this region, because it was so strongly influenced by snowmelt. The designation of Functionally Independent was largely influenced by the uncertainty related to historical water temperatures and the relatively long run coho salmon needed to make to this area, a type of life history the TRT determined to be an important component of the greater diversity of the ESU.

4. Discussion

The TRT based its determination of historical population structure of SONCC Coho Salmon ESU on a simple conceptual model of spatially dependent demographics of 59 populations considered to be historically present. These populations were classified based on their viability-in-isolation and self-recruitment. We believe that the interaction of these two characteristics provided us a measure of population independence and allowed us to categorize the role of each population played in the ESU. Our analysis of population structure was strongly constrained by the lack of data available for consideration; however our approach was intentionally consistent with the approaches taken by TRTs working in more data-rich areas of California and the Pacific Northwest (Currens et al. 2002; Lindley et al. 2004; Lawson et al. 2006). Technical Recovery Teams in California and the Pacific Northwest have expressed great confidence in inferences based on geographical information, followed by, in order of declining strength of inference, information on migration rates, population genetics, life history and phenotypic variation, population dynamics, and, lastly, environmental and habitat characteristics (Lindley et al. 2004; Bjorkstedt et al. 2005; Lawson et al. 2006). We believe our goal to have an approach that was consistent, reproducible, and transparent was met by our rule-based approach.

In general, the historical population structure of coho salmon in the SONCC ESU was characterized by small-to-moderate-sized coastal basins where high quality habitat is in the lower portions of the basin and three large basins where high quality habitat was located in the lower portions, middle portions of the basins provided little habitat, and the largest amount of habitat was located in the upper portions of the sub-basins. Populations that were determined to have minimal demographic influence from adjacent populations and were viable-in-isolation were classified as Functionally Independent (19 populations). Populations that appeared to have been viable-in-isolation but were demographically influenced by adjacent populations were classified as Potentially Independent (12 populations). Small populations of coho salmon that do not have a high likelihood of sustaining themselves over a 100-year time period in isolation and receive sufficient immigration to alter their dynamics

and extinction risk were classified as Dependent (27 populations). One population was designated as an Ephemeral population.

4.1. Uncertainty

The ability to develop models and draw inferences of historical population structure (or future population trajectories) is inherently limited by uncertainty. The quality of these analyses, or predictions, depends strongly on how well one understands both the current state of the system of interest and the processes that underlie the historical development of the current state or its future trajectory. It is clear that coho salmon in coastal basins of southern Oregon and northern California face greater risk of extinction under current circumstances than they faced under historical (pre-European influence) conditions. Although we recognize this general trend, our understanding of the current status of coho salmon in this region is imprecise (Weitkamp et al. 1995; California Department of Fish and Game 2004; Good et al. 2005), and available data were sparse and provided a poor foundation for rigorous analysis of the processes that influence these populations. In place of detailed, local information, it was necessary to draw on data and analyses developed elsewhere and to apply what has been learned to similar issues in the SONCC Coho Salmon ESU. Our uncertainty may be greatest in how well our IP model performs as a proxy for habitat capacity and the threshold value of 34 IP km used to define our viable-in-isolation line. As discussed earlier, this value was based on a simple habitat-based model of Oregon Coast coho salmon populations (Nickelson and Lawson 1998). There are inherent regional and inter-basin differences in habitat productivity that are not accounted for by using a single threshold. In addition, historical habitats may have been more productive and stable than current conditions that were used by Nickelson and Lawson (Nickelson and Lawson 1998; Lawson et al. 2006). The TRT examined what difference a 50% reduction (17 IP km) or a 50% increase (51 IP km) in our threshold value would have on our classification of populations. Of the coastal populations, three Dependent populations (Pistol River, Wilson Creek, and Elk Creek) would have been reclassified as Potentially Independent with a reduction of the threshold and both Ephemeral populations (Hubbard and Euchre creeks) would have been reclassified as Functionally Independent populations. Three Potentially Independent populations (Maple Creek/Big Lagoon, Little

River, and Bear River) would be reclassified as Dependent populations with an increase of the threshold. The majority of our classifications would not be affected by a reasonable change to the viability-in-isolation threshold.

4.2. Diversity Strata

The delineation of populations in this report forms the foundation for later development of viability criteria at the population scale and the integration of population information into viability criteria at the ESU scale. Viability of the ESU will necessarily incorporate variability in population type as well as diversity and spatial structure within the ESU. In anticipation of developing of viability criteria at the population scale and integration of population information into viability criteria at the ESU scale, we identify groups of populations that span the diversity and distribution that currently exists or historically existed within the ESU. We refer to these groups as 'diversity strata' to reflect our primary focus on the issue of diversity, broadly defined, as the basis for delineating these groups. By "diversity" we mean (1) diversity of (potential) selective environments (Williams and Reeves 2003), (2) diversity of phenotypes, including life history types, and (3) diversity of genetic variation, both neutral and selected. Different amounts of information are available for each of these three categories of diversity, but our understanding of the processes that generate such diversity strongly suggests that diversity of different types will be correlated with one another at various spatial scales, and through the inclusion of diversity in selective environments, will be correlated with geographic structure as well. The development of diversity strata will provide a basis for future efforts to identify ESU configurations, or sets of populations that, by virtue of the location, composition, and viability of the populations, are expected to yield a viable ESU. To ensure that the results of this exercise allow the spatial structure of the ESU to be sufficiently represented in subsequent analyses, we consider spatial information explicitly, although diversity information is primary, in delineating diversity strata. It is important to note that although the concept of a "diversity stratum" is intended to capture important structure at a scale between that of an individual population and an ESU, it does not necessarily form to a biological concept. Rather, diversity strata are described in terms of geography and a generally similar set of environmental and ecological conditions. Note that the role of a given

population in satisfying diversity elements of ESU-level viability criteria will depend on the contribution of the appropriate portion of that population to satisfying the criteria for a given diversity stratum.

The TRT organized the independent and dependent populations of coho salmon in the SONCC ESU into diversity strata largely based on the geographical arrangement of the populations and the multivariate analysis of basin-scale environmental and ecological characteristics (Figure 9). The SONCC Coho Salmon ESU is characterized by three large coastal basins that penetrate far inland to high elevation areas influenced by snowmelt and warmer summer and colder winter temperatures and smaller coastal basins characterized by moderate air temperatures, low elevation, and relatively high precipitation levels. Therefore, the primary diversity strata are the interior and coastal sub-basins. The interior sub-basin strata were divided into substrata representing the three major sub-basins of the Rogue, Klamath, and Eel basins. However, sufficient geographical and environmental variability occurs within the Klamath basin, therefore the Klamath basin was split into sub-strata of the Klamath River (upstream of the confluence with the Trinity River) and the Trinity River. The lower portions of these three large basins were included in the coastal basins sub-strata because they are more similar to other coastal basins in terms of the environmental and ecological characteristics examined than interior portions of the large basins. In addition, the lower portions of the large basins were more geographically proximate to the coastal basins. The Van Duzen River was included with the lower portion of the Eel River in the coastal basin stratum.

Across the coastal basins of the SONCC Coho Salmon ESU, there existed sufficient geographical and environmental variability resulting in the TRT dividing the coastal basins into three sub-strata. The northern sub-stratum includes basins from the Elk River to the Winchuck River, including the lower portion of the Rogue River. These basins were very similar in the clustering analysis of environmental and ecological characters (Figures 3-5). The central substratum includes coastal basins from the Smith River to the Mad River, including the lower portion of the Klamath River. This stratum is characterized by several larger coastal basins (Smith River, Redwood Creek, and Mad River) and smaller coastal systems that include lagoons (McDonald Creek and Maple Creek/Big Lagoon). The southern

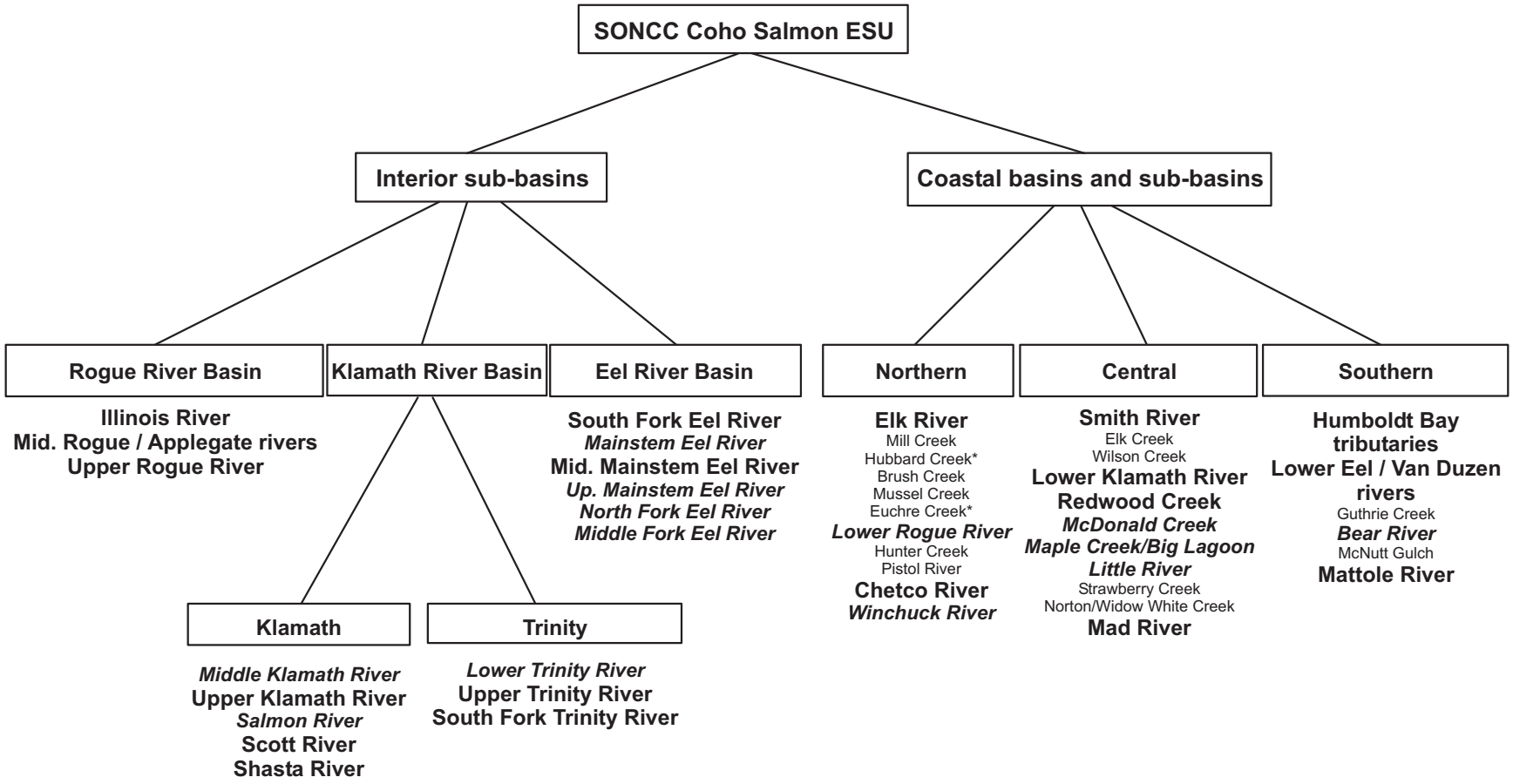


Figure 9. Arrangement of historical populations of the Southern Oregon/Northern California Coasts Coho Salmon ESU into diversity strata. Functionally Independent populations are listed in bold font, Potentially Independent populations are listed in bold italic font, other listed populations are Dependent populations (Note: Hubbard Creek* and Euchre Creek* are Ephemeral populations).

stratum includes the Humboldt Bay tributaries south to the Mattole River, including the lower Eel River and Van Duzen River.

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6. Appendices

6.1. Appendix A - Intrinsic Potential

Since we lack information concerning the historical distribution of coho salmon through a large portion of the SONCC Coho Salmon ESU and lack the biological data necessary to assess carrying capacity directly, we made use of habitat-based proxies for historical use and environmental capacity as a measure of a population's carrying capacity. To develop such proxies, we implemented a GIS model that predicts the distribution of species-specific "intrinsic potential" (IP) for habitat suitable for spawning or juvenile rearing ((Burnett et al. 2003)[8], also see Agrawal et al. (2005)).

In brief, the model predicts the potential for a stream reach to exhibit habitat characteristics suitable for a specific life history stage as a function of the underlying geomorphic and hydrologic characteristics of the landscape. In general, we use mean gradient, mean annual discharge, and valley constraint of stream reaches as the basis for our analysis. Valley constraint is defined as the ratio of the width of the valley floor (floodplain) and the width of the active stream channel. IP is calculated as the geometric mean of suitability scores, which range from 0-1 and describe the potential that a stream reach with a specific value for a given characteristic will exhibit suitable habitat. We used this approach to generate predictions of IP for spawning and rearing habitat of coho salmon using approaches developed by (Burnett et al. 2003)

To develop a description of the historical distribution of coho salmon throughout their in the SONCC ESU, we implemented the model developed by Burnett et al. (Burnett et al. 2003) to predict the IP of stream reaches to exhibit habitat characteristics suitable for coho salmon (Plate 9). Preliminary examination of the output from the IP model indicated regional discrepancies between historical records and the extent of areas with high IP for spawning and rearing habitat. These discrepancies were most apparent in portions of the Central California Coast (CCC) Coho Salmon ESU, but were also apparent in portions of the SONCC Coho Salmon ESU, where an additional factor, water temperature, is likely to be a major determinant of habitat suitability. Therefore, we developed a secondary analysis, based on

[8] http://www.fsl.orst.edu/clams/

temperature, to screen the results from the IP model for coho salmon in the CCC Coho Salmon ESU (see below) and incorporated those findings to the SONCC IP model results.

Temperature mask — Summer water temperatures in the interior portions of some larger drainages in the SONCC and CCC Coho Salmon ESUs (e.g. Rogue, Klamath, Eel, and Russian rivers) can approach or exceed the tolerable limits for juvenile coho salmon (Eaton et al. 1995). In cases where this occurs, temperature might preclude coho salmon from using areas that, based on geomorphic and hydrologic characteristics, would otherwise be suitable. Comprehensive data on water temperatures were not available for the SONCC and CCC ESUs. Therefore, to identify areas where temperature might limit the distribution of coho salmon, we combined information on the historical distribution of coho salmon (e.g., Spence et al. (2005)) and mean August air temperature to identify a threshold temperature above which juvenile coho salmon generally do not occur. This analysis found that coho salmon were rarely reported as present in watersheds where the lowest mean August air temperature in the basin exceeded 21.5ºC (Agrawal et al. 2005); this temperature is comparable to the maximum tolerable water temperature for coho salmon reported by Eaton et al. (1995). We therefore used 21.5ºC as the threshold to modify results from the IP model by excluding habitat in areas that historically may have been excessively warm for coho salmon. Plate 10 summarizes the results of this exercise for coho salmon in the SONCC ESU.

The use of the IP model to assess coho salmon habitat rests on two assumptions. First, we assume that the suitability curves that translate information on geomorphic and hydrologic characteristics into IP apply to watersheds in the SONCC Coho Salmon ESU as they do for the Oregon Coast Range where it was originally developed to predict the distribution of areas with varying degrees of potential to exhibit suitable rearing habitat for juvenile coho salmon. Lacking local data from which to develop region-specific curves to predict the potential for suitable juvenile rearing habitat as a function of the characteristics of stream reaches, we must assume that either the suitability curves based on data from the Oregon Coast Range apply also to watersheds in southern Oregon and northern California, or (somewhat less strongly) that the relationship between watershed characteristics and habitat potential throughout the SONCC Coho Salmon ESU differs from that observed in Oregon in a uniform and consistent

way. An extensive literature search provided no basis for choosing alternative suitability curves for the SONCC ESU (Agrawal et al. 2005).

Second, we assume that the differences in geomorphic structure and processes between the Oregon Coast Range and the SONCC Coho Salmon ESU, although present, do not require us to modify the IP components (gradient, discharge, valley-width constraint). One of the most substantial differences among coastal watersheds in Oregon and California is the amount and timing of precipitation, especially as one moves south along the coast. We attempted to account for this variation by estimating regional models for mean annual discharge as a function of catchment area and mean annual precipitation (Agrawal et al. 2005). The relations estimated for coastal watersheds north of Cape Mendocino were almost identical to that reported for coastal Oregon watersheds. We considered if a geomorphic approach might confirm or offer an alternative to transposing IP criteria from the Oregon Coast Range to the Klamath and Franciscan (Eel River) provinces. The hypothesis is that juvenile coho salmon favor a certain channel type (bar-pool or pool-riffle) that form under geomorphic conditions that can be identified from small-scale maps (e.g., 10-m DEM). These conditions (gradient, discharge, valley-width constraint) are the same as those used in the IP index but are linked to habitat by geomorphic conditions that form bar-pool channels. In these channels, pools form as the zones of flow concentration between alternate bars; the spreading of flow and sediment transport emerging from a pool is associated with sediment deposition on the next bar downstream, from which flow spills into a concentration zone, and so forth. This pool-forming tendency creates a minimum spacing of pools, but bends and obstructions can influence the size and spacing of individual pools. As sediment-storage features, bar evolve with changing boundary conditions, flow events, and sediment inputs. The result is a more complex and dynamic morphology than in channels without bars, and similarly, more complex habitats, including backwaters along bar margins. Finally, bar evolution is associated with lateral migration of channels and the formation and maintenance of floodplains and side channels.

The next most favorable channel type would be plane-bed (or forced-pool), which generally occurs in steeper valleys. In such channels, pools and bars do not form in straight uniform reaches but may be forced by large obstructions, bends, or sills. Forcing features such

as wood jams or large sediment inputs can cause some channel migration but such channels tend to be very stable except for infrequent disturbance. Abundant wood, which would characterize pristine basins in the Oregon Coast range, could make plane-bed channels highly favorable for juvenile coho salmon. Wood is less plentiful in the Klamath Mountains but probably equally so in the redwood coastal zone.

One should be able to predict the occurrence of bar-pool channels from drainage area, gradient, and valley confinement, just as used in IP. The strongest association would be expected for gradients <2% and some minimum floodplain width/active channel width. Of course, the transition between bar-pool to plane-bed (and plane-bed to step-pool) over gradients of any governing condition is gradual rather than step-wise. Evidence for the 2% break comes from the classification scheme of (Montgomery and Buffington 1997) for channels in Washington, and from the upper limit of dimensionless pool volumes vs channel gradient (Buffington et al. 2002) for channels in northern California and southern Oregon. Median dimensionless pool volume is the median residual pool volume in a reach (study reaches characteristically having around 10 pools) scaled by unit channel volume (the volume of a channel segment at bankfull stage having a length of one bankfull channel width).

In the final analysis, we found little to suggest a revision of the existing IP gradient curves for the SONCC Coho Salmon ESU. The IP model used seems consistent with the association of bar-pool and plane-bed channel types with gradient. Discharge is a weak factor at best in channel types, and it is uncertain if the same criteria could be transferred from the Oregon Coast Range to the California provinces. There should be an association in California between the existence of floodplains (i.e., valley-width constraint), bar-pool channels, and juvenile coho salmon habitat, but we could not find a defensible alternative to the use IP index adopted from Oregon for California.

Intrinsic Potential-based metrics of population carrying capacity — To make use of IP as a proxy for population carrying capacity, we integrate IP over the length of stream within each watershed that is accessible to anadromy to give a measure of habitat potential at the watershed scale. In doing so, we interpret IP as a likelihood that suitable habitat will occur, and assume that IP is linearly related to habitat. High quality freshwater habitat has been

suggested as being a critical characteristic of a watershed that enables populations to endure periods of poor ocean survival (Nickelson and Lawson 1998). In practice, we make the assumption that the carrying capacity of a watershed is linearly proportional to the integrated, IP-weighted extent of stream accessible to anadromy. For coho salmon freshwater rearing habitat has been shown to be a strongly limiting factor, without regard for any assumption regarding the intrinsic productivity of each population.

6.2. Appendix B - Environmental data

The following tables present environmental data (Table B1) and the results(Table B2) of the Principal Components Analysis used to examine ecological and environmental conditions throughout the SONCC Coho Salmon ESU.

Appendix Table B1. Environmental data used in principal component analysis. See Appendix Table B2 for codes and data descriptions; location numbers correspond to numbers in Table 1.

			Air temperature (Cº)							EcoRegion					Lithology			
Basin	ID	PPT	Mean	Min	Max	Range	ELEV	SNWI	PEAK	Klamath	Chap	Coast	ECascades	Cascades	Volc	Sed	Cry	All
Elk R.	1	303.30	11.80	6.90	16.70	9.80	431.38	0.00	4.00	0.00	0.00	1.00	0.00	0.00	0.00	0.75	0.14	0.10
Hubbard Ck.	3	217.10	11.70	7.30	16.20	8.90	107.25	0.00	4.00	0.00	0.00	1.00	0.00	0.00	0.00	0.42	0.00	0.58
Brush Ck.	4	294.30	12.10	7.40	16.80	9.40	312.03	0.00	4.00	0.00	0.00	1.00	0.00	0.00	0.00	0.62	0.38	0.00
Mussel Ck.	5	268.60	12.20	7.60	16.70	9.20	233.13	0.00	4.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
Euchre Ck.	6	270.40	12.20	7.60	16.70	9.10	256.73	0.00	4.00	0.00	0.00	1.00	0.00	0.00	0.00	0.88	0.04	0.05
Lower Rogue	7a	250.90	12.30	6.80	17.90	11.10	440.88	0.00	4.00	0.40	0.00	0.60	0.00	0.00	0.00	0.89	0.08	0.02
Ilinois R.	7b	211.90	11.00	4.70	17.30	12.60	812.66	16.58	4.20	1.00	0.00	0.00	0.00	0.00	0.17	0.42	0.32	0.09
Applegate R.	7c-1	99.70	9.30	3.40	15.30	11.80	956.37	115.47	4.25	1.00	0.00	0.00	0.00	0.00	0.45	0.33	0.15	0.08
Middle Rogue	7c-2	132.20	11.20	5.30	17.00	11.70	647.30	3.65	4.50	0.99	0.00	0.01	0.00	0.00	0.20	0.39	0.32	0.09
Upper Rogue	7d	100.80	8.40	1.80	15.10	13.30	1076.50	234.78	6.00	0.41	0.00	0.00	0.00	0.58	0.75	0.07	0.05	0.12
Hunter Ck.	8	271.20	12.50	7.50	17.40	9.90	463.97	0.00	4.00	0.44	0.00	0.56	0.00	0.00	0.00	0.74	0.26	0.00
Pistol R.	9	282.30	12.10	7.30	16.80	9.50	524.08	0.00	4.00	0.83	0.00	0.17	0.00	0.00	0.02	0.86	0.10	0.02
Chetco R.	10	282.50	11.60	6.50	16.70	10.20	584.13	0.03	4.00	0.87	0.00	0.13	0.00	0.00	0.03	0.68	0.27	0.02
Winchuck R.	11	222.80	11.90	7.60	16.20	8.70	291.11	0.00	3.00	0.36	0.00	0.64	0.00	0.00	0.00	0.96	0.01	0.03
Smith R.	12	264.90	11.10	5.60	16.60	11.00	647.55	25.01	4.20	0.75	0.00	0.25	0.00	0.00	0.09	0.43	0.40	0.08
Wilson Ck.	14	196.50	11.70	7.30	16.10	8.80	201.68	0.00	4.00	0.00	0.00	1.00	0.00	0.00	0.00	0.90	0.00	0.10
Lower Klamath R.	15a	209.20	11.30	5.20	17.40	12.20	578.25	21.11	4.50	0.58	0.00	0.42	0.00	0.00	0.00	0.87	0.11	0.02
Mid Klamath R.	15b	185.40	10.80	3.60	18.00	14.40	971.03	126.11	4.60	1.00	0.00	0.00	0.00	0.00	0.02	0.58	0.40	0.00
Upper Klamath R.	15c	77.30	8.20	2.00	14.30	12.30	1228.40	186.16	5.60	0.51	0.00	0.00	0.42	0.08	0.62	0.23	0.13	0.01
Salmon R.	15d	141.70	10.00	1.90	18.10	16.20	1297.60	260.91	6.50	1.00	0.00	0.00	0.00	0.00	0.18	0.50	0.30	0.01
Scott R.	15e	78.50	9.50	1.70	17.40	15.70	1319.60	165.85	5.60	1.00	0.00	0.00	0.00	0.00	0.17	0.46	0.27	0.10
Shasta R.	15f	61.40	9.20	1.80	16.60	14.80	1227.00	149.97	6.50	0.60	0.00	0.00	0.19	0.21	0.58	0.14	0.10	0.18
So. Fk. Trinity R.	15g	129.50	10.90	3.20	18.70	15.50	1078.50	123.71	4.70	1.00	0.00	0.00	0.00	0.00	0.01	0.84	0.15	0.01
Lower Trinity R.	15h	162.10	11.38	3.12	19.64	16.52	945.09	158.92	2.00	1.00	0.00	0.00	0.00	0.00	0.04	0.73	0.23	0.00

Appendix Table B1 continued.

			Air temperature (C°)							EcoRegion					Lithology			
Basin	ID	PPT	Mean	Min	Max	Range	ELEV	SNWI	PEAK	Klamath	Chap	Coast	ECascades	Cascades	Volc	Sed	Cry	All
Upper Trinity R.	15i	128.77	11.88	4.53	19.23	14.70	1283.75	82.01	3.44	1.00	0.00	0.00	0.00	0.00	0.03	0.52	0.42	0.03
Redwood Ck.	16	180.20	11.10	4.80	17.40	12.60	533.00	42.91	4.00	0.40	0.00	0.60	0.00	0.00	0.00	1.00	0.00	0.00
Maple Ck.	18	167.00	11.30	6.10	16.50	10.30	290.20	0.00	4.00	0.00	0.00	1.00	0.00	0.00	0.00	0.97	0.00	0.03
Little R.	19	156.50	11.40	6.40	16.40	10.00	297.80	0.00	4.00	0.00	0.00	1.00	0.00	0.00	0.00	0.81	0.00	0.19
Mad R.	22	160.50	10.80	3.90	17.70	13.80	785.30	104.65	4.00	0.68	0.00	0.32	0.00	0.00	0.00	0.96	0.00	0.04
Jacoby Ck.	23a	153.80	11.50	7.20	15.80	8.50	283.90	0.00	5.00	0.00	0.00	1.00	0.00	0.00	0.00	0.83	0.00	0.17
Freshwater Ck.	23b	134.20	11.60	7.40	15.80	8.50	181.40	0.00	5.00	0.00	0.00	1.00	0.00	0.00	0.00	0.64	0.00	0.36
Elk R.	23c	144.00	11.60	7.20	16.00	8.80	234.50	0.00	5.00	0.00	0.00	1.00	0.00	0.00	0.00	0.83	0.00	0.17
Salmon Ck.	23d	129.80	11.80	7.60	16.00	8.30	181.70	0.00	5.00	0.00	0.00	1.00	0.00	0.00	0.00	0.53	0.00	0.47
Lower Eel R.	24a-1	203.79	12.00	6.70	17.30	10.60	309.60	3.65	5.00	0.25	0.00	0.75	0.00	0.00	0.00	0.75	0.00	0.25
Van Duzen R.	24a-2	134.07	10.90	4.10	17.70	13.70	713.70	81.33	4.00	0.63	0.00	0.37	0.00	0.00	0.00	0.92	0.02	0.06
So. Fk. Eel R.	24b	160.32	12.40	5.90	19.00	13.40	495.80	1.04	4.00	0.14	0.00	0.86	0.00	0.00	0.00	0.97	0.02	0.02
Lower Mainstem Eel R.	24c	173.49	12.60	4.40	20.80	16.40	610.30	25.48	5.00	0.95	0.00	0.05	0.00	0.00	0.00	0.99	0.01	0.00
No. Fk. Eel R.	24d	125.30	12.10	3.80	20.50	16.50	906.70	57.75	4.00	1.00	0.00	0.00	0.00	0.00	0.02	0.97	0.02	0.00
Mid. Fk. Eel R.	24e	266.19	11.70	4.40	19.00	14.50	1118.60	66.73	4.50	1.00	0.00	0.00	0.00	0.00	0.02	0.92	0.03	0.04
Upper Mainstem Eel R.	24f	119.41	12.90	4.80	21.10	16.30	666.50	0.18	5.00	1.00	0.00	0.00	0.00	0.00	0.01	0.95	0.00	0.04
Upper Eel R.	24g	155.57	12.30	5.20	19.40	14.10	1059.60	6.52	5.00	0.86	0.14	0.00	0.00	0.00	0.05	0.92	0.02	0.01
Guthrie Ck.	25	126.10	12.00	7.80	16.20	8.40	212.78	0.00	4.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
Bear R.	26	173.60	11.80	6.90	16.70	9.90	456.20	0.00	4.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
Mattole R.	28	196.10	12.20	7.30	17.10	9.80	408.40	0.00	4.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00

Appendix Table B2. Environmental variables used in multivariate analysis, loadings and percent variance explained by the first three principal components, and data sources.

Variable	Code	Loadings			Data source
		PC1	PC2	PC3	
Mean elevation (m)	ELEV	0.3390	-0.1605	-0.0113	(United States Geological Survey 2002)
Snow index	SNWI	0.3306	0.0319	-0.0121	(Daly et al. 1994)
Percent area volcanic	Lith-Volc	0.2915	0.2668	-0.0123	
Average mean annual range of temperature	T-Range	0.2696	-0.3126	0.1719	(Daly et al. 1994)
Percent area Klamath Mountain Ecoregion	Eco-Klamath	0.2522	-0.3277	-0.1240	
Month of peak flow	PEAK	0.2016	0.1990	0.2786	(Daly et al. 1994)
Percent area Cascades Ecoregion	Eco-Cascades	0.1912	0.2522	0.1050	
Percent area Eastern Cascades Ecoregion	Eco-ECascades	0.1761	0.2153	0.0340	
Percent area crystalline	Lith-Cry	0.1480	-0.1259	-0.6334	
Average maximum air temperature	T-Max	0.0363	-0.4682	0.2153	(Daly et al. 1994)
Percent area Chapparal-Oak Ecoregion	Eco-Chap	0.0167	-0.1237	0.3592	
Percent area alluvial	Lith-ALL	-0.0678	0.3025	0.1150	
Average mean annual precipitation	PPT	-0.2209	-0.1019	-0.4148	(Daly et al. 1994)
Percent area sedimentary	Lith-Sed	-0.2477	-0.2649	0.2937	
Average mean air temperature	T-Mean	-0.2977	-0.2552	0.0739	(Daly et al. 1994)
Percent area Coast Range Ecoregion	Eco-Coast	-0.3076	0.2314	0.0731	
Average minimum air temperature	T-Min	-0.3532	0.0792	-0.0776	(Daly et al. 1994)
Percent variation explained		42.97	21.36	8.97	
Cumulative percent variation explained		42.97	64.33	73.31	

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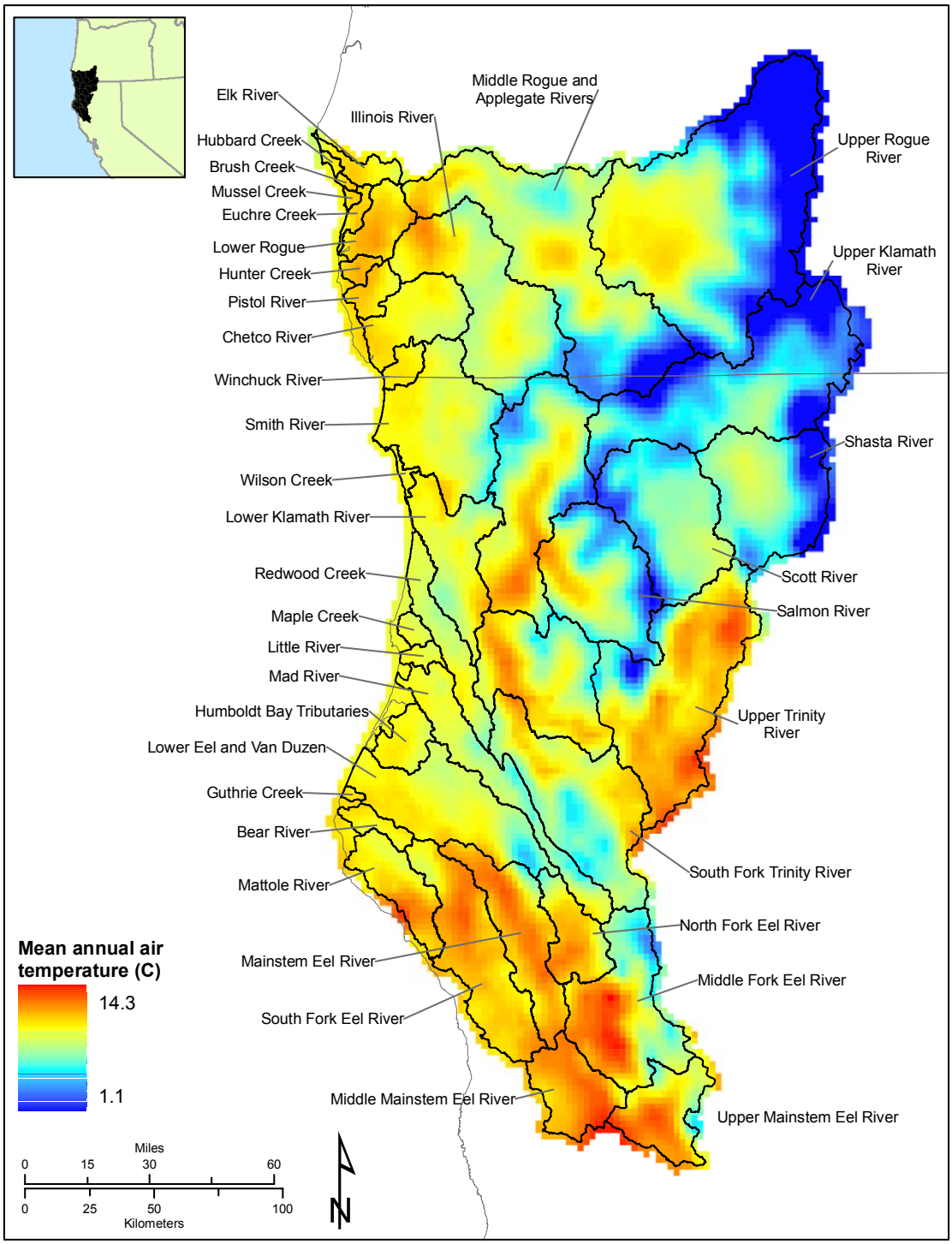

Plate 1. Mean annual air temperature across the Southern Oregon/Northern California Coasts Coho Salmon ESU.

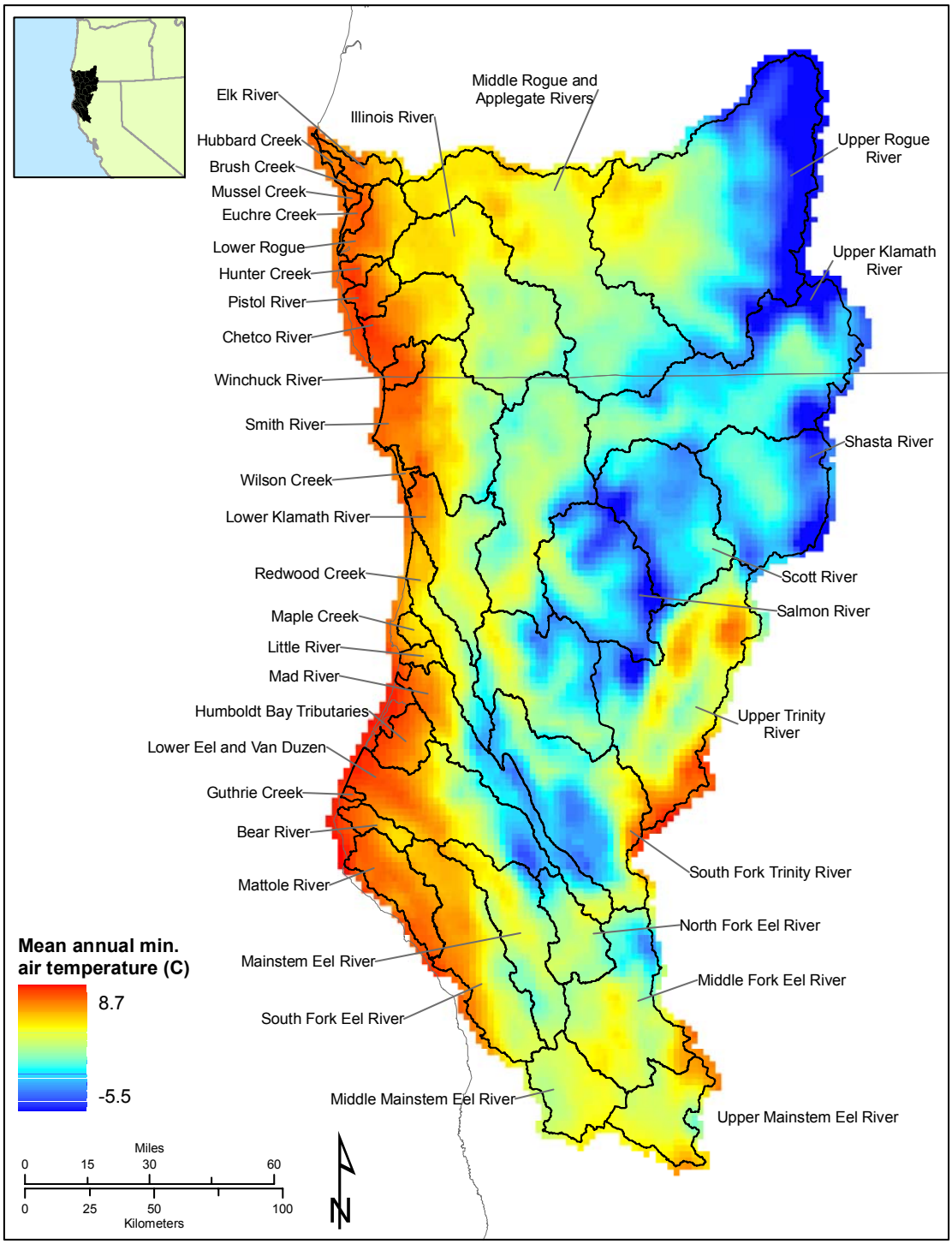

Plate 2. Mean annual minimum air temperature across the Southern Oregon/Northern California Coasts Coho Salmon ESU.

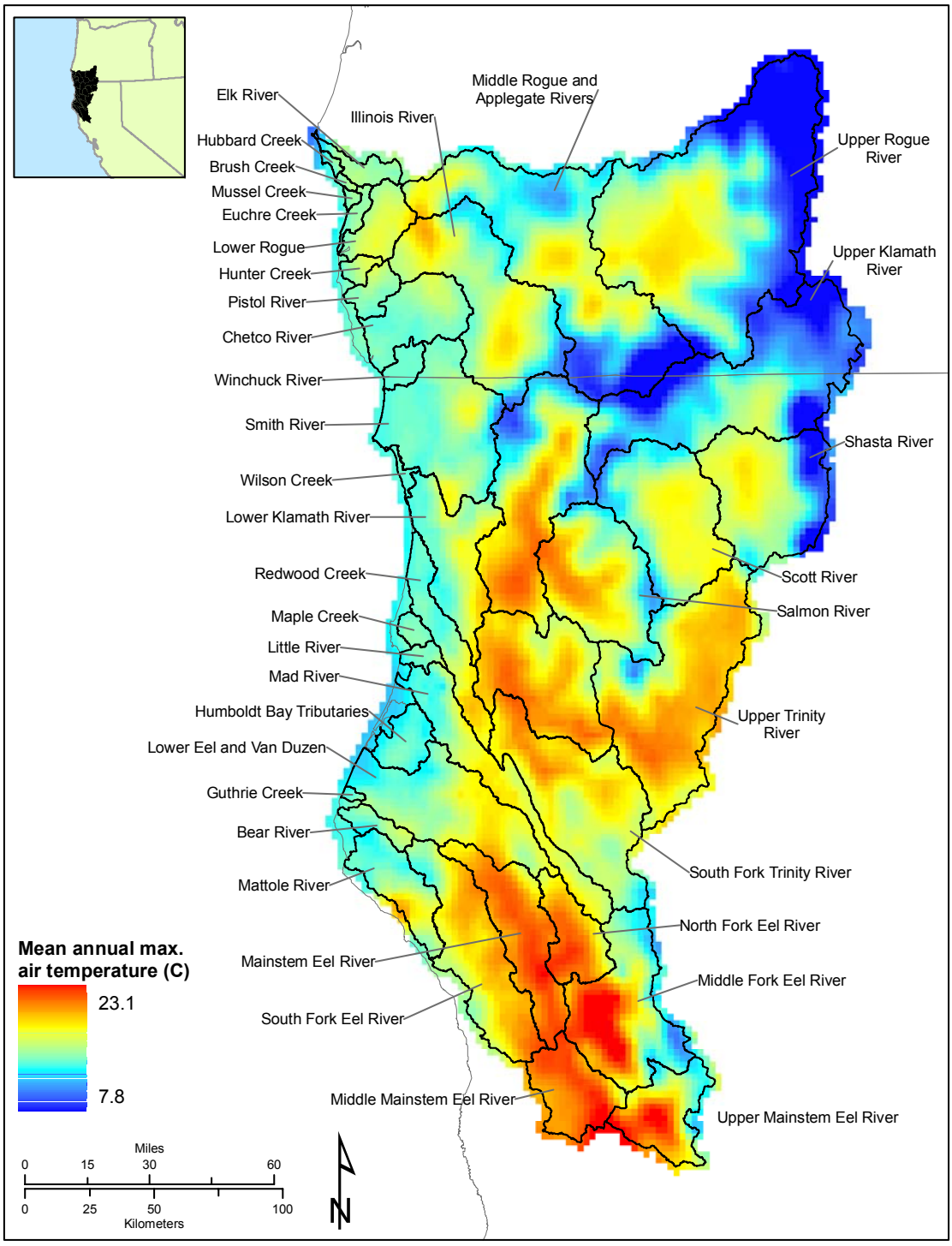

Plate 3. Mean annual maximum air temperature across the Southern Oregon/Northern California Coasts Coho Salmon ESU.

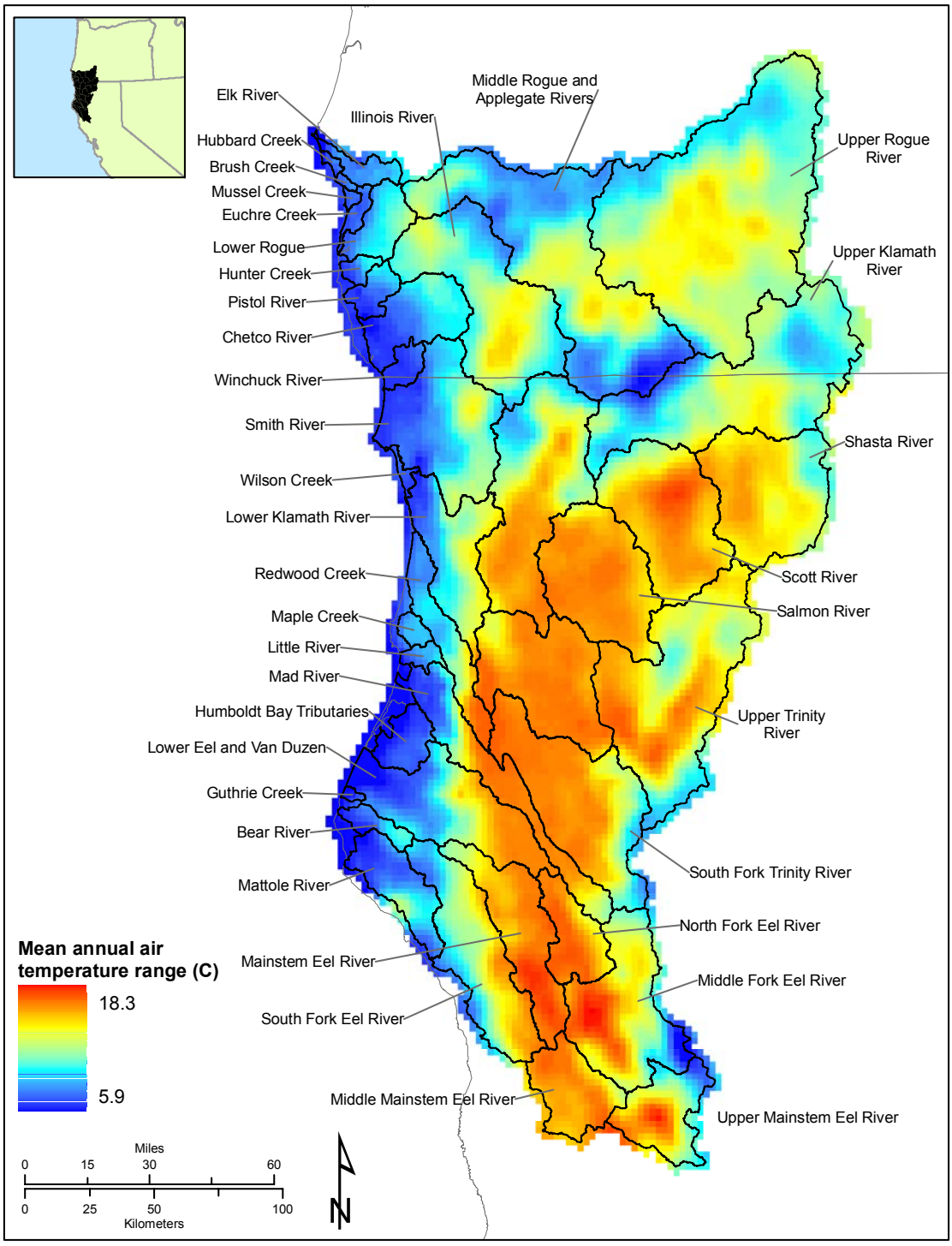

Plate 4. Mean annual air temperature range across the Southern Oregon/Northern California Coasts Coho Salmon ESU.

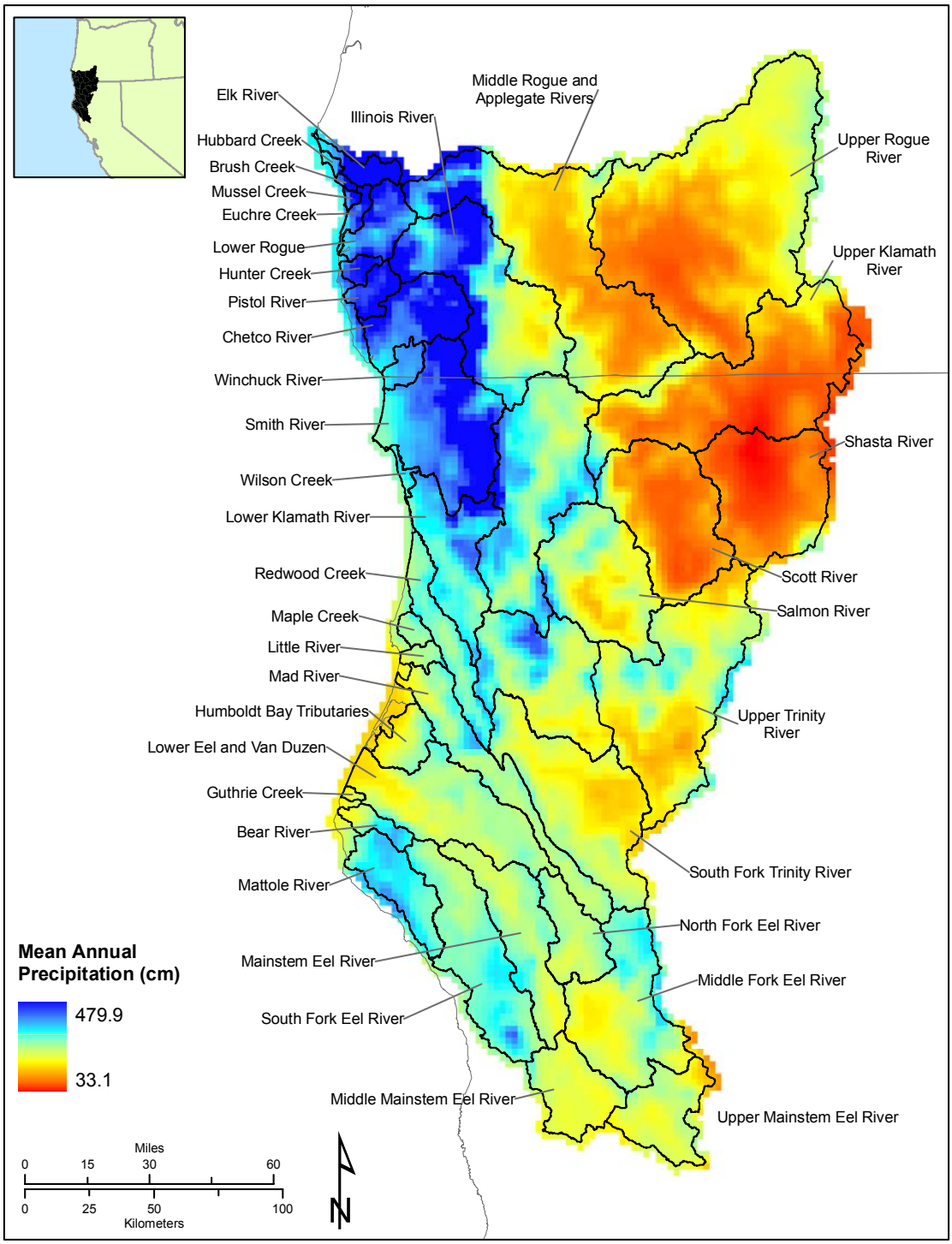

Plate 5. Mean annual precipitation across the Southern Oregon/Northern California Coasts Coho Salmon ESU.

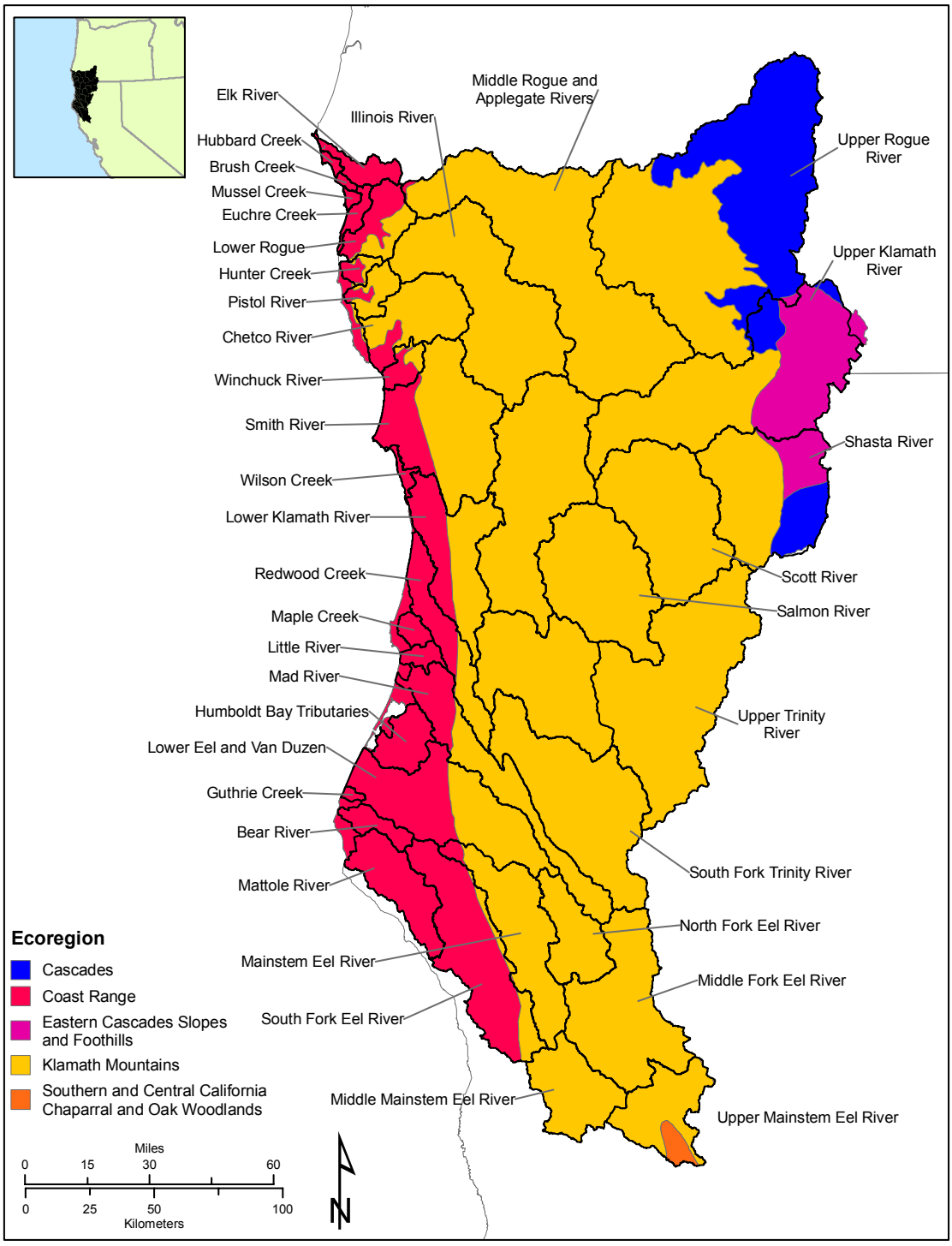

Plate 6. Ecoregions across the Southern Oregon/Northern California Coasts Coho Salmon ESU.

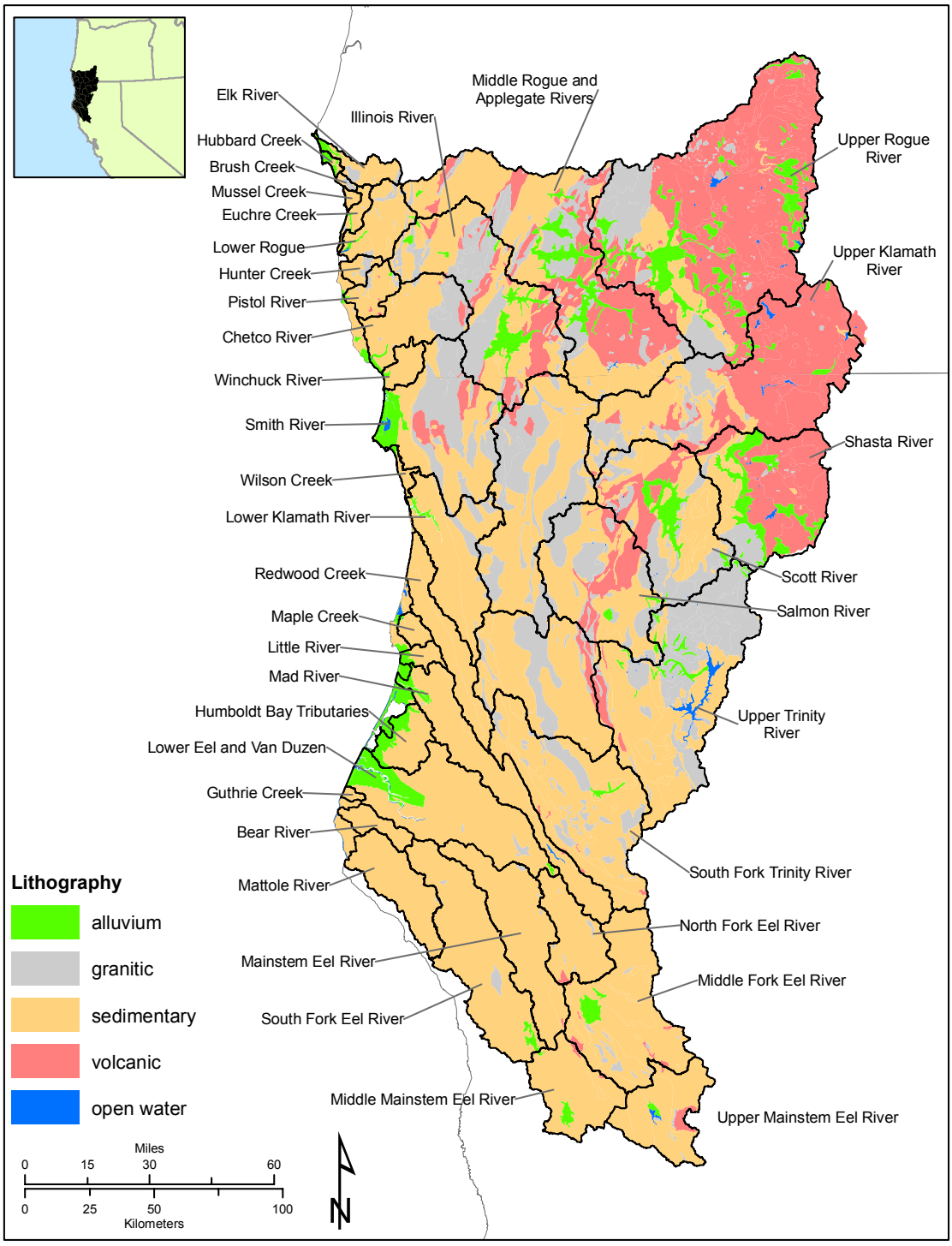

Plate 7. Geology across the Southern Oregon/Northern California Coasts Coho Salmon ESU.

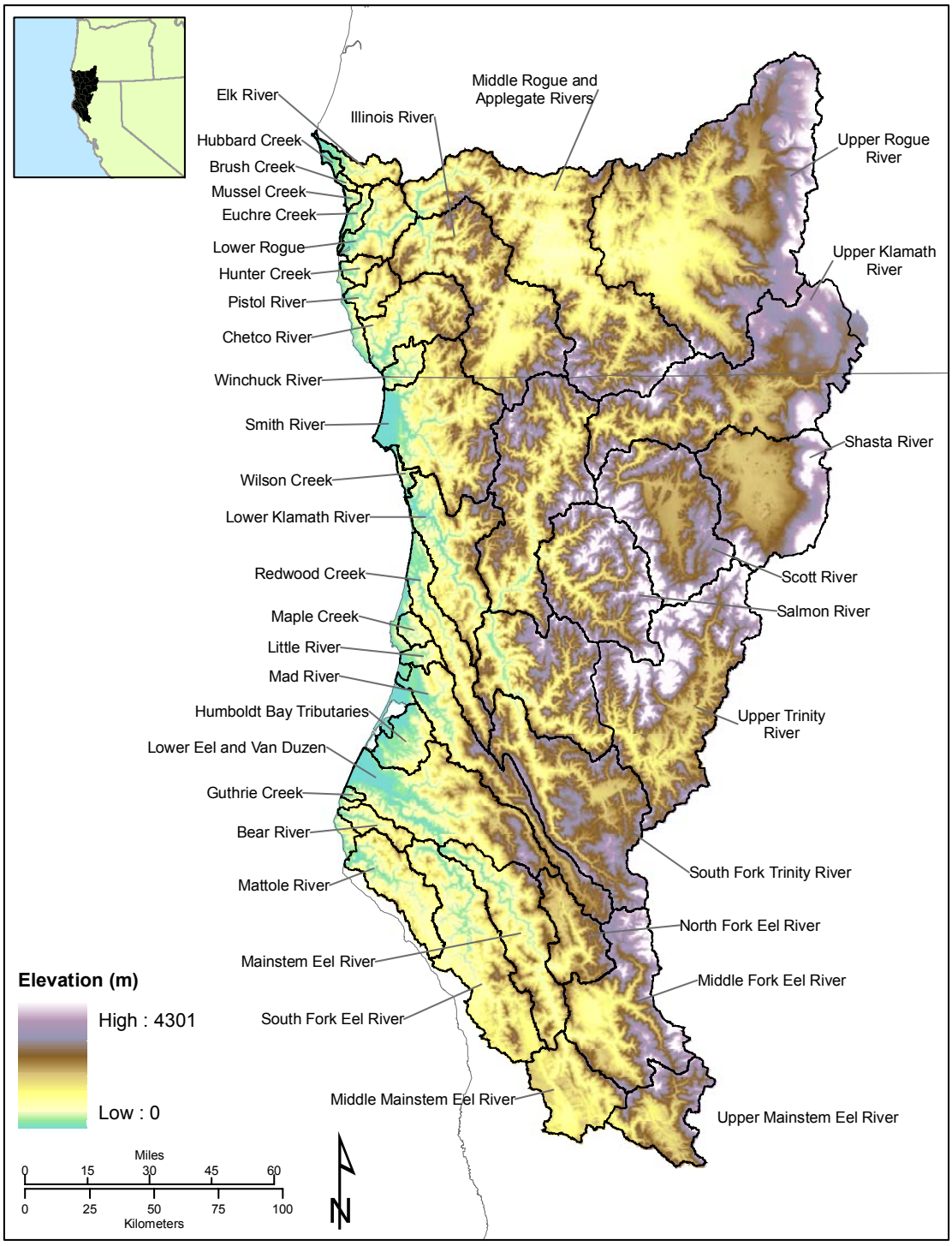

Plate 8. Elevation values across the outhern Oregon/Northern California Coasts Coho Salmon ESU.

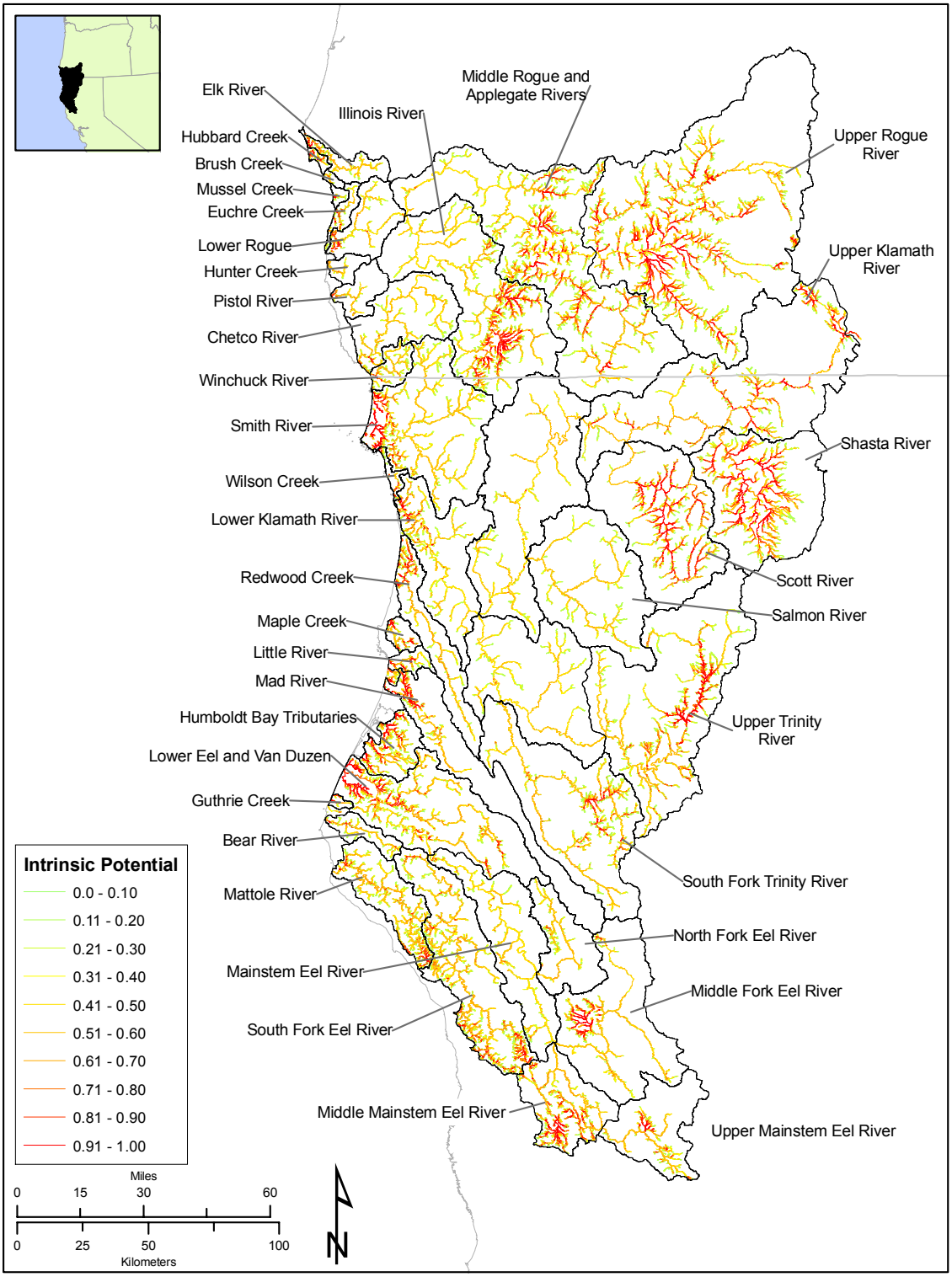

Plate 9. Intrinsic Potential for coho salmon across the Southern Oregon/Northern California Coasts Coho Salmon ESU.

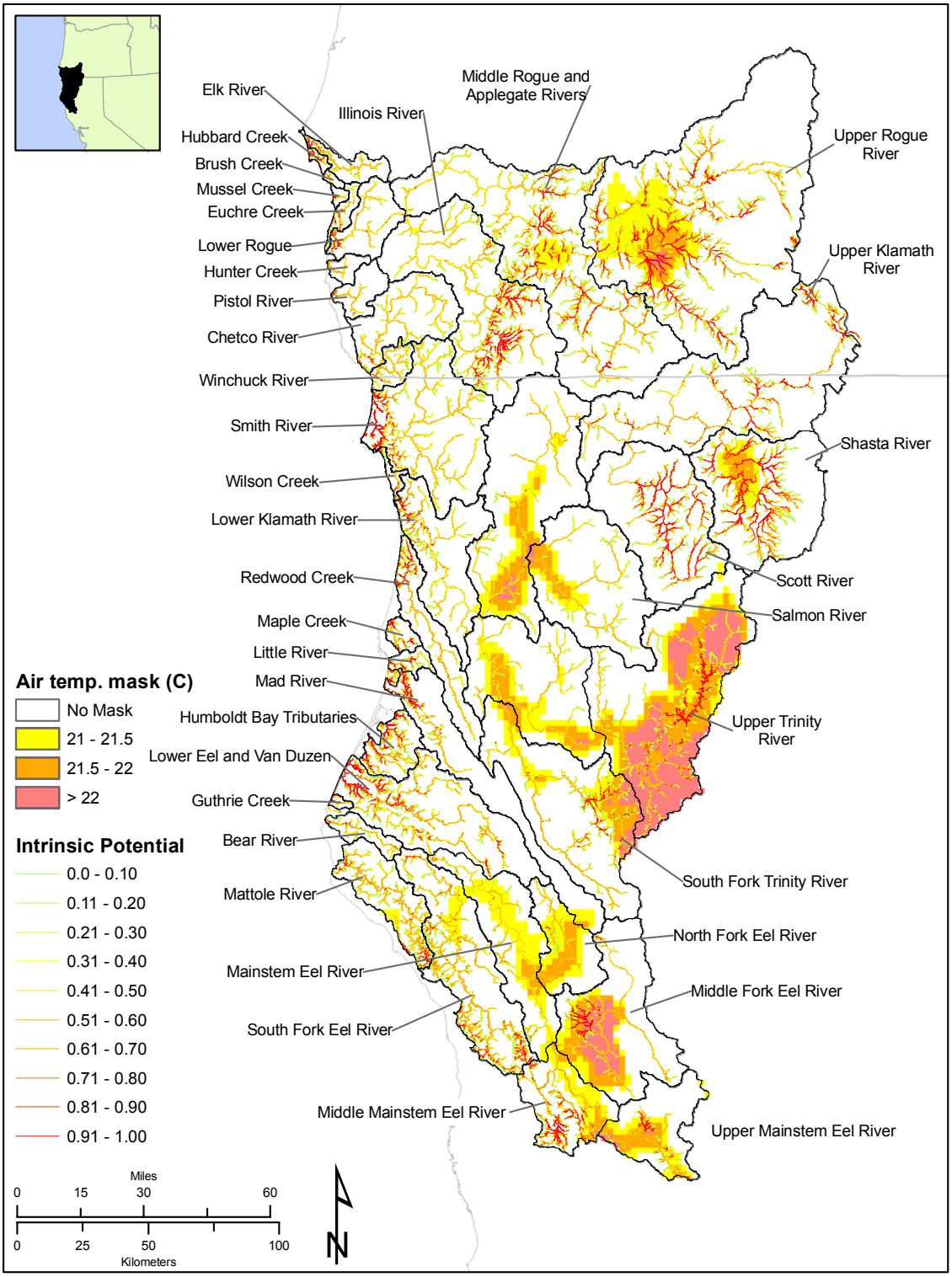

Plate 10. Intrinsic Potential for coho salmon across the Southern Oregon/Northern California Coasts Coho Salmon ESU, including areas where coho salmon are likely to be excluded by warm temperature indicated by temperature mask.

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