NOAA Technical Memorandum NMFS

OCTOBER 2005

AN ANALYSIS OF HISTORICAL POPULATION STRUCTURE FOR EVOLUTIONARILY SIGNIFICANT UNITS OF CHINOOK SALMON, COHO SALMON, AND STEELHEAD IN THE NORTH-CENTRAL CALIFORNIA COAST RECOVERY DOMAIN

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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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Executive Summary

The Technical Recovery Team (TRT) for the North-Central California Coast Recovery Domain (NC-CCRD) has been charged with evaluating the historical population structure of ESUs of coho salmon, Chinook salmon and steelhead that occupy coastal watersheds between the Klamath River (exclusive) and northern Monterey Bay. The main text of this report presents the conclusions of the TRT regarding historical population structure of four ESUs (summarized below), and discussion of analysis, assumptions, and uncertainties that underlie these conclusions.

Our analytical framework extends the original concepts developed by McElhany et al. (2000) by considering independently two characteristics of a population: *viability*, defined in terms of probability of extinction over a specified time frame, and *independence*, defined in terms of the influence of immigration on a population's extinction probability. Following McElhany et al. (2000), we define a "viable" population as a population having a low ($<$5%) probability of going extinct over a 100-year time frame, and define an "independent" population as one for which exchanges with other populations have negligible influence on its extinction risk, estimated over a similar time frame. By arranging populations in "viability–independence" space, and setting appropriate thresholds to distinguish "viable" populations from "non-viable" ones on one hand, and "independent" from "dependent" on the other, we are able to define four types of populations:

- "Functionally Independent Populations" are those with a high likelihood of persisting over 100-year time scales and conform to the definition of independent "viable salmonid populations" offered by McElhany et al. (2000, p. 3).
- "Potentially Independent Populations" have 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.
- "Dependent Populations"[1] have a substantial likelihood of going extinct within a 100-year time period in isolation, yet receive sufficient immigration to alter their dynamics and reduce extinction

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[1] Dependent populations (and, by extension, the watersheds that support them) serve at least three roles within an ESU. First, in the case of catastrophic disturbance, nearby dependent populations can support normally independent populations by providing a small, proximate source of colonists. Second, although they are not themselves dominant sources of dispersers within the ESU, dependent populations increase connectivity within an ESU by allowing dispersal among populations to occur in incremental steps. Third, since they are more subject to genetic drift and inputs of genetic material from other populations, small populations can serve as "evolutionary experiments" more readily than can large populations, such that maintaining conditions that support the existence of small populations may contribute importantly to the diversity evolutionary potential of

risk.

- "Ephemeral Populations"[2] have a substantial likelihood of going extinct within 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 at high densities relatively rarely and to be occupied at all for relatively short periods of time.

To apply this analysis to salmon and steelhead ESUs, we first define distinct demographic units of salmon and steelhead, defined on the basis of two rules, each of which reflect the fact that the anadromous life history places an extremely high premium on a successful transition from saltwater to a suitable freshwater habitat to close the life cycle. Our first rule defines each spawning group that occupies a direct tributary to the Pacific Ocean as a demographic unit separate from analogous groups in other direct ocean tributaries. Our second rule is that spawning groups within a large basin (including tributaries of a common estuary) may comprise multiple populations if sufficient physical, behavioral, or selective barriers to effective dispersal exist. To support evaluation of potential structure according to this rule, we developed an ordination analysis of watershed environmental characteristics, which identifies important regional structure within the ESU. (This analysis also supports the designation of "diversity strata", discussed below.) To support development of the set of demographic units to be considered for each species, we also used a synthesis of historical records and results from a model designed to predict the potential for species- and life-history-stage- specific habitat to occur at a reach scale and thus, the distribution of habitat potential within a watershed.

A number of types of information can be brought to bear to support the analysis, of which we relied most heavily on three: geographic structure, population genetic structure, and life history variation. Although data are generally sparse for the ESUs in the NCCCRD, we are fortunate to have a molecular genetic data for each ESU that supports analysis of population genetic structure. Analysis of genetic data yielded three general results: (1) concordance between population genetic structure and the geographical arrangement of samples, (2) signals of isolation-by-distance, and (3) evidence that dispersal among tributaries within a basin tends to be greater than dispersal among basins. These results support the postulates that underlie our rules for defining demographic units, and further, provide support for the assumptions of a simple model that allows a comprehensive synthesis of historical population status within the ESU based largely on geographic structure. Life history variation was used solely to differentiate populations within an ESU on the basis of major differences in run-timing (e.g., summer and winter steelhead, fall-run and spring-run Chinook salmon.).

The geographical model required that, for each population, we develop (1) a measure of "viability-in-isolation", which is based on the probability of extinction in complete isolation from all other pop-

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the ESU. These three criteria argue strongly that "dependence" should not be equated with "expendable", although it is clear that such populations will serve a different role in contributing to ESU viability than will larger populations. Note that a set of small populations that are dependent on larger populations can themselves exhibit a degree of "mutual dependence" and increased viability as a consequence of bilateral dispersal.

[2] Ephemeral populations are likely to be rare, and to occur almost without exception at the edge of an ESUs range. For two of the three species considered in this report, the NCCCRD spans or includes the southern end of the species (coastal) range, so ephemeral populations are perhaps more likely to be observed in this region.

ulations, and (2) an estimate of self-recruitment, i.e., the proportion of recruits to a population that originate in that population, which, as a measure of the degree to which each population's dynamics are determined internally, serves as a measure of population independence. Methods for calculating population-specific values for these two parameters are discussed in detail in the main text of the report, but rest on (1) estimates of habitat capacity derived from a GIS model as a proxy measure for viability-in-isolation as a proxy for (relative) extinction risk, and (2) comparisons of population-specific self-recruitment rates to the fidelity (homing) rate as an indicator of whether a population is more strongly affected by internal dynamics than by dispersal processes. Self-recruitment is derived from a simple dispersal model that includes information on the size of a population and the size and spatial distribution of neighboring populations. This framework amounts to a "connectivity-viability" model for *ranking* the status of populations within an ESU. Of course, the status of individual populations is not static over time, and the predicted position of a population in viability-independence space should be envisioned as a central point about which a population's true state fluctuates as a function of perturbations to itself and neighboring populations.

We applied the geographic "connectivity-viability" model to each ESU as a major element of our analysis of historical population structure. However, in our interpretation of the results from this model, we also take into account potential biases and uncertainties in the underlying inputs to the model, particularly those that derive from regional patterns in environmental conditions (see main text of report for detailed discussion). As noted previously, we also take into account any relevant information on life history variation in evaluating population structure, with a particular emphasis on distinguishing populations on the basis of major differences in run-timing. After evaluating the historical population type (e.g., "potentially independent") for all demographic units in an ESU, we arrange these populations into diversity strata on the basis of groups identified in our ordination analysis of watershed-scale environmental characteristics. Diversity strata represent an important level of structure (although not necessarily biological structure) between the population and ESU, and offer a useful framework for accounting for diversity and spatial structure in the evaluation of ESU viability under current conditions and future scenarios. Figures on the following pages summarize our conclusions regarding the historical population structure of each ESU in the NCCCRD. Note that not all dependent populations are included in these figures.

The analyses described in this report necessarily incorporate a broad range of assumptions, which are discussed in great detail in the main text. We emphasize, however, that this uncertainty is likely to have relatively minor consequences for subsequent development of ESU viability criteria, given that appropriate consideration of spatial structure and diversity is included in evaluation of viability at both scales of individual populations and each ESU as a whole.

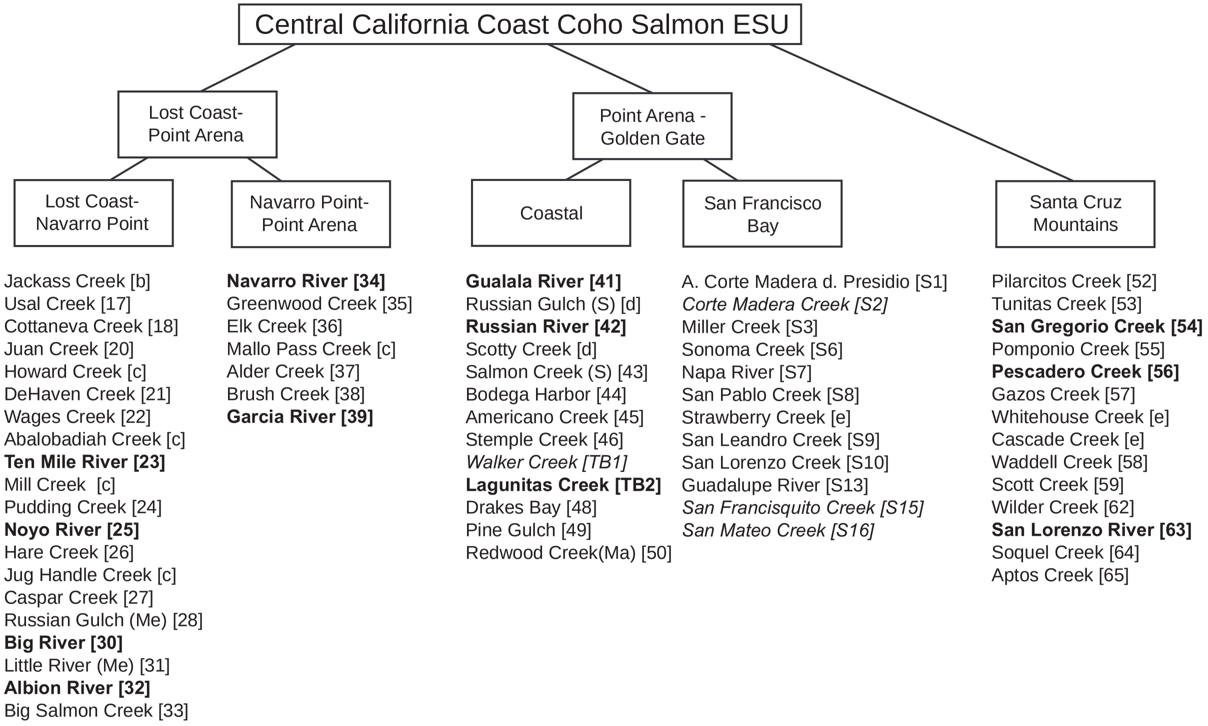

Figure A1. Historical structure of the CCC-Coho ESU. Functionally independent populations are listed in bold font. Potentially independent populations are listed in italic font. Dependent populations are listed in regular font. See text in main report for detailed discussion.

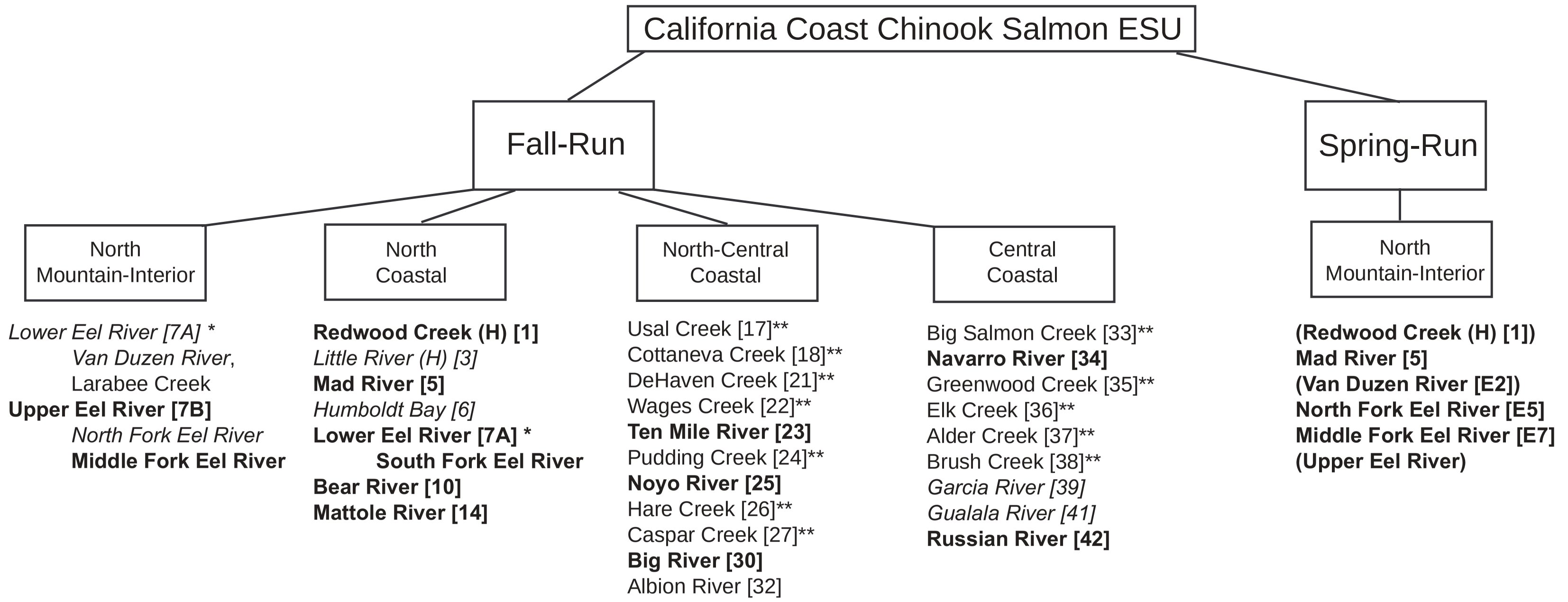

Figure A2. Historical structure of the CC-Chinook ESU. Functionally independent populations are listed in bold font. Potentially independent populations are listed in italic font. Dependent populations are listed in regular font. Populations indicated by a single asterisk are listed under multiple diversity strata occupy environmentally diverse basins or watersheds. Populations indicated by a double asterisk are dependent populations in small watersheds, and are expected to be critically dependent on dispersal for occupancy. Spring-run Chinook salmon populations listed parenthetically are those for which potential historical existence is tentatively inferred from environmental correlates. See text in main report for detailed discussion.

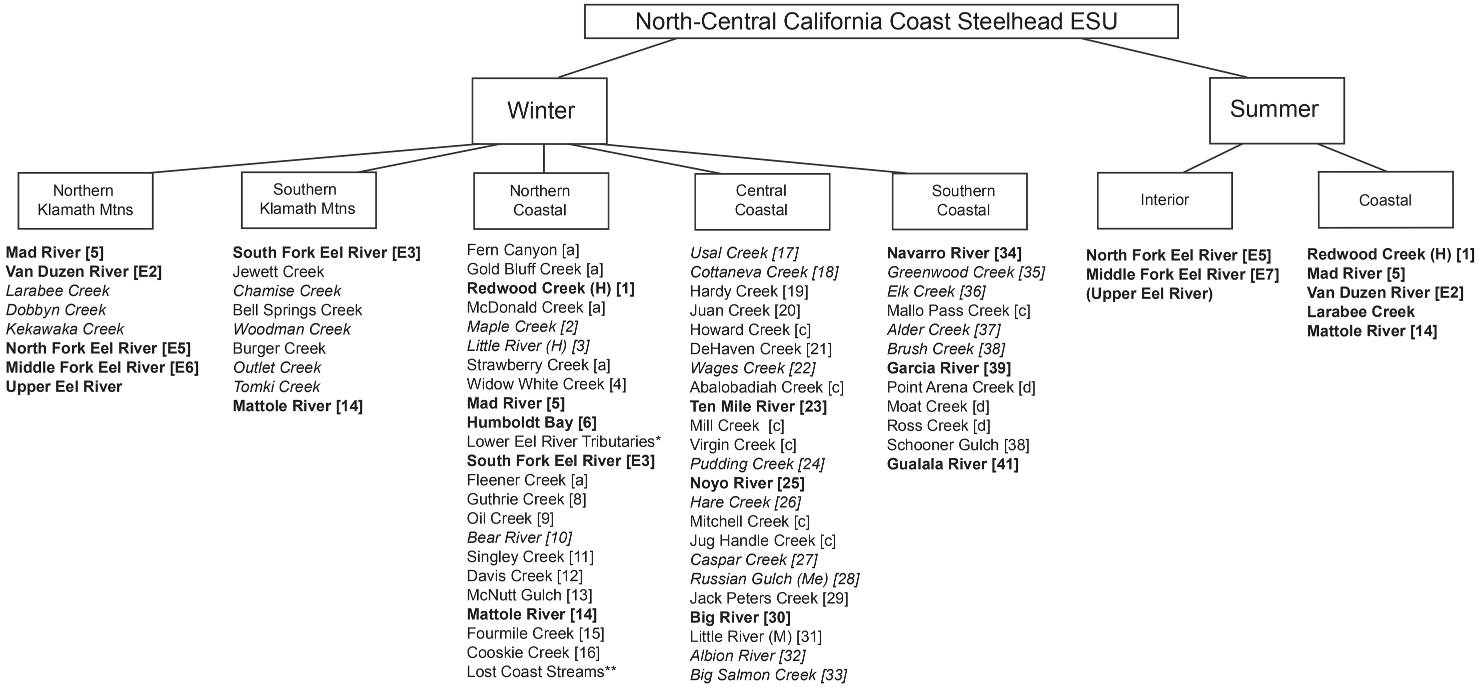

Figure A3. Historical structure of the NC-Steelhead ESU. Functionally independent populations are listed in bold font. Potentially independent populations are listed in italic font. Dependent populations are listed in regular font. Not all dependent populations have been included in this figure. See text in main report for detailed discussion.

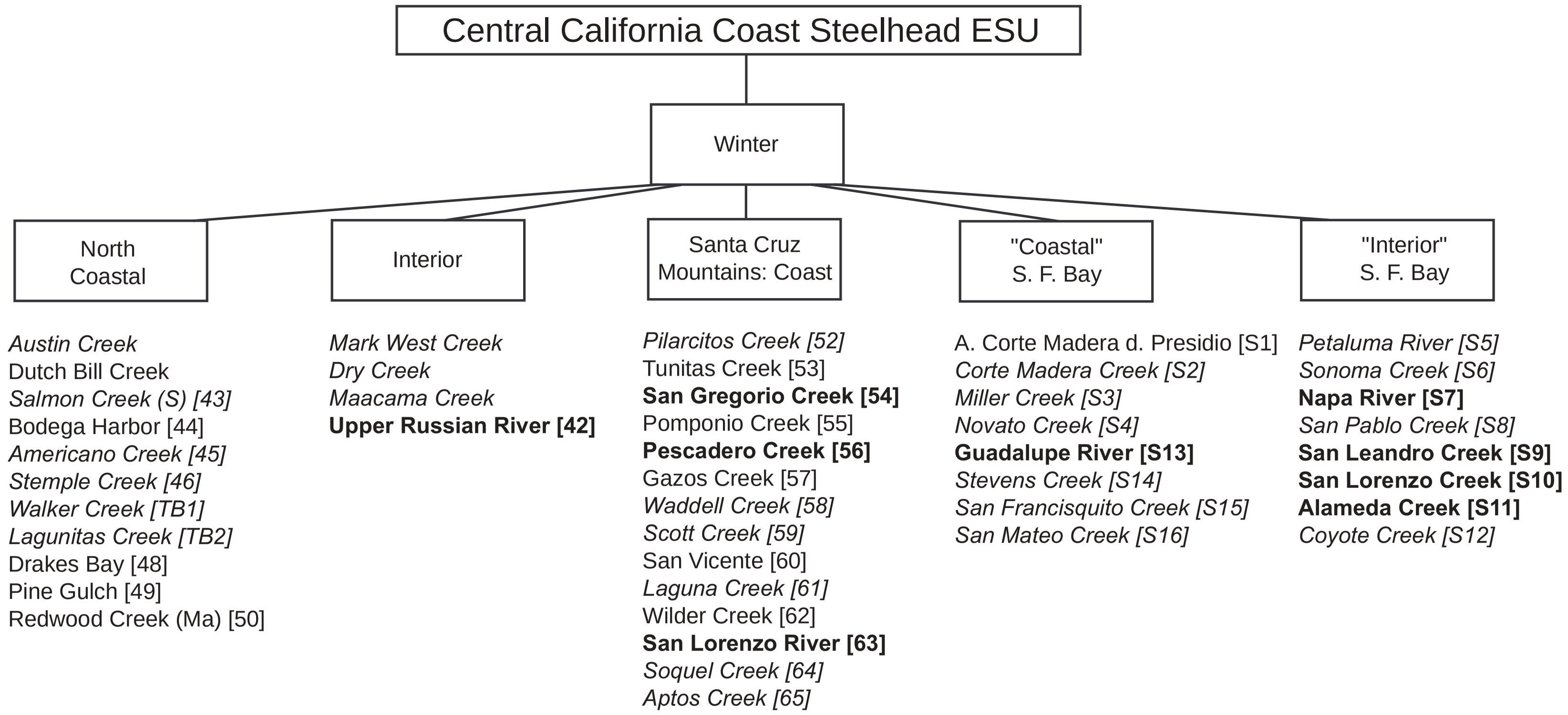

Figure A4. Historical structure of the NC-Steelhead ESU. Functionally independent populations are listed in bold font. Potentially independent populations are listed in italic font. Dependent populations are listed in regular font. Not all dependent populations have been included in this figure. See text in main report for detailed discussion.

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1 Introduction

1.1 Purpose and scope of this report

As the Technical Recovery Team (TRT) for the North-Central California Coast Recovery Domain (NCCCRD; Figure 1.1)[1] we have been assigned the task of developing biological viability criteria for four Evolutionarily Significant Units (ESUs) currently listed under the federal Endangered Species Act (ESA): California Coastal Chinook salmon ("CC-Chinook"; *Oncorhynchus tshawytscha*), Central California Coastal coho salmon ("CCC-Coho"; *O. kisutch*), North-Central California Coastal steelhead ("NC-Steelhead"; *O. mykiss*), and Central California Coastal steelhead ("CCC-Steelhead"; *O. mykiss*). A critical first step in this process is to define the relevant biological structure within each ESU and the temporal and spatial scales relevant to this structure (Meffe and Vrijenhoek, 1988; McElhany et al., 2000)[2]. The priority of this step reflects the importance of understanding population characteristics that contribute to populations' viability and thus their contribution to the persistence of the ESU.

In this document, we delineate historical population structure for each of the four ESUs. We focus on historical population structure, as it is the result of ecological and evolutionary dynamics that played out across the physical and ecological landscape before disruptions associated with the establishment and development of industrial European-American culture over the past two centuries. Thus, the historical population structure and dynamics of an ESU reflect the conditions for which we are most certain that the ESU was likely to persist over long time scales. That said, we do not propose that historical conditions are the benchmark for population or ESU viability. Rather, we consider historical population structure to be a baseline of sorts for evaluating the status of an ESU under current or projected conditions. Increasing divergence from this baseline almost certainly decreases the ability of the ESU to persist. The functional relationship between departure from historical conditions and extinction risk for the ESU is probably non-linear, such that the loss of a few populations–particularly small populations–from

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[1] The NCCCRD encompasses coastal watersheds from Redwood Creek (Humboldt County) in the north, to Aptos Creek (Santa Cruz County) in the south, including tributaries of San Francisco and San Pablo Bays. The NCCCRD overlaps with the Southern Oregon - Northern California Coast Recovery Domain (SONCCRD) in the area between Redwood Creek in Humboldt County and the Mattole River (inclusive). In the region of overlap, the TRT for the NCCCRD is responsible for developing viability criteria for Chinook salmon and steelhead and the TRT for the SONCRD is responsible for coho salmon.

[2] McElhany et al. (2000) outlines the general framework put forth by NMFS for evaluating ESU structure and developing biological viability criteria. This document is commonly referred to as the "VSP paper" (for "viable salmonid populations") in reference to its focus on independent populations and the qualities that generally correlate with viable populations. We refer to this document by formal citation.

an otherwise intact ESU may not greatly reduce ESU viability, whereas the loss of key populations or the loss of populations from an already diminished ESU will have more profound implications for the persistence of the ESU. Uncertainty associated with the form of this relationship must be accounted for in assessing the viability of any proposed ESU configurations that departs from historical conditions. Understanding the historical population structure of an ESU is essential to reducing the consequences of this uncertainty, as information on the historical role of specific populations in the ESU supports a biologically relevant context for recovery planning. Simply put, populations that were important to ESU persistence in the past, if restored or preserved, are likely to be important to ESU persistence in the future.

This report sets the stage for analysis of current status at the population level, development of population-specific viability criteria, and elaboration of guidance on how populations should be arranged to achieve a viable ESU (McElhany et al., 2000). The results of these analyses will be presented in a later report and, in combination with the historical population structure presented here, will represent the core of the scientific advice provided by the TRT to the team charged with developing delisting criteria[3] and the recovery plan for achieving these criteria.

In this report, we consider population structure under historical conditions, by which we mean population structure under pristine conditions that existed greater than 200 years ago and would exist presently had anthropogenic disturbances associated with European-American civilization not occurred. Since this temporal scale is essentially fixed, the uncertainty arising from this time frame can not effectively be reduced. Historical uncertainty does not influence our analysis in a consistent way across the NCCCRD. For example, our uncertainty regarding historical conditions and the distribution and status of anadromous salmon is greatest in the region surrounding the San Francisco Bay[4]. This area has been exposed to substantial anthropogenic disturbance since the 1800s and we have few records from which to reconstruct the distribution of salmon and steelhead in these watersheds (Leidy et al., 2003, 2005; Spence et al., 2005). We encounter similar level of uncertainty in the Russian River basin (Steiner Environmental Consulting, 1996). Moreover, since these areas coincide with the southernmost distribution of coastal Chinook salmon and the analogous inland boundary of the southern distribution of coho salmon, historical uncertainty is not readily countered through interpolation of information from populations to either side. Compounding this issue, the few early records that are available often provide ambiguous information as the taxonomy of salmonids was still unsettled at that time. Areas further from San Francisco have also been subject to disturbance, but these impacts typically took place later, were of a nature that allowed the pristine condition to be recognized or reconstructed from historical records or geographic information relatively easily, or occur in a more central part of the species range, which allows us to draw inference from information collected nearby.

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[3] Delisting criteria necessarily go beyond biological viability criteria to include criteria regarding the underlying causes of population and ESU decline and to address any societal requirements that can not be accounted for in solely biological terms. In contrast, viability criteria are focused on the biological characteristics of a population or an ESU that are consistent with low risk of extinction over long time horizons.

[4] Generally, “San Francisco Bay” refers to the San Francisco Bay-San Pablo Bay estuary, from the Golden Gate to the Carquinez Straits.

To some degree, the spatial scale of our task is also defined, albeit not explicitly, so there is some minimum contribution of uncertainty due to the coarse resolution of our study that cannot be eliminated. Here, however, we do have some control, and we can minimize the degree of uncertainty in our analyses by focusing at sufficiently large scales that satisfy the minimum resolution for the questions at hand. Some of the work performed in the course of our analyses, particularly that which draws on GIS technology, is performed at a high spatial resolution. However, we generally consider the results from these analyses after aggregation at the scale of river basins, and in the case of large systems, major sub-basins. Aggregation at this scale reduces the consequences of minor errors in the underlying information, and reduces the uncertainty in our conclusions. Of course, effectively developing and implementing recovery actions will require more detailed information; however, such detail will not be especially useful in reducing the uncertainty in our assessment of historical population structure within ESUs, a task that is necessarily large in scope and for which a coarse-grained approach is satisfactory.

Structure of this report

This report consists of four main chapters: this introductory chapter, and a chapter for each species[5] that we consider. Throughout the report, we review information on data sets or analyses used in the course of this exercise that do not appear elsewhere in the literature. For the most part, however, data sets and analyses brought to bear in this report are presented in greater detail as journal articles or technical memoranda that are or shortly will be available.

Much of the remainder of this introductory chapter serves two purposes. First, we develop a conceptual framework for identifying and classifying populations that make up an ESU. This framework rests on the concept of “independent populations” as put forth by McElhany et al. (2000) (see also Esler, 2000) and reflects the ongoing evolution of ideas and approaches to identifying relevant structure within an ESU. From a practical standpoint, this approach also satisfies a need to accommodate certain pragmatic issues that arise in evaluating the population structure of coastal ESUs. Second, we provide a general overview of how we apply this framework to each ESU, which includes a review of types of information relevant to our task, the general availability of each type of information for ESUs in the NCCCRD, the analytical frameworks in which we bring these data to bear on the question of historical population structure, and how we synthesize available data to draw our conclusions.

1.2 Accounting for uncertainty

Uncertainty pervades almost every aspect of our analysis, and limits our ability to develop compelling models from which we can draw strong, detailed inference regarding historical population structure of salmon and steelhead ESUs in the NCCCRD. Much of this uncertainty stems from the information available for analysis. Historical records are very limited, and in many cases, are of uncertain value due to the degree of anthropogenic influence that occurred before information on salmon populations was

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[5] The NC-Steelhead and CCC-Steelhead ESUs are considered jointly in one chapter to take advantage of integrated analyses of geographic and genetic information that span the full range of the NCCCRD.

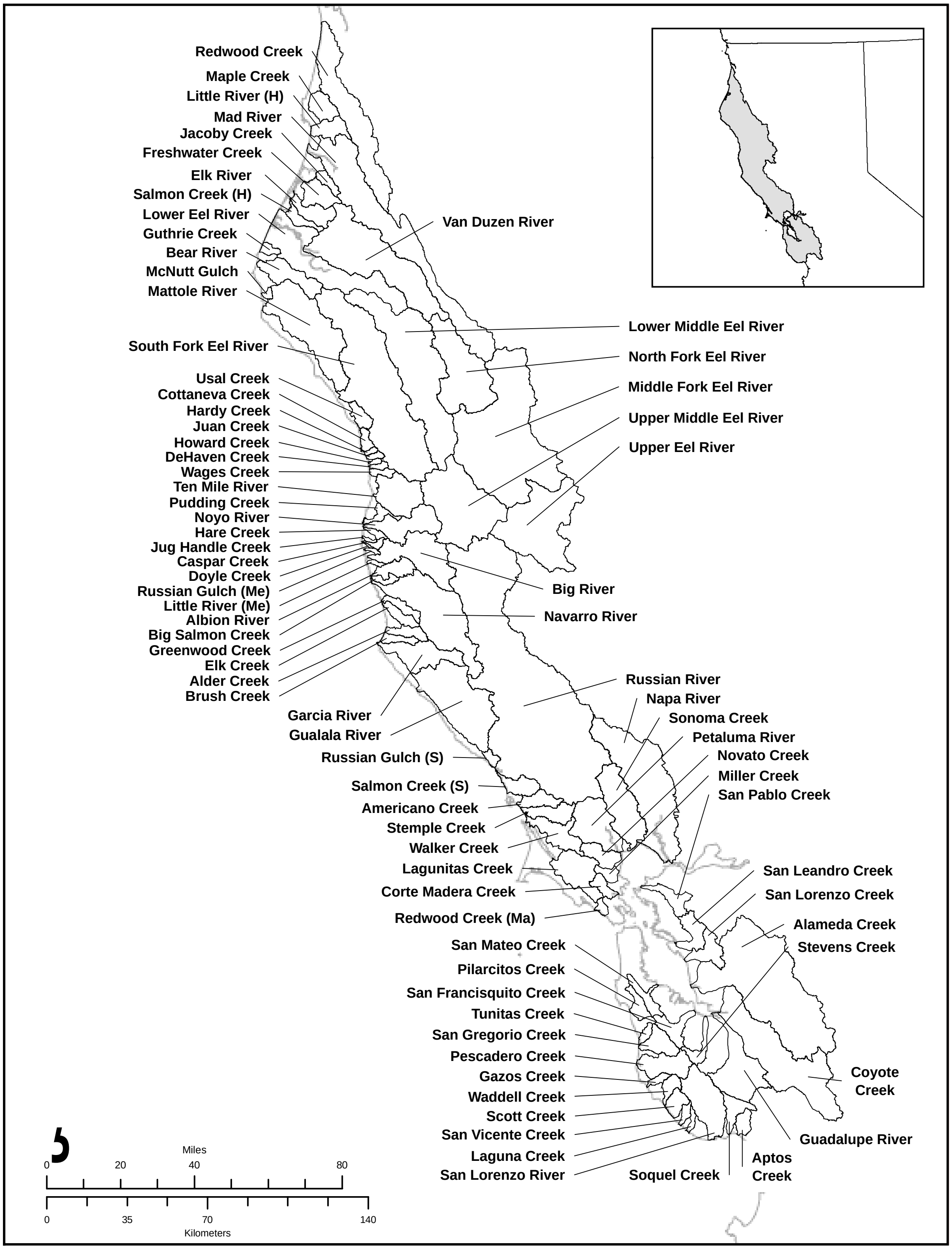

Figure 1.1. The North-Central California Coast Recovery Domain, with selected watersheds.

rigorously recorded[6] and the fact that the salmonid taxonomy was not well resolved until well into the 1900's. Moreover, recent data are sparse and provide a somewhat limited basis for inferring historical population structure, particularly in areas where substantial disturbance has occurred.

Uncertainty also arises in the course of analysis. As is the case in any analytical exercise, we make various assumptions regarding the processes that lead to the observed data or in how available data correspond to a quantity of interest. Some of these assumptions are formalized in a model, but many, such as "this model is (or these data are) an adequate and appropriate description (representation) of nature", have a more subtle nature and often go unstated. Violations of assumptions can have important consequences for what can be learned from the data or the analysis. In order for results of analyses to be interpreted appropriately, it is therefore essential to understand both where and how assumptions are likely to be violated and how the consequences of such violations are likely to manifest in the results. We therefore take time throughout this report to outline the assumptions that underpin our work in some detail, pay special attention to where violation of an assumption might underlie substantial bias that must be considered in interpreting the results of our work, and attempt to outline the consequences for our conclusions should our assumptions be wrong. In most cases, we describe the consequences of violating an assumption in terms of the expected direction and plausible magnitude of any difference between our simple models and reality. Just as importantly, since we recognize that some assumptions are unavoidable and not readily evaluated, we also seek to develop analyses that yield relevant results that are robust to violation of our assumptions, and to interpret these results in a similarly robust manner.

One particular sort of analysis brings with it a set of assumptions that, if violated, have potentially pernicious consequences for our conclusions. These analyses involve cases in which we seek to offset the lack of local information by drawing on data and analyses developed for populations and ESUs of salmon and steelhead elsewhere in California and the Pacific Northwest. For example, a substantial literature focuses on the study of factors that affect salmon and steelhead populations, and this line of research has recently extended to spatial scales concordant with the range of ESUs (Burnett et al., 2003; Steel et al., 2004). In doing so, differences in geography, history, and environment constrain the strength of inferences that can be drawn from such studies when applied to the NCCCRD, and potentially increase uncertainty or inject bias in our analysis. Moreover, the potential for uncertainty to arise from such extrapolation is further compounded by the fact that the NCCCRD spans the southernmost extreme of the coastal distribution for two of our three species: coho salmon and Chinook salmon. The response of a species to conditions at the edge of its distribution and the nature of the conditions themselves are expected to differ substantially from patterns observed in more central parts of the range, and this raises the possibility that serious biases can arise when information from elsewhere is brought to bear in coastal California. Unfortunately, this sort of uncertainty is beyond any quick fix. Nevertheless, given the very real potential for bias to be imported unwittingly with insights gained from somewhat more detailed studies elsewhere, we must bear these issues in mind to guide appropriate interpretation of any model results and evaluation of their relevance to the NCCCRD.

Despite the emphasis we place on explicit recognition of assumptions and consideration of potential

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[6] Historical photographs of the effects of land use practices as early as the late 1800s are available at, e.g., http://www.krisweb.com/.

uncertainty, we also note that, for the most part, violations of our assumptions and the consequences of uncertainty are not devastating to the conclusions presented in this report. Our conclusions regarding "where the lines are drawn" include uncertainty, and our assumptions guide the scale at which these lines are drawn. Therefore, violating these assumptions might lead to conclusions that differ from reality. However, subsequent consideration of spatial structure and diversity in evaluating viability at both population and ESU scales, strongly mitigate the consequences of such uncertainty or bias for achieving recovery of an ESU.

1.3 A conceptual approach for evaluating population structure of an ESU

Technical aspects of recovery planning focus primarily at two levels of biological structure: the ESU and the populations that comprise each 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. In particular, rates of exchange among distinct units at these two levels of biological structure are expected to differ—dispersal among populations within an ESU is expected to greatly exceed dispersal between ESUs—which has important implications for divergence at different biological scales (Moritz et al., 1995). ESUs (ideally) are defined in terms of deep evolutionary divergences, and represent major independent lineages with a species. Thus, ESUs are most usefully considered as genetic units, each of which exhibits a unique evolutionary history and adaptive potential, and within which variation and structure change on time scales of tens to hundreds of generations. Variation and structure within a species (i.e., among ESUs) typically occurs on even longer time scales. In contrast, populations are units within which individuals and subpopulations typically interact most strongly at time scales of days to a few generations. At these scales, populations often are more usefully considered in primarily demographic terms for which genetic information can support inference or provide useful context for interpretation[7]. The distinction between ESU and population is especially clear with respect to the time scale of the "forseeable future" (on the order of a few decades to a few centuries at best) that guides recovery planning. At these time scales, ESUs are essentially constant structures, loss of which is irrevocable, whereas the populations that make up an ESU are more dynamic entities.

With this in mind, we adopt a conceptual approach to identifying and classifying populations that explicitly recognizes the link between scale, with respect to both space and time, and biological structure. We developed this framework in concert with the Oregon-Northern California Coast (ONCC) TRT (Lawson et al., 2004) in an effort to promote a consistent basis for recovery planning throughout northern California and coastal Oregon. This approach differs from those developed elsewhere in the Pacific Northwest in ways that reflect important differences among Recovery Domains with respect to

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[7] This is not to say that genetic processes are irrelevant at the scale of populations. After all, populations, which represent "samples" of the genetic content of an ESU, are the units within (and among) which many of the processes that drive evolution take place. Our focus on demographic characteristics of populations—particularly with respect to independence—is based on the observation that genetic dynamics most strongly influence the short-term dynamics of populations under a somewhat limited set of conditions (e.g., inbreeding during a population bottleneck).

the geometry of the landscape. Over much of the NCCCRD, watersheds vary widely in size, and are distributed along a generally linear coastline. In contrast, Recovery Domains in the Pacific Northwest span radially structured landscapes, such as the Puget Sound or interior basins of the Columbia River. Such differences in the geometry have important implications for the potential dynamics of an ESU and its constituent populations (e.g., Fagan, 2002) that we accommodate explicitly in our analysis.

Conceptual definition of a "population"

At the core of this exercise 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.

In extending this concept, McElhany et al. (2000) sought a definition that would support the delineation of "independent" populations, which, by virtue of being independent units, offer a means to simplify the complex issue of assessing ESU structure and risk (see also Esler, 2000). McElhany et al. (2000, p. 3) define an "independent" population as "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."

In general, we follow the broad concepts outlined by McElhany et al. (2000). However, we find that a simple dichotomy between "independent" and "non-independent" populations does not adequately capture important variability among populations and the relative nature of population independence, and thus neglects variation among populations with respect to their role in each of the ESUs under consideration. We therefore extend the concepts in McElhany et al. (2000) to develop a population classification scheme that includes the properties of individual populations and interactions among populations without compromising the definition of a population as a discrete biological unit, yet is approachable in a meaningful way with limited data. We choose, therefore, to evaluate the role of demographic units—defined according to a set of simple rules—within the ESU, rather than to delineate biological units that satisfy some definition of population independence.

Rules for identifying populations: underlying principles and application

Physical isolation of populations, whether due to geographic separation or behavior, is necessary for population divergence. Such divergence can be relatively trivial and reversible (e.g., changes in allele frequency at selectively neutral loci), or profound and reinforcing (e.g., adaptation to local environments with its attendant alteration of the genetic and phenotypic character of populations). Behavioral and geographic isolation act synergistically in anadromous salmonids. These fish exhibit strong fidelity to their natal watershed as they return to freshwater in preparation for spawning (Quinn, 1993), and this homing behavior is expressed across a landscape that favors hierarchical subdivision and presents variable selective environments across a broad range of spatial scale. These processes gives rise to a continuum of biological structure with important breaks (e.g., populations and ESUs) arising at various

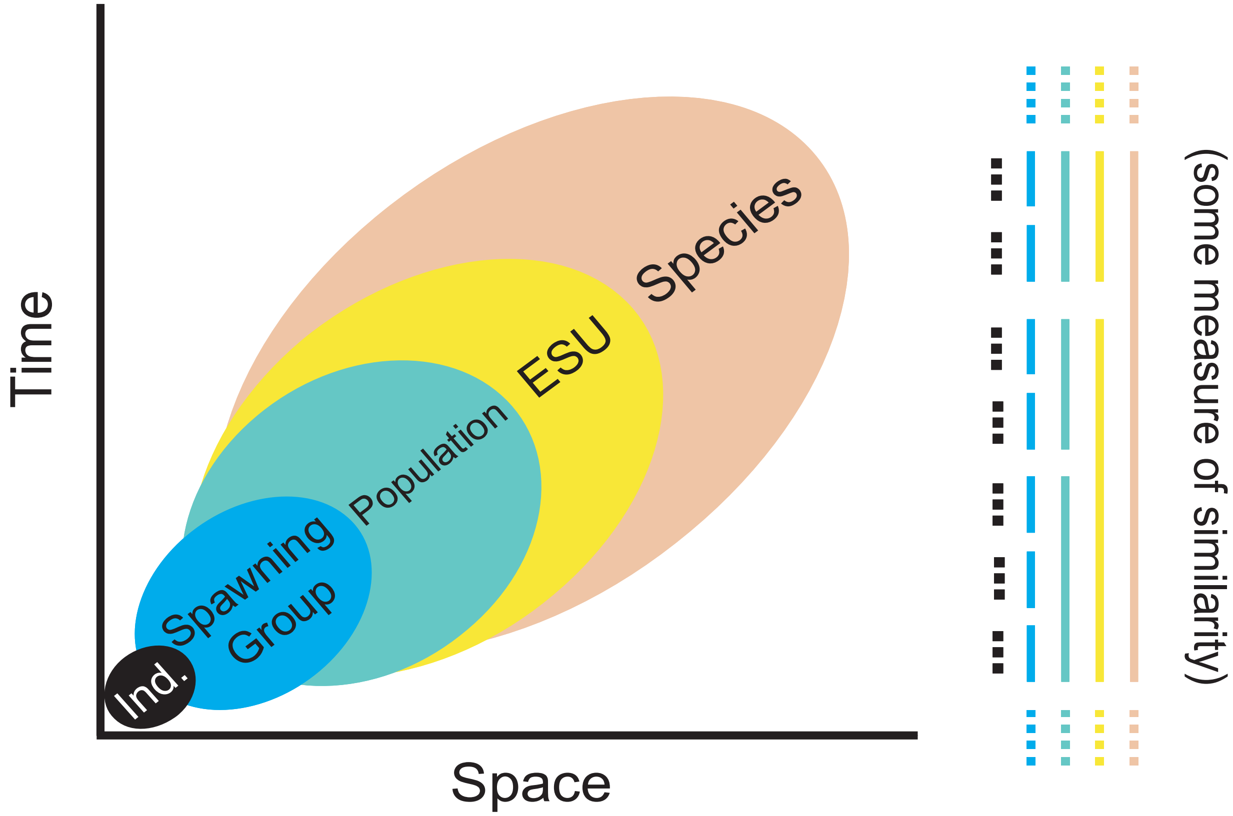

Figure 1.2. Conceptual schematic of hierarchical continuum of biological structure. Bars on the right of the diagram depict inferences of similarity at different resolutions.

locations in space on ecological and evolutionary time scales (Figure 1.2). Where these breaks lie depends on the life history of a species and the structure of the landscape on which this life history plays out.

Because comprehensive analysis of ESU structure along the full continuum of biological structure is not possible, we structure our analysis by first defining the demographic units to be evaluated. We adopt two rules to accomplish this. These rules reflect the fact that the anadromous life history places an extremely high premium on a successful transition from saltwater to a suitable freshwater habitat to close the life cycle. Homing behaviors are an obvious adaptation for enabling individuals to reach habitats with a high probability of being suitable for reproduction (as evidenced by their own birth and survival). Within a species, the nature of the imprinting process appears to accommodate more “error” as fish move to increasingly local scales; however, the scale at which homing behaviors break down and populations are well mixed is uncertain.

Our first rule defines each spawning group that occupies a direct tributary to the Pacific Ocean as a demographic unit separate from analogous groups in other direct ocean tributaries; these units are the subject of subsequent evaluation. This rule derives from two underlying concepts. The first is the overarching premise that population structure of anadromous salmon is determined by the structure of freshwater spawning and rearing habitats, strong fidelity to natal streams, and migration pathways that allow dispersal[8] among these habitats. The second is the postulate that saltwater-freshwater boundaries present a greater constraint on dispersal among populations than do analogous boundaries (e.g., confluences) within freshwater systems or estuaries, such that dispersal within a basin is greater than dispersal among basins[9]. The combination of these concepts yields a rule for defining demographic units that explicitly accommodates the simple fact that an individual can not belong to multiple populations.

In implementing this rule, we initially treat all spawning groups in watersheds that drain into a common estuary (e.g., Humboldt Bay, Tomales Bay, and San Francisco Bay) as a single, composite population subject to subsequent analysis. In each case, salmon and steelhead that spawn and rear in the tributaries of a particular estuary share a common access to the coastal ocean, and the estuary itself presents a weaker, less consistent barrier to dispersal than does the full-strength saltwater barrier of the open coast. Estuarine barriers to dispersal are likely to be especially weak during the winter months when spawning migrations of coho salmon and winter steelhead coincide with the period of seasonally intense rainfall and river discharge. For example, under historical conditions, an extensive layer of freshwater covered much of San Francisco Bay during the winter and spring, to the degree that obligatory freshwater species of fish with affiliations to the Sacramento-San Joaquin basin are widely distributed among the tributaries of the northern and southern arms of the Bay (Snyder, 1905). We therefore assume that the potential for migration among tributaries to an estuary is greater than among watersheds that drain directly to the Pacific.

Our second rule is that spawning groups within a large basin (including tributaries of a common estuary) may comprise multiple populations if sufficient physical, behavioral, or selective barriers to effective dispersal exist. As noted above, we assume that dispersal (straying) within a basin is more likely than straying among basins with different ocean-entry points. However, we are interested in "absolute" measures of population structure and must therefore consider conditions not covered by the first rule under which population structure might occur. Specifically, we must consider what might allow two spawning groups within a basin to satisfy some absolute measure of differentiation and to be thus considered separate populations. Two conditions can contribute to sufficient differentiation among spawning groups for population structure to arise within a basin: (1) extensive gaps in the spatial distribution of suitable spawning and rearing habitats, and (2) substantial environmental heterogeneity at the watershed scale can create conditions that limit effective dispersal within a basin and lead to population structure. Spatial separation between spawning groups, if the distance is sufficiently large relative to the accuracy and precision of the homing response, can effectively limit dispersal so that population structure arises. Environmental heterogeneity can present substantially different cues for the homing response and thus indirectly structure populations by reducing the likelihood of straying, and can present different selec-

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[8] Throughout this report, we use "migration" to refer to the movement of individuals among habitats through the course of the life cycle, and use "dispersal" (commonly referred to as "straying") to refer to the movement of individuals from one population to another population. *Dispersal* typically occurs when a fish *migrates* back to freshwater, but arrives in a watershed other than that in which it was born. Note that our use of "dispersal" in discussion of genetic data departs from the convention in the population genetic literature which traditionally uses "migration" to refer to movement *among* populations.

[9] Indirect measures of migration derived from population genetic data support this assumption; details are presented in each of the species-specific chapters.

tive regimes that favor divergence among populations such that immigrants have reduced reproductive success. Covariation in homing cues and selective regimes is likely to yield synergistic effects: the existence of the divergent selective pressures will tend to reinforce selection for more accurate homing, and more accurate homing will increase the potential for variable selective regimes to drive population differentiation. Likewise, environmental heterogeneity and spatial separation are likely to act together in cases where conditions favor population divergence.

For the NCCCRD, application of the first rule yields a large set of demographic units for consideration, especially for winter-run steelhead, which can effectively spawn and rear in very small coastal watersheds. We therefore adopted a rough set of criteria based on (1) predictions of habitat potential[10] and (2) historical records of species occurrence (e.g., Spence et al., 2005) to generate a tractable set of demographic units for further consideration. We used a synthesis of model results and historical evidence to reduce the potential for incorporating the consequences of a "shifting baseline" for the range of an ESU into our analysis of historical structure[11] We subsequently developed thresholds for including watersheds in analysis of the geographical structure of an ESU (see 1.5.1: Geographical Analysis, p. 24). A set of 129 watersheds (including aggregated estuaries) directly tributary to the Pacific Ocean was retained for further consideration (Table 1.1).

Table 1.1 is functionally comprehensive with regards to the array of watersheds occupied by anadromous salmon in the NCCCRD; the listed watersheds include over 99% of the stream kilometers in the NCCCRD, represent almost all of the areas that have the potential to provide suitable freshwater habitats, and include all streams for which we have historical records of presence of salmon or steelhead in the NCCCRD[12]. (Given the cosmopolitan distribution of winter steelhead, we chose to have the list of watersheds tend towards inclusiveness.) Table 1.1 anticipates application of the second rule, in that we identify major subbasins within the Eel River and tributaries to three estuaries (Humboldt Bay, Tomales Bay, and San Francisco Bay) for subsequent consideration. Per our second rule, we examine environmental variability in these areas and throughout the ESU below (§1.5.6: Environmental and ecological diversity), but defer consideration of the biological significance of environmental heterogeneity to the appropriate species-specific chapters of this report.

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[10] We used the modeling framework of Burnett et al. (2003) to predict the intrinsic potential (IP) of watersheds to exhibit suitable habitat for freshwater life history stages of each species. This analysis is discussed in further elsewhere in this report and in Agrawal et al. (2005).

[11] Comprehensive data on topics as basic as historical distribution of a species are often lacking for much of coastal California (e.g. Weitkamp et al., 1995; Busby et al., 1996; Myers et al., 1998; West Coast Salmon Biological Review Team, 2005, but see Spence et al., 2005). Although the lack of rigorous efforts to document the distribution of fish (or subsequent loss or obscurity of historical records) are likely to blame for much of this uncertainty, two other factors contribute to uncertainty in the historical record. First, in some cases, environmental impacts were substantial before any known records were produced. For example, salmon populations in the Russian River were in dramatic decline in the 1880s (Steiner Environmental Consulting, 1996). Second, during the early period when fish populations were being surveyed, the taxonomy of Pacific salmon was still very much unsettled. Thus, species identifications may be suspect in some cases.

[12] Some streams for which we have historical records of a species are extremely small, and it is highly likely that the observations represent a rare event rather than consistent occupancy. Such streams are not retained in our analyses of geographic structure, but are listed in Table 1.1.

Table 1.1. Historical presence of salmon and steelhead in selected watersheds in the NC-CCRD.

	ESU			
Watershed [ID]*	**CCC-Coho**	**CC-Chinook**	**NCCC-Steelhead**	**CCC-Steelhead**
Butler Creek [a]	-		W	-
Boat Creek [a]	-		W	-
Fern Canyon [a]	-		W	-
Squashan Creek [a]	-		W	-
Gold Bluff [a]	-		W	-
Redwood Creek (H) [1]	-	F, (Sg?)	W, Su	-
McDonald Creek [a]	-		W	-
Maple Creek [2]	-		W	-
Little River (H) [3]	-	F**	W	-
Strawberry Creek [a]	-		W	-
Widow White Creek [4]	-		W	-
Mad River [5]	-	F, (Sg?)	W, Su	-
Humboldt Bay [6]	-	F	W	-
Jacoby Creek [H1]	-	F	W	-
Freshwater Creek [H2]	-	F	W	-
Elk River (H) [H3]	-	F	W	-
Salmon Creek (H) [H4]	-	F	W	-
Eel River [7]	-		W, Su***	-
Lower Mainstem Eel River [E1]	-	F	W	-
Van Duzen River [E2]	-	F, (Sg?)	W, Su	-
South Fork Eel River [E3]	-	F	W, Su	-
Lower Middle Mainstem Eel River [E4]	-	F	W, Su	-
North Fork Eel River [E5]	-	F, Sg	W, Su	-
Upper Middle Mainstem Eel River [E6]	-	F	W, Su	-
Middle Fork Eel River [E7]	-	F, Sg	W, Su	-
Upper Mainstem Eel River [E8]	-	F	W, (Su?)	-
Fleener Creek [a]	-		W	-
Guthrie Creek [8]	-		W	-
Oil Creek [9]	-		W	-
Bear River [10]	-	F	W	-
Singley Creek [11]	-		W	-
Davis Creek [12]	-		W	-
Domingo Creek [a]	-		W	-
McNutt Gulch [13]	-		W	-
Peter Gulch [a]	-		W	-
Mattole River [14]	-	F, (Sg?)	W, Su	-
Fourmile Creek [15]			W	-
Cooskie Creek [16]			W	-
Randall Creek [b]			W	-
Spanish Creek [b]			W	-
Oat Creek [b]			W	-
Big Creek [b]	x†		W	-
Big Flat Creek [b]			W	-

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	ESU			
Watershed [ID]*	**CCC-Coho**	**CC-Chinook**	**NCCC-Steelhead**	**CCC-Steelhead**
Shipman Creek [b]			W	-
Gitchell Creek [b]			W	-
Horse Mountain Creek [b]			W	-
Telegraph Creek [b]			W	-
Humboldt Creek [b]			W	-
Whale Gulch [b]	x†		W	-
Jackass Creek [b]	x††		W	-
Little Jackass Creek [b]			W	-
Usal Creek [17]	x	F**	W	-
Cottaneva Creek [18]	x	F**	W	-
Hardy Creek [19]	x		W	-
Juan Creek [20]	x		W	-
Howard Creek [c]	x		W	-
DeHaven Creek [21]	x	F	W	-
Wages Creek [22]	x	F	W	-
Chadbourne Gulch [c]			W	-
Abalobadiah Creek [c]	x††		W	-
Seaside Creek [c]			W	-
Ten Mile River [23]	x	F	W	-
Inglenook Creek [c]			W	-
Mill Creek [c]			W	-
Virgin Creek [c]			W	-
Pudding Creek [24]	x	F**	W	-
Hare Creek [26]	x		W	-
Noyo River [25]	x	F	W	-
Digger Creek [c]			W	-
Mitchell Creek [c]	x†		W	-
Jug Handle Creek [c]	x		W	-
Caspar Creek [27]	x	F**	W	-
Doyle Creek [c]	x†		W	-
Russian Gulch (Me) [28]	x		W	-
Jack Peters Creek [29]			W	-
Big River [30]	x	F	W	-
Little River (Me) [31]	x		W	-
Buckhorn Creek [c]			W	-
Dark Gulch [c]			W	-
Albion River [32]	x	F	W	-
Big Salmon Creek [33]	x		W	-
Navarro River [34]	x	F	W	-
Greenwood Creek [35]	x		W	-
Elk Creek [36]	x	F**	W	-
Mallo Pass Creek [c]	x††		W	-
Alder Creek [37]	x	F**	W	-
Brush Creek [38]	x	F**	W	-
Garcia River [39]	x	F	W	-

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	ESU			
Watershed [ID]*	**CCC-Coho**	**CC-Chinook**	**NCCC-Steelhead**	**CCC-Steelhead**
Point Arena Creek [d]			W	-
Moat Creek [d]			W	-
Ross Creek [d]			W	-
Galloway Creek [d]			W	-
Schooner Gulch [40]	x		W	-
Slick Rock Creek [d]			W	-
Signal Port Creek [d]			W	-
Fish Rock Gulch [d]	x[†]		W	-
Saint Orres Creek [d]			W	-
Gualala River [41]	x	F	W	-
Miller Creek [d]			W	-
Stockhoff Creek [d]			W	-
Timber Cove Creek [d]			W	-
Kolmer Creek [d]			W	-
Fort Ross Creek [d]	x		W	-
Russian Gulch (S) [d]	x		-	W
Russian River [42]	x	F	-	W
Scotty Creek [d]	x		-	W
Salmon Creek (S) [43]	x	F**	-	W
Bodega Harbor [44]			-	W
Americano Creek [45]	x	F**	-	W
Stemple Creek [46]	x[††]	F**	-	W
Tomales Bay [47]	x	F**	-	W
Walker Creek [TB1]	x	F**	-	W
Lagunitas Creek [TB2]	x	F**	-	W
Drakes Bay [48]			-	W
Pine Gulch [49]	x		-	W
Redwood Creek (Ma) [50]	x		-	W
San Francisco Bay [51]	x	F**	-	W
Arroyo Corte Madera Del Presidio [S1]	x		-	W
Miller Creek [S2]			-	W
Corte Madera Creek [S3]	x		-	W
Novato Creek [S4]			-	W
Petaluma River [S5]		F**	-	W
Sonoma Creek [S6]			-	W
Napa River [S7]	x[††]	F**	-	W
San Pablo Creek [S8]	x		-	W
Strawberry Creek [e]	x		-	W
San Leandro Creek [S9]	x		-	W
San Lorenzo Creek [S10]	x[††]		-	W
Alameda Creek [S11]	x[†††]		-	W
Coyote Creek [S12]	x[†††]	F**	-	W
Guadalupe River [S13]		F**	-	W
Stevens Creek [S14]			-	W
San Francisquito Creek [S15]	x[††]		-	W

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	ESU			
Watershed [ID]*	**CCC-Coho**	**CC-Chinook**	**NCCC-Steelhead**	**CCC-Steelhead**
San Mateo Creek [S16]	x		-	W
San Pedro Creek [f]			-	W
Pilarcitos Creek [52]	x††	-	-	W
Canada Verde Creek [f]			-	W
Tunitas Creek [53]	x		-	W
San Gregorio Creek [54]	x		-	W
Pomponio Creek [55]			-	W
Pescadero Creek [56]	x		-	W
Butano Creek [f]	x		-	W
Gazos Creek [57]	x		-	W
Whitehouse Creek [f]	x††		-	W
Cascade Creek [f]	x††		-	W
Green Oaks Creek [f]			-	W
Ano Nuevo Creek [f]			-	W
Waddell Creek [58]	x		-	W
Scott Creek [59]	x		-	W
Molino Creek [f]			-	W
San Vicente Creek [60]	x		-	W
Liddell Creek [f]			-	W
Laguna Creek [61]	x††		-	W
Baldwin Creek [f]			-	W
Wilder Creek [62]	x††		-	W
San Lorenzo River [63]	x		-	W
Rodeo Creek Gulch [f]			-	W
Soquel Creek [64]	x		-	W
Aptos Creek [65]	x		-	W

For CCC-Coho ESU, “x” indicates historical presence. For CC-Chinook ESU, “F” indicates fall-run, “Sg” indicates spring-run, and “(Sg?)” indicates possible historical spring-run based on environmental conditions. For the steelhead ESUs, “W” indicates winter, “Su” indicates summer, and “(Su?)” indicates possible summer based on environmental conditions. Note that given the cosmopolitan distribution of winter steelhead, this table is likely to tend towards inclusiveness. “-” indicates watersheds in the range of a different ESU.* Watersheds with identical names are distinguished by county: “(H)”, Humboldt; “(Me)”, Mendocino; “(S)”, Sonoma, and “(Ma)”, Marin. Watersheds with approximately 8 IP km or more for winter steelhead are assigned a number, all other watersheds with greater than 1.6 IP km for winter steelhead are assigned a region-specific letter: [a] north of Cape Mendocino; [b] Lost Coast; [c] Mendocino Coast; [d] Point Arena to the Golden Gate; [e] San Francisco Bay; [f] South of San Francisco. Basins indicated in bold type include sub-basins indicated in italic type. ** Watershed is included among potential watersheds historically occupied by fall-run Chinook on the basis of exhibiting greater than 2.5 IP km for fall-run Chinook and, in the case of San Francisco Bay tributaries, being identified as potential Chinook-bearing streams. *** Summer steelhead may have been historically widespread in the Eel River basin (Jones, 1992). † Coho salmon have been observed in these watersheds, but they do not meet the minimum size for inclusion in subsequent analysis. †† No definitive historical record for coho salmon, but included in analysis based on exceeding minimum size threshold and environmental similarity to neighboring watershed with historical presence of coho salmon. ††† Historical evidence (not necessarily definitive) for coho salmon, but environmental conditions substantially different from those expected for watersheds known to harbor robust populations of coho salmon.

Classifying populations: a conceptual approach

Once populations are designated according to the rules stated above, we need to classify them in a biologically meaningful way that will allow us to consider the role of each population (or group of populations) in the dynamics and persistence of the ESU. In doing so, we are guided by work of McElhany et al. (2000), who developed the concept of an “independent population” and reviewed the characteristics expected of a population that is “viable”, i.e., having a low ($<$5%) probability of going extinct over a 100-year time frame. Unfortunately, these concepts, as developed in McElhany et al. (2000) do not readily accommodate the broad range of population sizes and potentially rich structure that emerges from application of our population definition across the NCCCRD and other coastal ESUs[13].

A “connectivity-viability” model for evaluating the population structure of an ESU

Our conceptual approach implements the original concepts developed by McElhany et al. (2000) by considering independently two characteristics of a population: viability, defined in terms of probability of extinction over a specified time frame, and independence, defined in terms of the influence of immigration on this extinction probability. Following McElhany et al. (2000), we define a viable population as a population having a low ($<$5%) probability of going extinct over a 100-year time frame, and define an independent population as one for which exchanges with other populations have negligible influence on its extinction risk, estimated over a similar time frame. Under this definition, whether a population is considered independent does not depend on the current state or predicted fate of a population (i.e., a population’s historical persistence or whether the population is more or less likely to be extant 100 years into the future), but rather depends only on whether the probability that a population will go extinct is affected by the presence or status of any other such group. In other words, the independence of a population is not a function of its probability of going extinct over 100-year time scales; it is a function of the *independence* of this probability on interactions with other populations.

We begin 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[14] to be used as a measure of the degree to which each population’s dynamics are determined internally [15]. Viability-in-isolation is a function of numerous

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[13] McElhany et al. (2000) recognize potential problems that might arise from attempts to identify independent populations and subsequently to evaluate the viability of these populations, and propose two approaches to evaluating a population identified as independent that subsequent analysis suggests is not viable (McElhany et al., 2000, p. 27): (1) the population in question was misidentified as independent and should correctly be considered as part of a larger unit, or (2) the population is indeed independent and not viable, and represents an “ephemeral” population. The first solution does not address the situation where a putative population is influenced by immigration from more than one other population, and thus, in the absence of relevant data, invokes a spatially-specific assumption regarding where the population boundary lies.

[14] “Self-recruitment” is a term borrowed from the literature on recruitment dynamics of reef fishes (e.g Swearer et al., 2002) that describes the proportion of recruits to a population that originate in that population. In the case of anadromous salmonids, “self-recruitment” is the proportion of a populations’ spawning run that is of native origin.

[15] Consideration of the relative degree to which population dynamics are determined by internal processes (e.g., birth and death) and external processes (e.g., immigration and emigration) is conceptually similar to the approach to describing population structure put forth by Thomas and Kunin (1999).

population characteristics that can be distilled down 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 use a time frame of 100 years as the time frame for evaluating viability, and consider 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[16]. For convenience, we often refer to such populations simply as "viable" populations in this report. 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 other population that is a potential source of immigrants and the rate at which individuals from each donor population disperse to the recipient population.

By using "viability-in-isolation" and "self-recruitment" to specify two axes, and setting appropriate thresholds to distinguish "viable" populations from "non-viable" ones on one hand, and "independent" from "dependent" on the other, we are able to define four types of populations (Figure 1.3):

- "Functionally Independent Populations" are those with a high likelihood of persisting over 100-year time scales and conform to the definition of independent "viable salmonid populations" offered by McElhany et al. (2000, p. 3).

- "Potentially Independent Populations" have 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.

- "Dependent Populations" have a substantial likelihood of going extinct within a 100-year time period in isolation, yet receive sufficient immigration to alter their dynamics and reduce extinction risk.

- "Ephemeral Populations" have a substantial likelihood of going extinct within 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 at high densities relatively rarely and to be occupied at all for relatively short periods of time.

Note that self-recruitment and viability-in-isolation are not independent parameters (Figure 1.3), but are linked through a common dependence on population size. Thus, large populations are more likely to be both viable-in-isolation and exhibit dynamics only weakly affected by immigration, but small populations are likely not to be viable-in-isolation and more strongly influenced by immigration. Moreover, in the case of populations exposed to different selective environments, asymmetric dispersal can be expected to exacerbate this pattern by reducing productivity in smaller population by countering the potential for local adaptation to occur (Kawecki and Holt, 2002; Lenormand, 2002). The distribution of

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[16] In their analysis of historical population structure in the Oregon Coast Coho ESU, Lawson et al. (2004) use the term "persistent" to mean what we refer to as "viable-in-isolation". We prefer the latter term as it is unambiguous with respect to the conditions under which viability or persistence is being evaluated. We use the term "persistent" to describe populations that are more or less continuously extant, regardless of whether such persistence is conditional on the presence of other populations

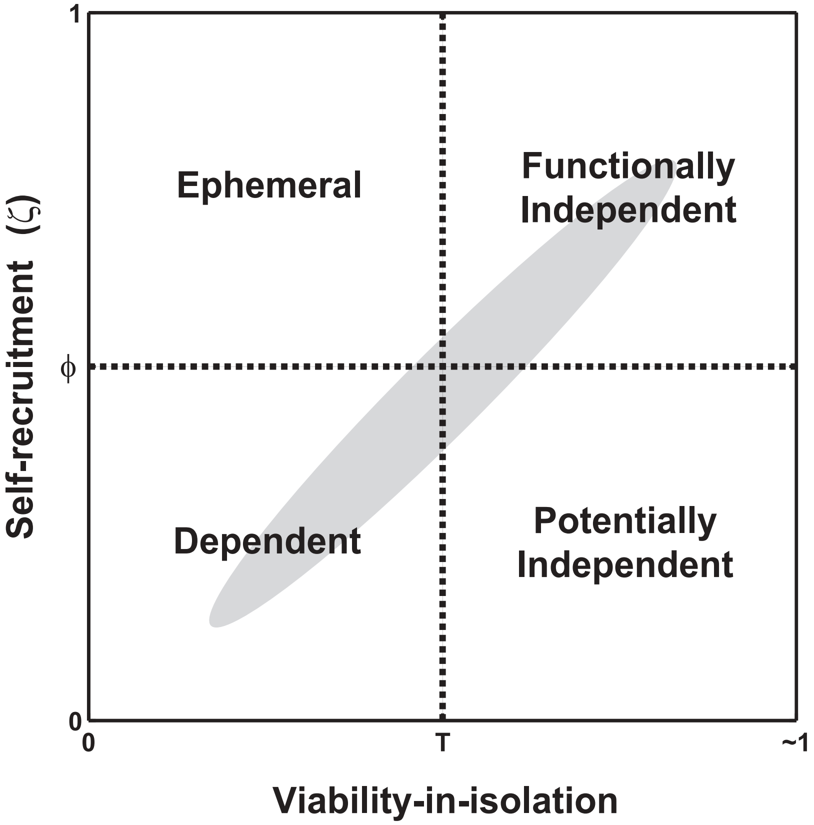

Figure 1.3. Conceptual arrangement of population types as a function of viability-in-isolation and self-recruitment. Since viability-in-isolation and self-recruitment are are not independent, populations typically are distributed along a diagonal between the dependent and functionally independent quadrants, indicated here by the shaded oval. Critical values for viability-in-isolation and self-recruitment are indicated by "T" and "ϕ", respectively. See text for definitions of each population type and further discussion.

populations in viability-independence space depends on the details of how the populations are arranged on the landscape and the nuances of dispersal.

It is important to note that some unavoidable circularity arises when applying our conceptual approach and subsequently moving on to more formal viability analyses. We seek to classify populations, in part, as a function of their viability-in-isolation. In practice, this will require us to revisit population classifications once the issue of population viability is evaluated for each population. As such, classifications presented here represent results based on assumptions or hypotheses regarding how populations of anadromous salmonids operate. We discuss this important point in greater detail below.

Absolute and practical thresholds for viability-in-isolation and independence

Viability-in-isolation. Strictly speaking, the concept of viability-in-isolation is based on comparing an absolute measure of a given population's extinction risk to a specified threshold (e.g., a 5% probability of going extinct over a 100-year time horizon). Ideally, estimates of absolute extinction probability from a robust population viability analysis for each population, preferably based on a model capable of estimating and excluding the influence of immigration on population viability, would be used to arrange populations along the viability-in-isolation axis. In practice, estimates of absolute extinction probabilities are notoriously sensitive to model parameters and structure. Selecting a quasi-extinction threshold reduces this sensitivity to some degree, but at a cost to the rigor of our the definition of viability-in-isolation. In any case, the data necessary to parameterize such a model are not available for populations of salmon and steelhead in the NCCCRD.

Recognizing these limitations, we instead focus 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 focus on measures of historical carrying capacity—a robust predictor of population size—as a metric of population viability[17].

Specifically, we assume that viability-in-isolation is linearly proportional to (a suitable proxy for) population carrying capacity, even though the actual relationship is likely to be non-linear, although similarly monotonic[18]. Note that even if robust estimates of historical carrying capacity were available, any model that we might use to develop the underlying relation between carrying capacity and

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[17] Strictly speaking, since we wish to apply this threshold across the ESU, we must assume that the extinction probability of an isolated population at the threshold carrying capacity is constant, regardless of where it lies in the geographical range of the ESU. In other words, although the curve that describes the marginal effect of carrying capacity on extinction probability can vary over space as a function of variation in other parameters that help determine extinction probability, we assume that this curve intersects the definition of a viable population (e.g., 5% probability of extinction over a 100 year time horizon) at the same carrying capacity regardless of where a population is located. Thus, in making this assumption, we implicitly assume that other parameters that affect extinction probability are constant or covary in such a way that this condition is satisfied.

[18] For example, theoretical studies of extinction risk show that for populations in which environmental stochasticity is the sole cause of variability in population size over time, the extinction rate $\Pr[E]$ is an inverse function of carrying capacity with a form like $\Pr[E] \propto K^{-2}$ (Lande, 1993).

extinction probability will yield predictions of absolute extinction probabilities that are sensitive to assumptions regarding model structure and other population characteristics, such as intrinsic productivity and the mean and variance of instantaneous population growth rates. We therefore chose to use a simple linear relationship between viability-in-isolation and population carrying capacity, which in addition to being simple, embodies a precautionary approach: the viability of large populations is less likely to be overestimated, and the importance of small populations is less likely to be underestimated.

Given the uncertainty inherent in estimating extinction risk, what this exercise boils down to on a practical level is *ranking* populations according to an estimate of their extinction risk, which in some ways limits the utility of a threshold demarcating those populations that are viable-in-isolation from those that are not. Nevertheless, we develop for each species a threshold for viability-in-isolation, in terms of our estimates (proxies) of historical carrying capacity, and use this threshold to guide our interpretation of population structure. In doing so, however, we augment our precautionary approach by setting thresholds for viability-in-isolation somewhat higher than might be thought absolutely necessary; we do so to focus attention on what are likely to have been the most robust populations in the ESU and to minimize risks associated with uncertainty regarding both where the true threshold lies and how well our estimate of historical carrying capacity reflects extinction risk. Regardless, we expect that extinctions (or close calls) are expected to affect populations below our thresholds with sufficient frequency to play a substantial role in their dynamics and evolution over relatively short time frames (i.e., on temporal scales of many decades to many centuries).

Self-recruitment. Extinction probabilities are highly sensitive to the rate of immigration to a population, particularly at levels of dispersal for which populations are not strongly coupled (e.g., Hill et al., 2002). Indeed, very small rates of immigration to a population can stave off extinction, a phenomenon sometimes referred to as the "rescue effect" (Brown and Kodric-Brown, 1977; Hanski, 1994b; Hill et al., 2002). Unfortunately, dispersal parameters are difficult to estimate and few estimates are available for naturally-spawning salmonid populations (summarized in McElhany et al., 2000, Table A1, p. 40). Uncertainty in rates of dispersal among populations (and thus rates of immigration to specific populations), coupled with the sensitivity of extinction probabilities to immigration makes the task of setting an absolute threshold for population independence effectively impossible. We therefore choose to sacrifice the rigor of the definition of population independence proposed by McElhany et al. (2000) for the flexibility and ready application of a relative measure of independence based on self-recruitment.

To develop this measure, we draw from the literature concerning two broad categories of metapopulation structure that seem particularly relevant to anadromous salmonids: "source-sink" and "mainland-island" (or "core-satellite") structures. In both of these structures, constituent populations differ with respect to their ability to persist in isolation. In a "source-sink" metapopulation, "source" populations occupy habitats that support sufficient production to maintain a positive steady state abundance in the absence of immigration, whereas "sink" populations do not (Pulliam, 1988; Cooper and Mangel, 1999). Source populations are also identifiable as producing more emigrants than they receive immigrants (per capita), while the reverse is true of sink populations. Dispersal among populations can complicate this picture: substantial dispersal into a productive habitat can mask the ability of a population to act as a source–such populations are called "pseudo-sinks" and can be difficult to differentiate from actual sinks (Watkinson and Sutherland, 1995). In a "mainland-island" metapopulation, the "mainland" is a generally large population that is effectively immune to extinction over reasonable time scales (barring large-scale, catastrophic disturbance) (Hanski, 1994a). "Island" populations are smaller populations that are more susceptible to extinction, whether due to demographic and genetic processes that have increased effect in small populations or increased vulnerability to environmental variation. Both of these metapopulation concepts address variability in productivity, whether explicitly (source-sink) or implicitly as a function of extinctions that zero out long-term productivity in island populations.

In each case, populations that exhibit dynamics dominated by internal processes are (typically) central to the persistence of the metapopulation. In general, these "core" populations receive fewer migrants than they produce, which results in a rate of self-recruitment that exceeds the fidelity rate[19] of the population. Indeed, this is the formal definition of a source population. We therefore use the fidelity rate as an operational threshold for differentiating populations with dynamics dominated by internal processes from those strongly influenced by external dynamics. Typical modeling frameworks used to calculate self-recruitment yield self-recruitment rates that scale with the fidelity rate. This insensitivity lends stability to conclusions based on relative self-recruitment values, but does not avoid the issue of determining what level of absolute external influence is sufficient to render a populations' extinction risk dependent on the dynamics of other populations. Thus, 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.

Interpreting population status and ESU structure within the connectivity-viability framework.

Given the intractability of developing absolute measures of viability-in-isolation and self-recruitment, the connectivity-viability framework is reduced to a model for ranking the status of populations within an ESU. Given that viability-in-isolation is a monotonically increasing function of population carrying capacity, and that self-recruitment is a monotonically increasing function of the ratio between a population's carrying capacity and that of each of its neighbors, the order in which populations fall out in viability-independence space is quite robust to assumptions regarding the form of these relationships. In other words, as long as the assumption of monotonicity holds, population A, on average, will always be more viable and have greater self-recruitment than population B (or *vice versa*).

The position of individual populations in viability-independence space, however, is not static over time. Rather, a population's status at any point in time is a function of its state (e.g., abundance, productivity, etc.) and that of its neighbors. Likewise, when a population is severely perturbed or goes extinct due to catastrophe or a sustained period of low productivity, other populations' positions in viability-independence space will shift until the population recovers or is recolonized (see also Thomas and Kunin, 1999). Thus, the position of a population in viability-independence space predicted by the

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[19] The fidelity rate is the per capita probability that an individual will attempt to return to its natal watershed, and is defined as one minus the dispersal rate. In our analysis, we assume that all individuals that survive to maturation arrive in some population, and do not suffer a reduced expectation for reproductive success, so that there is no subsequent cost of dispersal.

connectivity-viability model should be envisioned as a central point of sorts—a long-term mean—about which the population's true state fluctuates through time. For example, a dependent population can become an ephemeral population as a consequence of the source population(s) on which it is dependent being diminished or extirpated. Such emergent ephemeral populations are not destined to go extinct immediately following reductions in immigration, and may persist for long periods in isolation, particularly if the population is a not a true sink (i.e., the population exhibits a positive growth rate and would persist under deterministic conditions). Recovery of the source population will re-establish the dependency of these populations[20]. Likewise, a population that on average acts as a potentially independent population, can act as a functionally independent population if its larger neighbors are diminished or extirpated.

Within this framework, small dependent populations may appear "ephemeral" in cases where immigration from other populations is sufficient to alter the population's extinction dynamics, but the probability of extinction remains so high that immigration appears to serve more to increase the rate of recolonization than to support a persistent population. However, we expect true ephemeral populations (as defined above) to be rare, and to occur almost without exception at the edge of an ESUs range. Indeed, the requisite combination of small size and isolation implies that this must be so, as the geographical structure necessary for an ephemeral population is likely to favor divergence between groups of populations on either side of the area where ephemeral populations occur. For coho salmon and Chinook salmon, the NCCCRD spans or includes the southern end of the species (coastal) range, so ephemeral populations are perhaps more likely to be observed in this region.

Dependent populations and potentially independent populations are net sinks, yet still contribute dispersers to other populations. Thus, dependent populations (and, by extension, the watersheds that support them) serve at least three roles within an ESU. First, in the case of catastrophic disturbance, nearby dependent populations can support normally independent populations by providing a small, proximate source of colonists. Second, although they are not themselves dominant sources of dispersers within the ESU, dependent populations increase connectivity within an ESU by allowing dispersal among populations to occur in incremental steps[21]. Third, since they are more subject to genetic drift and inputs of genetic material from other populations, small populations can serve as "evolutionary experiments" more readily than can large populations, such that maintaining conditions that support the existence of small populations may contribute importantly to the diversity evolutionary potential of the ESU. Given our uncertainty with respect both to the degree of dispersal among populations and to where lies the actual threshold between populations that are viable-in-isolation and those that are not, these three criteria argue strongly that "dependence" should not be equated with "expendable", although it is clear that such populations will serve a different role in contributing to ESU viability than will larger populations.

Note that, to a degree, a set of small populations that are dependent on larger populations can them-

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[20] If the source does not recover, such populations are a signature of so-called "extinction debt" in a metapopulation that has not yet declined to the steady-state distribution supported by the remaining source populations (Hanski and Ovaskainen, 2002).

[21] Graph-theoretic approaches support identification of such populations more rigorous evaluation of their role within an ESU (Urban and Keitt, 2001; Lindley et al., 2004).

selves exhibit a degree of mutual dependence as a consequence of bilateral dispersal. The connectivity-viability framework, does not support evaluation of the potential for networks of small populations to persist in the absence of a source population that is viable-in-isolation [22], although the potential role of such a composite population can be evaluated if some measure of the composite population's viability-in-isolation can be developed.

1.4 Anticipated structure of population and ESU viability criteria

Before turning attention to the application of our conceptual definition of population independence, we think it useful to provide some brief background on our motivation for developing an approach that offers a broader set of possible population classifications. In beginning this exercise, we found it is useful to consider the goal of the technical recovery planning process and to anticipate the structure of the viability criteria we will offer to guide ongoing recovery planning. A general structure for viability criteria has emerged from continuing discussions among the Chairs of TRTs working throughout California and the Pacific Northwest and reflects a synthesis of experience and input from the TRTs themselves and recommendations from external review (e.g., the Recovery Science Review Panel). In this structure, population-specific criteria are expected to vary in nature according to the likely role of each population within each ESU. Viability criteria will be quantitative to a degree dependent on the role of each population in ESU viability, but the degree of rigor necessary is likely to differ among population classes. ESU-level viability criteria will integrate population-specific criteria within diversity-based strata (see below) that must be represented to ensure ESU viability. We tailored our approach to population structure to directly address these needs.

Thus, ESU viability criteria that form the basis for delisting criteria might be constructed something like:

- X% of functionally independent populations in the ESU are demonstrably viable, with at least N viable functionally independent populations in each diversity stratum (see below); viable functionally independent populations satisfy specific criteria based on the four parameters emphasized in McElhany et al. (2000): spawner abundance, productivity, spatial structure, and diversity.

- All remaining functionally independent populations maintain a level of abundance and productivity indicative of viability and thus consistent with continued persistence, but demonstration that such populations comprehensively satisfy viability criteria for each of the four parameters listed above is not necessarily required.

- Y% of potentially independent populations populations maintain a level of abundance and productivity consistent with continued persistence and with their role in the ESU.

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[22] Removal of all populations that exceed the viable-in-isolation threshold results in a similar diagonal distribution of populations in viability-independence space (Figure 1.3); however, the largest remaining populations will fall in the ephemeral quadrant. Evaluation of the persistence of a set of populations so structured requires additional information on factors that determine absolute rates of extinction and recolonization (Hanski, 1998; Gosselin, 1999)

- $Z\%$ of habitats capable of supporting dependent populations are occupied as an indicator of the status of other populations and connectivity within the ESU.

Of course, ESU viability criteria that are eventually developed by the TRT are likely to differ somewhat in structure, and, in any event, will almost certainly be somewhat more specific than the example presented here. The general structure outlined above, however, is consistent with the direction taken by other TRTs and offers a logical framework for focusing restoration and evaluation efforts on populations critically important to ESU viability.

Stratifying ESUs

ESU viability criteria necessarily incorporate variability in population type as well as diversity and spatial structure within the ESU McElhany et al. (2000). Therefore, to set the stage more completely for development of viability criteria at the population scale and integration of population information into viability criteria at the ESU scale, we go beyond delineating individual populations to 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 diversity, broadly defined, as the basis for delineating these groups. By “diversity” we mean (1) diversity of (potential) selective environments, (2) diversity of phenotypes, including life history types, and (3) diversity of genetic variation, both neutral and selected. We have available to us differing amounts of information 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. Results of this analysis will provide a basis for future work to identify or sets of populations (“ESU configurations”) that, by virtue of the location, composition, and viability status of the component populations, are expected to yield a viable ESU. We expect that recommendations emerging from analyses focused on diversity concerns will largely satisfy ESU viability criteria for spatial distribution of populations. However, to ensure that the results of this exercise allow the spatial structure of the ESU to be sufficiently represented in subsequent analyses, we also consider spatial information in delineating diversity strata.

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, we emphasize that it does not necessarily conform to a level of biological structure. Rather, diversity strata are described in terms of geography and a generally similar set of environmental and ecological conditions. We expect that phylogeny will correlate with the structure and arrangement of diversity strata; however, we generally do not incorporate phylogeny explicitly into the definition of diversity strata. Therefore, although it is impossible for an individual to belong to two populations, it is possible for a population that occupies an environmentally diverse watershed to contribute to multiple diversity strata at the ESU level. 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.

1.5 Analysis and synthesis for evaluating population structure of an ESU

Once the set of putative demographic units to be considered has been delineated, various types of information can be brought to bear to evaluate their role in the ESU under historical conditions. TRTs active elsewhere in California and the Pacific Northwest have expressed greatest confidence in inferences based on geographical information, followed in order of declining strength of inference, by information on migration rates, population genetics, life history and phenotypic variation, population dynamics, and, lastly, environmental and habitat characteristics (Currens et al., 2002; Myers et al., 2003; Lindley et al., 2004; Lawson et al., 2004). The remainder of this introductory chapter is devoted to (1) a general overview of the types of data we have available to us, the analytical approaches we use to bring these data to bear on the task at hand, and the nature and implications of assumptions we must make in the course of our analyses and with respect to the data themselves, and (2) discussion of how various types of information are synthesized to develop conclusions regarding historical population structure and how such syntheses are expected to differ among species as a consequence of differences in life history.

Analysis of population structure in the four ESUs reviewed here is strongly constrained by the sparse nature of the data available for consideration; however, our approach is intentionally consistent with the approaches taken by TRTs working in more data-rich areas of California and the Pacific Northwest (Currens et al., 2002; Myers et al., 2003; Lindley et al., 2004; Lawson et al., 2004). As will become apparent from the emphases placed on particular types of information in the rest of this section, we rely heavily on (1) information that is readily available and analyzed in a GIS to examine the distribution of potential freshwater spawning and rearing habitats and spatial environmental variability, and (2) molecular genetic information. Evaluations and analyses of ESU-specific data are presented and discussed in the appropriate chapters.

1.5.1 Geographic structure

Population structure of salmon and steelhead is a consequence of more-or-less accurate homing to natal streams, and reflects the nested, dendritic structure of freshwater habitats across the landscape. Spawning habitat, in particular, tends to occur in spatially discrete areas, and the distribution of both spawning and rearing habitats under natural conditions is largely determined by physical processes controlled by characteristics of watersheds (e.g., topography, hydrology, vegetation, etc.), that are effectively constant over millennial timescales (Frissell et al., 1986; Montgomery and Buffington, 1998). Geographical descriptions of the distribution, extent, and discreteness of these habitats therefore support strong inference regarding the population structure of anadromous salmonids.

Unfortunately, comprehensive information on the historical distribution of spawning and rearing areas is generally unavailable for large expanses of the NCCCRD. Our efforts to assemble and evaluate available historical records for each ESU yielded presence-absence data of varying sophistication and reliability (Spence et al., 2005; Agrawal et al., 2005). We therefore also implemented a suite of models in GIS to develop predictions of habitat potential as a function of more or less constant physical characteristics of the landscape (Agrawal et al., 2005); this work is discussed in some detail below, and in more specific detail in each of the species-specific chapters. Both sources of information were used to construct set of watersheds to be considered in our analyses (Table 1.1); however, the GIS exercise also provides information on the size and location of populations that can be synthesized with the connectivity-viability framework described above.

Intrinsic potential: model-based predictions of habitat potential for anadromous salmonids

A population's position along both axes of viability-independence space (Figure 1.3) is a function of population size, which, since the long-term average position is of interest, can be approximated by an estimate of a population's carrying capacity. Since we lack the biological data necessary to assess carrying capacity directly, we make use of habitat-based proxies for 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, see Agrawal et al., 2005, for technical details regarding our implementation of the model).

The concept of a stream's intrinsic potential to exhibit suitable habitat for a particular species or life stage emanates from a hierarchical perspective of fish-habitat relationships (*sensu* Frissell et al., 1986; Montgomery and Buffington, 1998). In this view, landform, lithology, and hydrology interact to govern movement and deposition of sediment, large wood, and other structural elements along a river network. These larger-scale characteristics and processes thereby control gross channel morphology at the scale of stream segments or reaches, as reflected in the frequency and characteristics of constituent habitat units (e.g., pools, runs, riffles, side-channels, etc.). The intrinsic potential concept assumes that this hierarchy of organization, structure, and dynamics of physical habitat is reflected in the biological organization of stream communities. In the case of salmonids, the biological response manifests itself as heterogeneity in the distribution, abundance, and productivity of different species and life stages within a basin's stream network. The underlying framework for the intrinsic potential models used in this analysis assumes that channel gradient, some index of valley width, and mean annual discharge, which are three primary indicators of landform and hydrology, serve as reasonable predictors of channel morphology and hence the potential for a particular reach to express habitat conditions favorable to a particular salmonid species at some stage of its life. These characteristics are effectively constant features of the landscape, and thus are provide basis for predicting both potential habitat under historical conditions, and the potential for physical processes to recreate suitable habitat if left to operate more or less naturally. Among-species or life-stage differences in habitat affinities are accommodated through species-specific curves relating suitability to the three physical metrics.

More specifically, under the modeling framework used for our analysis, a given IP model predicts the potential for each stream reach[23] in a basin to exhibit habitat characteristics suitable for a particular species during a specific life history stage as a function of the underlying geomorphological and hydrological characteristics of the landscape. In general, we use mean gradient, mean annual discharge, and valley constraint[24]. IP for each reach is calculated as the geometric mean of suitability scores, which

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[23] Within the IP modeling framework, stream reaches are sections of stream or river approximately 50-200 m in length and are generally defined with respect to geomorphological features.

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

range from 0-1 and describe the marginal likelihood 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 three habitat characteristics onto species- and life-history-stage-specific suitability curves based on the functional relationship between the value of a habitat characteristic and its marginal influence on the likelihood that suitable habitat will occur (Burnett et al., 2003; Agrawal et al., 2005)[25]. 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 likelihood that suitable habitat will occur.

We used this approach to generate predictions of IP for spawning and rearing habitat of coho salmon and winter steelhead using approaches developed by Burnett et al. (2003), and for spawning habitat of fall-run Chinook salmon using suitability curves based on the work of the Umpqua Land Exchange Project (see citations in Agrawal et al., 2005, b). Specifics for each species are reviewed in the appropriate chapter. We do not use the intrinsic potential model to predict IP for summer steelhead or spring-run Chinook salmon. Although the intrinsic potential model might be expected to offer reasonable predictions for the spawning habitats for these species and rearing habitat for juvenile summer steelhead, the intrinsic potential model is not designed to predict the potential of stream reaches to exhibit critical over-summer habitat requirements for adults of these two species (e.g., summer holding pools).

IP-based metrics of population carrying capacity.

To make use of IP as a proxy for population carrying capacity, we calculate a weighted sum of the linear length of stream within each watershed that is accessible to anadromy, using IP scores to weight the contribution of each stream reach, and express the results in units of IP-km to give a measure of habitat potential at the watershed scale. In doing so, we interpret IP probabilistically, so that IP-km describes a watershed in terms of its (expected) equivalent length of continuous high quality habitat[26]. Our use of an aggregated measure of historical habitat follows from the suggestion that the amount of high quality freshwater habitat in a watershed strongly affects the ability of a population to endure periods of poor ocean survival (e.g. Nickelson and Lawson, 1998, for coho salmon). To accommodate uncertainty associated with both the quality of available habitat and the baseline level of bias in the predictions of the IP model, we adopt a precautionary approach to setting thresholds for viability-in-isolation.

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channel.

[25] 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 by Lawson et al. (2004) 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).

[26] Alternatively, we might have considered using a measure based on “high” IP. However, given the way that IP is calculated, defining a meaningful definition for high IP is somewhat problematic, and the results from applying such a threshold are likely to be especially susceptible to bias associated with latitudinal variation in hydrology. We therefore limit our use of non-integrated IP measures to informal examination of where areas of relatively high potential are located in a basin and whether such areas appear to contribute significantly to the total integrated measure of IP-km for a watershed.

Assumptions related to use of IP as a measure of population size. Translating IP into a measure of population size appropriate for use in the connectivity-viability analysis described above entails assumptions beyond those required in the application of the IP model to coastal California (i.e., the assumption that the IP model itself is an adequate description of habitat potential in the NCCCRD). In particular, we must assume that population carrying capacity scales monotonically with an integrated measure of habitat quality and extent.

In practice, we make the assumption that, for each species, the carrying capacity of a watershed is linearly proportional to the integrated, IP-weighted extent of stream accessible to anadromy. For populations with dynamics described by the familiar Ricker and Beverton-Holt stock-recruitment models, carrying capacity is a function of habitat capacity, of which we might consider IP-km to be an estimate, and the intrinsic productivity of the population (i.e., the Ricker α), which governs how well the population is able to exploit available habitat capacity (Mousalli and Hilborn, 1986). Therefore, to use a measure of habitat capacity to predict carrying capacity directly, we either must have information on productivity for each population, whether from empirical estimates or model predictions, or assume that a single productivity value applies to all populations. We make the latter assumption, from which follows the assumption of a linear relation between habitat capacity and carrying capacity[27].

We are fairly comfortable in assuming that habitat capacity exhibits a linear relation to IP-km for coho salmon and steelhead, for which freshwater rearing habitat has been shown to be a strongly limiting factor. Bradford et al. (2000) provide empirical evidence that "hockey-stick" (*sensu* Barrowman and Myers, 2000) models adequately describe spawner-recruit relations for coho salmon in British Columbia. In such models, carrying capacity of populations is independent of intrinsic productivity and depends entirely on habitat capacity. Moreover, Lawson et al. (2004) provide direct support for a linear relation between IP-km and population size, based on a comparison between IP-based predictions of watershed capacity and estimates of maximum historical abundance for Oregon Coast coho salmon. Comparable analyses are not available for steelhead, but their extended period of juvenile residence in freshwater supports the use of a similar set of assumptions as those developed for coho salmon. Note, however, that despite the strong case for a linear relation between IP-km and carrying capacity for coho salmon and steelhead, we must still assume a common intrinsic productivity and similar assumptions regarding other population parameters, as these parameters are directly linked to our assumption that carrying capacity is a predictor of viability-in-isolation.

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[27] For the Ricker model, formulated as $N_{t+1} = \alpha N_t^{-\beta N_t}$, carrying capacity $\hat{N}$ can be expressed as $\hat{N} = \ln \alpha \beta^{-1}$. Assuming that the capacity parameter β is an inversely proportional to the amount of available habitat, i.e., $\beta \propto (\mathrm{IP} - \mathrm{km})^{-1}$, and that the productivity parameter α does not vary among populations, carrying capacity is proportional to IP-km: $\hat{N} = \alpha(\mathrm{IP} - \mathrm{km})$. An analogous result obtains for the Beverton-Holt model as well. This interpretation and the requisite assumption regarding population productivity are consistent with the definition of IP as the potential for high quality habitat to occur in a stream reach, rather than a measure of the quality of habitat in a given reach. A monotonic relationship between IP-km and carrying capacity is preserved even if population *productivity* exhibits an increasing relationship with IP-km. The relationship between K and IP-km may be disrupted if α is related to some measure of IP at the watershed scale, say, the average IP score within a watershed. If this were the case, a large watershed with low average IP and small watershed with high average IP could have the same IP-km, yet exhibit different carrying capacities as a consequence of differences in α depending on the statistical distribution of reach-specific IP values.

For Chinook salmon, many analyses of spawner-recruit data use a Ricker model to describe the underlying dynamics (e.g., Prager and Mohr, 2001), which therefore explicitly requires that population productivity be constant across populations for a linear relationship between habitat capacity and steady-state abundance to hold. In the case of Chinook salmon, however, the use of IP-km (a linear measure) as a predictor of habitat capacity is somewhat problematic, and an areal measure might be more suitable. However, translating an areal measure of IP for Chinook salmon into a habitat capacity measure is also not entirely straightforward. The relationship between area of spawning habitat and total stream bed area is not well characterized, and is likely to be itself nonlinear in a way that partially counters the general increase in streambed area with watershed size (i.e., as streambed area reach increases on a reach-by-reach basis, a decreasing proportion of the streambed remains suitable for spawning, Hanrahan et al., 2004). This is further confounded by the tendency for spawning Chinook salmon to exhibit a highly patchy distribution within a watershed. We therefore chose to retain use of IP-km as a linear measure of habitat capacity, with the expectation that what nonlinearity exists in the relationship between IP-km and habitat capacity will only exacerbate differences between large and small populations. We also explicitly accommodate potential nonlinearity in the assumptions we make in the course of developing our viability-in-isolation threshold for Chinook salmon.

Implementing the connectivity-viability model

Viability-in-isolation. Issues relevant to setting thresholds for dividing populations that are viable-in-isolation from those that are not have been discussed previously. The rationale for each species-specific threshold is presented for each species in the appropriate chapter.

Self-recruitment and connectivity. To synthesize geographical information into predictions of self-recruitment and population connectivity, we use a simple dispersal model to synthesize information on population location and a proxy for population size and produce estimates of self-recruitment and population connectivity. More specifically, we assume that each population exhibits some steady-state or expected abundance (prior to dispersal), $\hat{N}_i$, that reflects internal population dynamics as determined by the intrinsic productivity of the population and the capacity of its habitat.

The per capita rate of dispersal from population i to population j is given by d_{ij}, and the rate at which individuals successfully home to their natal population (i.e., the fidelity rate) is d_{ii}. The number of "native spawners" is then given by $d_{ii}\hat{N}_i$, and the number of immigrants to a population is $\sum_{j\neq i} d_{ij}\hat{N}_j$. Self-recruitment ($\zeta$) is defined as the proportion of individuals in a population returning to reproduce that originate in that population:

$$\hat{\zeta}_i = \frac{d_{ii}\hat{N}_i}{d_{ii}\hat{N}_i + \sum_{j\neq i} d_{ij}\hat{N}_j}. \tag{1.1}$$

The complement of self-recruitment is, of course, immigration. Notice that self-recruitment to and the composition of a population is a function of (1) the population's abundance and fidelity, (2) the rate of immigration from other populations, and (3) the size of the donor populations. Within this framework, we are also able to partition immigration to a population among donor populations so as to describe population-specific connectivity (ω_{ij}) as

$$\omega_{ij} = \frac{d_{ij}\hat{N}_j}{d_{ii}\hat{N}_i + \sum_j d_{ij}\hat{N}_j}, \tag{1.2}$$

which provides a measure of which how strongly each donor population influences the receiving population. Note that links between populations are generally asymmetrical: a large population is only weakly connected to a small population, whereas a small population is strongly connected to a larger donor. Connectivity is most useful as a metric for identifying key populations in analyses focused on ESU viability. In anticipation of this work, we present information on connectivity in the form of graphs (*sensu* Urban and Keitt, 2001), in which sink populations are linked to their sources according to the contribution of immigration to the sink. These results complement the distribution of populations in viability-independence space and support more direct comparison between geographical and genetic structure within an ESU.

Calculating self-recruitment and connectivity requires values for the $\hat{N}$s and ds. Recall that we assume that steady-state population size (carrying capacity) is directly proportional to IP-km. Since self-recruitment (ζ) and connectivity (ω) are proportions, we can therefore substitute watershed-specific IP-km as a measure of $\hat{N}$.

To calculate the d_{ij}s, we assume that fidelity to natal populations (d_{ii}) is constant and fixed across populations[28], and use one of the simplest theoretical dispersal functions[29], an exponential decline with distance (with parameter δ) in the per capita rate at which two populations exchange individuals (Cooper and Mangel, 1999), as the basis for calculating migration among populations. We assume that dispersers are equally divided into those that disperse north and those that disperse south, and that ESU boundaries are “open”, i.e., individuals are not forced to turn back at the ESU boundary (Figure 1.4)[30]. Our assumption of a exponential-decline-with-distance model for dispersal is supported by both theoretical and empirical study (Candy and Beacham, 2000; Hard and Heard, 1999; Labelle, 1992, T. Nickelson, Oregon Department of Fish and Game, *unpublished results*), although more complicated, spatially ex-

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[28] Our decision to use a fixed, per-capita fidelity rate rather than a purely distance-based approach has an empirical basis in the known homing abilities of anadromous salmon and has the theoretically appealing consequence of maintaining a consistent, readily interpreted metric for the source-sink status of a population.

[29] Such functions are typically referred to as “dispersal kernels” in the ecological literature on marine reserves (e.g., Botsford et al., 2001).

[30] The proportion of dispersers arriving at basin j from basin i is found by integrating the exponential “dispersal function” centered on basin i over an interval of coastline surrounding basin j. This interval is defined by the midpoints between basins j and $j-1$ and basins j and $j+1$. Note that “homing” is not calculated in this manner, but is set by the fidelity parameter. Thus, the integral of the dispersal function over the interval surrounding the focal population does not enter these calculations. Dispersal across the boundary of the ESU is calculated as the integral of the dispersal function over the interval defined by the distal edge of the attractive interval of the border basin (which is defined in part by the location of the nearest basin outside of the ESU) to infinity. Integrated values are corrected to sum to 1, subject to the constraint that total dispersal to the north and south are equal, and multiplied by $1-\phi$. Thus, all dispersal is accounted for, including losses across ESU boundaries. Dispersal, thus calculated, between basin i and basin j is d_{ij}.

plicit models are also suggested by empirical data (Pascual and Quinn, 1995)[31]

The arrangement of populations along the self-recruitment axis is somewhat sensitive to the shape of the dispersal function[32]. We therefore calculated self-recruitment for dispersal functions ranging from narrow (50% of dispersers expected to arrive within 10 km of their natal stream given continual habitat) to broad (50% of dispersers expected to arrive within 100 km of their natal stream); these results are presented in full for each ESU and integrated into the interpretation of the self-recruitment data.

The results of the analysis are also sensitive to the threshold for watersheds to be included as a putative population. Lowering the threshold for inclusion of a watershed increases the number of potential sites over which dispersing individuals are distributed, and thus attenuates the effect of dispersal from a donor population along the coast; however, criteria for inclusion that are too strict may obscure important gaps within the ESU by predicting artificially high rates of exchange among neighboring populations. Lacking a strong basis for choosing a specific threshold for including a putative population in the connectivity-viability analysis, we selected a threshold of 10% of the IP-km necessary to support a viable population.

Assumptions related to predicting IP in watersheds of coastal California. Our implementation of the IP model for juvenile coho salmon and winter steelhead 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 NCCCRD as they do in coastal Oregon streams. The IP model was constructed originally to predict the distribution of areas with varying degrees of potential to exhibit suitable habitat for juvenile coho salmon and steelhead in watersheds of the Coast Range of Oregon. 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 northern coastal California, or (somewhat less strongly) that the relationship between watershed characteristics and habitat potential throughout the NCCCRD 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 NCCCRD (Agrawal et al., 2005).

Second, and perhaps more importantly, we assume that the interaction of geomorphic structure and precipitation in northern California is similar to that observed in watersheds of coastal Oregon for which the IP model was originally developed, and as a consequence, that geomorphic and hydrologic

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[31] Other factors that plausibly affect the rate of exchange among populations, such as differences in the timing of spawning runs or accessibility of freshwater habitats, or differences in the “attractiveness” of watersheds as a function of discharge, underlying geology, or other environmental characteristics were not incorporated into the model. Such factors can readily be incorporated into the model by linking them to dispersal through an appropriate model. Lacking relevant data with which to ground such an exercise, we chose to retain a simple approach.

[32] The shape of the dispersal function determines the distribution over space of dispersers from a population. Changes in how individuals are distributed can have strong effects. If dispersal occurs over short distances a population receives immigrants concentrated from its close neighbors, whereas if dispersal occurs over broad distances, many populations contribute, albeit at a lesser intensity. Changes in dispersal distance influence the range of populations that contribute, which, since populations vary substantially in size, can have important effects for the total amount of immigration to a population.

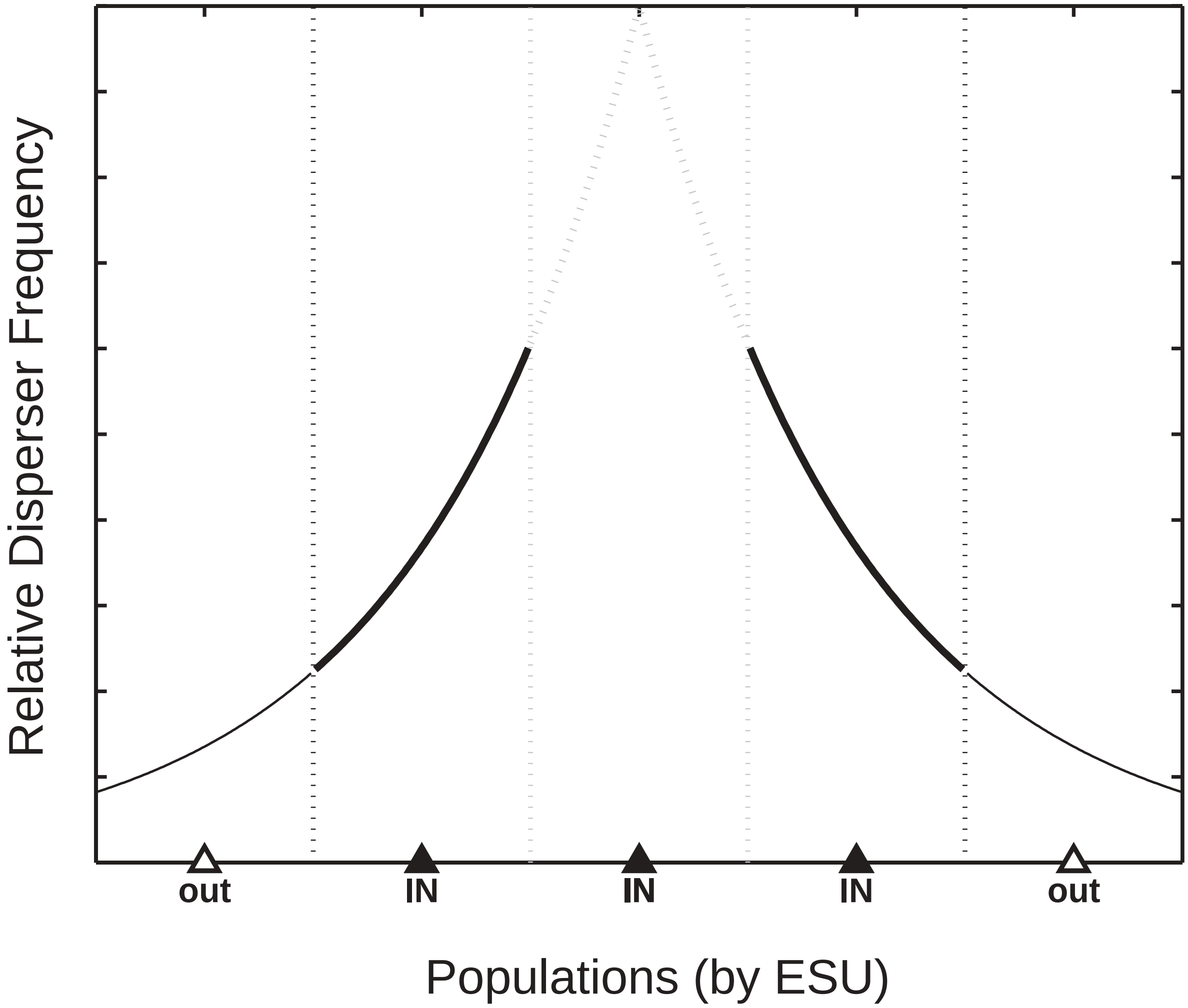

Figure 1.4. Schematic of dispersal model. Curved line indicates exponential decline of dispersal from central population. Area under heavy portions of curved line indicate weight for dispersal to populations in the same ESU as the source population. Area under the light portions of the curved line (out to infinite distance) indicate weight for dispersal out of the ESU. Since fidelity to natal population is set to the same value for each population, the central peak of the exponential function is not used.

processes that create salmonid habitat operate are also similar. 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 or inland of the coastal mountains. 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, but the relationships for watersheds south of Cape Mendocino and the San Francisco Bay region differed substantially from that for coastal Oregon.

Potential bias in predictions of IP in coastal California. The coarse relationships between precipitation and discharge developed for the NCCCRD are not likely to have captured fully the nature of hydrological differences between the two regions, as the models do not incorporate information on the timing of precipitation and the effects of temperature, both of which contribute to more dramatic drops in stream flow over the course of the summer than are observed in watersheds in Oregon. These differences are likely to have important consequences for the interpretation of IP predictions for California watersheds, and in particular are likely to give rise to bias that must be accounted for in how we use IP in the course of our analysis. In the case of juvenile coho salmon and steelhead, it is likely that results from the IP model will exceed the true amount of summer juvenile habitat over much of the NCCCRD and that such bias will increase towards the southern and interior portions of the NCCCRD[33] Moreover, juvenile coho salmon and steelhead in warmer, drier watersheds in the NCCCRD are more susceptible to drought conditions than populations in wetter (on average) watersheds.

Unfortunately, in neither case do we have sufficient empirical data to support estimation of how these differences manifest in terms of IP for a given species and life history stage. We therefore use a qualitative index of bias ranging from “low” to “severe” to guide our interpretation of IP-based results from subsequent analysis. For juvenile coho salmon and steelhead, we based this index on a comparison of the ratio of watershed averages of mean annual precipitation to mean annual temperature. For watersheds in southern coastal Oregon (e.g., Pistol River, Chetco River, and Elk River), this ratio is approximately 24 mm/°C. In the NCCCRD, this ratio ranges from below 4 mm/°C in the southeastern San Francisco Bay to over 16 mm/°C in northern, coastal watersheds. For fall-run Chinook salmon, we used mean precipitation during the month of October[34] as the relative basis for our bias index. In this case, we used apparent geographical breaks in precipitation patterns to define bias categories.

Our implementation of the IP model for spawning habitat of fall-run Chinook salmon rests on assumptions similar to those discussed in the preceding paragraphs for juvenile coho salmon and steelhead. In the case of fall-run Chinook salmon, we are less concerned by potential positive bias in the extent

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[33] To some degree, fog-drip in coastal forests can counter the effects of differences in precipitation patterns; we therefore use the (historical) presence of redwood or other conifer forests as ancillary information in determining potential bias in the IP model.

[34] Geographical patterns in (relative) mean precipitation are quite similar for September through December. We elected to use October precipitation patterns under the assumption that, even when aggregated in a climatology, these patterns will reflect both differences in the magnitude of precipitation and the effects of variation in the onset of winter storm season.

of available habitat, as (ocean-type) fall-run Chinook salmon reside in freshwater typically coincides with periods of high flow. Interaction between watershed size and the timing of winter storms is likely to affect how consistently fall-run Chinook salmon can enter freshwater during the appropriate time of year. However, fall-run Chinook salmon exhibit considerable flexibility with respect to the final phases of maturation and can endure considerable delays in gaining access to freshwater spawning habitats (Nicholas and Hankin, 1988).

Assumptions and the interpretation of the connectivity-viability model

The chain of analyses that culminate in the output of the connectivity-viability model entail a series of assumptions that address (1) the suitability of the hydrological model that underlies predictions of IP for watersheds in coastal California, (2) the relevance of the IP model as a predictor of habitat potential in watersheds of the NCCCRD, (3) the utility of an IP-based measure of habitat capacity–specifically, the IP-weighted sum of linear stream length–as a proxy for population carrying capacity, (4) the link between carrying capacity and population extinction risk, and (5) how individuals disperse among populations. By recognizing that the connectivity-viability model is simply a framework for ranking populations according to measures for viability-in-isolation and independence (self-recruitment), potential concern regarding many of the assumptions is greatly reduced. Few will disagree that a larger population is generally less likely to go extinct than a smaller one, and the conditions for such a reversal to hold over a broad range of sizes require dramatic trends in other population dynamics parameters that counter the contribution of carrying capacity. Likewise, slight adjustments to the dispersal model are not likely to disrupt the general patterns that larger populations are more likely to be independent than smaller ones, and that independence of a population of a given size increases with distance from larger populations.

It is far more critical for appropriate interpretation of our model to understand the consequences of violating the assumptions concerning predictions of carrying capacity based on the IP model. Recall that the most likely bias arising in the use of the IP model for coastal California is over-prediction of available summer rearing habitat (for coho salmon and steelhead) as a consequence of a north-to-south gradient in the dynamics that yield mean annual discharge as a function of catchment area and mean annual precipitation. We attempted to correct for such differences by developing region-specific models, but it is likely that the use of mean annual values obscures important differences in the temporal distribution of precipitation. Fortunately, the direction of such bias is consistent, and is expected to increase along a fairly clear north-to-south gradient, with the possible exception that the model is likely to yield better predictions of IP for watersheds draining the Santa Cruz Mountains south of San Francisco than it is for smaller coastal watersheds between Point Arena and the Golden Gate that do not exhibit strong orographic effects on precipitation.

The consequences of positive bias in IP-km for the results of the connectivity-viability model differ between the two axes. Positive bias in IP-km for a population means that it will be placed to the right of its real position along the “viability-in-isolation” axis. Therefore, conclusions regarding the historical viability-in-isolation of populations in the south part of the NCCCRD, especially San Francisco Bay, should be adjusted by shifting to the left to reflect the likelihood that these populations' carrying capacities are not as high as predicted by the IP model. The effect of bias in IP-km on self-recruitment is not likely to be as strong because (1) self-recruitment is a function of the *relative* population size, and (2) the set of significant donor populations is limited by the scales over which dispersal occurs. Since a recipient population and its (nearby) donor populations are likely to exhibit a similar degree of bias between true historical carrying capacity and predictions of carrying capacity based on IP-km, the effect of such biases on relative population size is likely to be small, which leads to similarly small consequences for predicted self-recruitment. Thus, we expect that the arrangement of populations along the self-recruitment axis will be relatively robust to regionally consistent bias arising from application of the IP model in the southern portions of the NCCCRD.

A final set of assumptions related to the connectivity-viability model centers on the deterministic, steady-state structure of the model. Given the scale and frequency of environmental variability and disturbance, including catastrophic disturbance, across the landscape, any given ESU rarely approaches the distribution of populations in viability-independence space predicted under the assumption of steady-state conditions (Reeves et al., 1995). Nevertheless, this distribution is useful in highlighting which populations are likely to contribute most strongly to ESU persistence and in differentiating the long-term role of populations within the ESU.

1.5.2 Dispersal Rates

Estimates of dispersal rates among populations and the reproductive success of immigrants to a population are useful for parameterizing and testing the assumptions of models such as the connectivity-viability model, and generally gaining insight to connectivity within an ESU or population. Few direct estimates of rates of dispersal among populations are available for any of the four ESUs in the NCCCRD (Shapovalov and Taft, 1954; McElhany et al., 2000), which limits the utility of such information for evaluating population structure within an ESU, save as they inform models of ESU 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 (see below) can be strongly influenced by the introduction of hatchery fish, since, depending on hatchery practices, introduced fish may stray at rates higher than naturally born fish (Pascual and Quinn, 1995). Therefore, any available estimates, especially if developed for hatchery fish or a population strongly influenced by hatchery fish must be considered cautiously.

1.5.3 Population genetics

Genetic information can be used to describe how genetic variation is distributed among and within populations or to gain insight to 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 putatively 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). For each of the ESUs in the NCCCRD, we have data of the latter type available from earlier studies based on allozyme markers (Bartley et al., 1992; Weitkamp et al., 1995; Busby et al., 1996) and more recent work based on microsatellites (e.g., Garza et al., 2004, and unpublished data developed by NOAA scientists and presented in this report). In each case, we have available to us data that span a range of spatial scales and thus better enable us to draw insights regarding population structure within an ESU. Detailed analysis of each data set is presented in the appropriate ESU chapter. Here, we offer some general information on the types of data considered, analyses conducted and what we can expect to learn from these analyses, and appropriate context for interpreting results from these analyses, i.e., model assumptions and anthropogenic influences.

Types of molecular genetic data

Several types of molecular genetic markers are commonly used in the study of biological population structure and in the delineation of population boundaries, including allozymes, mitochondrial DNA (mtDNA), and microsatellites. In most cases, genetic systems used for population studies are chosen because they are assumed to be neutral to the effects of selection, and thus reflect the effects of genetic drift within populations and gene flow among populations. Variability apparent in each type of molecular marker reflects a different time scales, and thus each type of molecular marker provides a lens best suited for resolving biological structure at a particular range of scales. For example, variation in allozyme markers accumulates much more slowly than genetic variation because a substantial amount of genetic variation at a locus is not reflected in the assays used to identify variation. As a consequence, allozyme data is often of limited use in resolving structure between closely related populations. In contrast, microsatellites, which are short repetitive regions of DNA scattered throughout the genome, are highly variable—a single microsatellite gene can have over 100 alleles in a given species—and accumulate variability rapidly. As a consequence, microsatellites provide a useful tool for investigating recent differentiation processes. See Avise (2004) for a more detailed discussion of the various types of molecular markers.

Analysis of genetic data

In bringing genetic data to bear on the question of historical population structure, we are most interested in results from analyses that provide insight into the relative scales at which structure is apparent and the mechanisms that determine the distribution of genetic variance within the ESU[35]. Three general analytical approaches provide the set of inferences that we consider in this report: (1) analyses of pairwise F_{ST} from the perspectives of both hierarchical structure and isolation by distance, (2) analysis of structure

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[35] Some of the genetic data available to us will also contribute to analyses of current status or recent population history, but we do not present results of such analyses, save where such information is required to support appropriate interpretation of population-ESU scale patterns.

in phylogeographic trees, including examination of concordance between population genetic structure and geographical structure, and (3) individual-based analyses of genetic variation (i.e., assignment tests) that identify individuals' ancestry and provide insight to connectivity among populations. Exact tests based on the Monte Carlo-Markov Chain-based method of Raymond and Rousset (1995) were also conducted to examine whether samples were drawn from the same underlying population to establish the presence of genetic structure within each data set. It should be noted that this test is very sensitive with microsatellite data and frequently finds significant differences on small temporal and spatial scales. For steelhead, the available data also support an analysis that is, at its core, an individual-based assignment analysis, but that examines the assignment of individuals at a larger scale to identify geographical locations where evidence of reduced gene flow consistently appears; this analysis is described in detail in the chapter dedicated to the two steelhead ESUs.

General assumptions. For all of the tests considered here, calculation of various values is based on models derived under certain assumptions regarding how genetic variation is distributed within and among populations and by implication the mechanisms that generate this structure. An overarching assumption for all tests below is that the populations being examined are at equilibrium with respect to factors that affect allele frequencies, such as genetic drift, selection and dispersal. This assumption can be violated in numerous ways, including how populations to be sampled are defined and samples are subsequently collected (e.g., kin-biased sampling or admixture of substantially different populations), and historical or recent departures from population dynamics that are expected to underlie a hypothetical equilibrium (e.g., population bottlenecks that greatly reduce effective population size). For the most part, the analyses presented here are robust to violations of these assumptions, and few of the samples in the data sets examined exhibit strong evidence of being out of equilibrium.

Analysis of pairwise F_{ST}. Pairwise F_{ST} is a measure of how genetic variance is distributed among populations, and is related to the level of dispersal among populations [36]. We compare the distribution of estimates[37] of pairwise F_{ST} among samples taken within the same basin to estimates of pairwise F_{ST} among samples collected in different basins to draw inference regarding hierarchical structure within an ESU. We also use F_{ST} to explore patterns of isolation-by-distance, by regressing estimates of pairwise F_{ST} on geographic distance, generally measured "as-the-fish-swims" along stream networks, between samples. From these analyses, we seek to evaluate our assumptions regarding the use of a hierarchically structured geographic model such as the connectivity-viability model as a way to synthesize information on the relative size and location of putative populations along the coast.

Samples that depart strongly from equilibrium expected under the assumption of constant population size, say as a consequence of inbreeding, recent severe bottlenecks, or biased sampling, often exhibit very large genetic distances from other populations, and thus can have undue influence in isolation-by-distance relationships. We therefore exclude such samples from analyses of isolation-by-distance.

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[36] More specifically, pairwise F_{ST} is the proportion of the standardized variance in allele frequencies between two population samples, i.e., the ratio of the variance between samples to the variance among individuals within each sample

[37] F_{ST} is estimated with the unbiased estimator Θ (Weir and Cockerham, 1984).

Phylogeographic trees. Phylogeographic trees are graphical illustrations of population relationships based on pairwise distances estimated from genetic data. In these analyses, we are more interested in the internal structure of the tree (i.e., the length of internal branches and how they join), which provides information on how populations are related to one another, and less interested in the length of the terminal branches, which reflect the degree of population differentiation. We present trees constructed by applying the neighbor-joining tree-building algorithm for tree construction (Saitou and Nei, 1987), to matrices of Cavalli-Sforza and Edwards (1967) (CSE) chord distance; this algorithm and measure of genetic distance are robust to variation in mutation rate across loci and fluctuations in population size, and are commonly used in analysis of genetic data from anadromous salmonids. Bootstrap analyses were used to evaluate the stability of tree branching patterns and determine the extent to which the signal is influenced by particular genes or alleles; the "majority rules" consensus tree is presented, which provides information on how well the data support internal branches. We also evaluated trees constructed with a maximum likelihood algorithm that considers the raw data, not mean genetic distances derived from population allele frequencies Felsenstein (2003); these trees proved to be essentially identical to the NJ trees, and are not presented. One of the principal uses to which we put phylogeographic trees, is as a means of examining more specifically the degree of concordance between population genetic structure and the spatial arrangement of populations. Our heavy reliance on bootstrap consensus trees is driven by our need to focus on internal structure and by uncertainty regarding the reliability of absolute estimates of genetic distance due to the influence of non-equilibrium factors.

Although departures from equilibrium related to variation in population size can lead to positive bias in estimates of genetic distances among populations, the effects of such violations are generally confined to the length of the terminal branches in a phylogeographic tree. The internal structure, which is where we focus our attention, is generally robust to such violations.

Individual-based analyses of genetic variation: assignment tests Assignment tests evaluate the most likely population of origin for a specific individual given its genotype, by comparing the individual genotype to a genetic profile based on the allele frequencies observed in each population sample (Paetkau et al., 1995; Nielsen et al., 1997)[38]. For these tests, as for the analyses presented above, it is assumed that each sampled population is in Hardy-Weinberg equilibrium. Thus, cases in which individuals are assigned with greater likelihood to a population other than the one in which they were collected are considered as evidence for recent migration. By focusing on the similarity of individuals to populations, such tests can powerfully resolve structure that is not readily discerned with measures that distill an entire population sample into a set of allele frequencies (e.g., F_{ST} or other genetic distances).

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[38] For the analyses presented here, each individual was assigned to its most likely population of origin by comparing it against allele frequency profiles calculated sans the individual being evaluated. Analyses were carried out using GeneClass2 (Piry et al., 2004) which implements the probabilistic method of (Paetkau et al., 1995) with a modification that uses a partially-Bayesian algorithm to estimate allele frequencies (Rannala and Mountain, 1997).

Assumptions and appropriate inference of historical population structure

Molecular data can be used to answer a broad array of questions related to population structure and dynamics (Avise, 2004). As noted above, for the purpose of drawing inference regarding historical population structure of each ESU, we are most interested in what can be learned from genetic samples regarding (1) macro-scale processes that underlie population and ESU structure, and (2) evidence for specific dispersal-mediated connections (or lack thereof) that provide evidence of important idiosyncratic dynamics at a local scale. In particular, we examine genetic data with the intent of inferring patterns that reflect macro-scale processes thought to underlie population and ESU structure, and thus provide insight to population structure under historical conditions.

There are several key issues one must consider when interpreting genetic data. First, the power of genetic data to support inferences regarding population structure is asymmetrical with respect to the question of whether to "lump" or to "split" two groups. Genetic analyses readily detect the effects of a lack of gene flow between groups, but are much less informative in determining whether two groups that show signs of gene flow are currently exchanging individuals, due to the need for sufficient time following isolation for divergence to arise. Likewise, since genetic structure is highly sensitive to very low levels of effective dispersal, genetic analyses are of limited use in determining whether two groups are exchanging demographically relevant numbers of individuals (Waples, 1998). Second, some of the most recent genetic techniques have tremendous power to resolve differences among samples, to the degree that the statistical significance and biological relevance of a result can be decoupled (Allendorf and Phelps, 1981; Waples, 1998; Hedrick, 1999). Finally, many of the analyses require assumptions regarding the underlying population and genetic dynamics (e.g., population at equilibrium, equal mutation rates, individuals are sampled randomly from the population, markers are in fact neutral, etc.); failure to satisfy these assumptions can bias inferences drawn from the analysis. In some cases, if samples are likely to depart from assumptions in a similar manner, analyses based on relative measures can still yield robust results. Finally, genetic patterns may not reflect natural processes. Artificial propagation, and especially out-of-basin stock transfers can disrupt historical patterns of genetic structure.

Stock transfers and the historical context of genetic data The latter point is particularly germane to our task. Many watersheds within the NCCCRD have received transplants derived from out-of-basin, even out-of-ESU broodstock (Weitkamp et al., 1995; Busby et al., 1996; Myers et al., 1998). For each species, we summarize historical records of among-basin and among-ESU transfers to basins in the NCCCRD to provide some context for interpreting available genetic information. Relevant information is brought to bear in each of the species-specific chapters that follow.

To evaluate the influence of among-basin transfers on observed population genetic structure, it is necessary to keep three issues in mind. First, the success of some of these introductions may have been limited (Utter, 2001). Early hatchery practices often involved releasing fry or fingerlings, a practice that was eventually abandoned because of marginal adult returns, and fish from other basins, and particularly those from outside an ESU (and particularly out-of-state), were more likely to be poorly adapted for the environmental conditions that occur in the watershed to which the fish were transferred. Second, the short duration of many out-of-basin transfers reduces the probability that these introductions left a lasting genetic signature. In contrast, introductions shortly before genetic surveys are more likely to yield measurable signals. Third, the degree to which out-of-basin introductions are likely to affect genetic population structure depends on both the number of introduced fish that successfully spawn as well as the size of the recipient population. Large transfers into small or strongly depressed populations are more likely than small transfers into large populations to have a lasting effect.

1.5.4 Life history and phenotypic diversity

To be informative with respect to population differentiation, variability in life history or other phenotypic characteristics must reflect (at least in part) underlying genetic variability (cf. Funk et al., 2005), in which case, phenotypic variability serves as a proxy for genetic information as well as evidence of potential variation in selective environments experienced by salmon. 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.

Comprehensive Status Review Updates were completed for all listed ESUs in 2003 (West Coast Salmon Biological Review Team, 2005). In preparing these updates, NMFS scientists compiled, summarized and analyzed all available data relevant to ESU status for consideration by the Biological Review Teams and, where possible, focused analysis and interpretation at the population level. We do not repeat these data in detail here, but rather draw from the Status Review updates only those few data sets that offer some information for analysis of population structure. Likewise, we do not attempt to present data that have been compiled on life-history variation, etc., in comprehensive detail. Rather, we cite specific examples that prove informative with respect to population structure.

1.5.5 Population dynamics

Analysis of correlations in time series of abundance for two putative populations can provide information on whether the two groups are demographically linked. A lack of correlation in abundance between two putative populations in close proximity to one another provides evidence that the two groups are not demographically coupled, i.e., dispersal between the populations is insufficient to erase the effects of variation that affects population dynamics at spatial scales corresponding to individual populations. Positive correlation suggests the possibility strong demographic links; however, correlation in environmental drivers of population dynamics at spatial scales that exceed the range of individual populations can confound such analyses. Thus, 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 only a few time series amenable to this sort of analysis for any ESU in the NCCCRD. Data that are not useful for evaluating correlations in populations' dynamics are not examined in this report, but have been considered elsewhere as part of the ESU status reviews (West Coast Salmon Biological Review Team, 2005).

1.5.6 Environmental and ecological diversity

We examine diversity associated with spatial variation in environmental and ecological conditions for two closely related reasons: (1) such diversity can contribute to viability at both the ESU and population level (McElhany et al., 2000), and (2) environmental variation often underlies biological structure, and can contribute to population structure within an ESU. In salmon and steelhead, spatial variation in selective pressures can favor local adaptations cued to specific watersheds or locations within a watershed and thus drive population differentiation (Taylor, 1991; Lenormand, 2002, but see Adikson1995). The potential for environmental and ecological heterogeneity to favor local adaptation is strongly dependent on rates of dispersal among populations, the degree to which selective regimes differ, and how intensely selection affects putative populations during the portion of the life cycle each is exposed to environmental conditions that differ from those experienced by other populations. Although spatial variation in environmental conditions can serve as an indicator of putative variation in selective regimes, inferences regarding population structure are sensitive to assumptions about dispersal rates and about the strength of divergent selection associated with 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. Despite the relatively low power for environmental information to resolve population structure independently, we characterize environmental and ecological variation across the NCCCRD (1) to serve as a foundation for considering the role of diversity in subsequent efforts to develop viability criteria for ESUs and populations, and (2) to identify areas that satisfy at least one prerequisite for population differentiation due to local adaptation.

Basin-scale multivariate analysis of environmental characteristics

We developed a multivariate analysis of environmental and ecological characteristics for watersheds in the Recovery Domain to serve two purposes. First, the analysis helps us to identify differences in ecological and environmental characteristics within large basins, which are useful in considering whether sub-basins within large basins might harbor separate populations. Second, by identifying 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 and extracted specific metrics for watersheds throughout the NCCCRD[39], and applied principle components analysis

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[39] Environmental data for selected watersheds of the NCCCRD were extracted from GIS datasets using two different types of joins in ArcInfo GIS (ArcGIS 8.3, Environmental Systems Research Institute, Redlands, CA): a spatial join between polygon coverages; and a spatial join between a polygon coverage and a raster (or grid) coverage. Polygon-polygon joins were used to extract information on lithology, which was subsequently converted to percent-coverage for a watershed. Lithographic categories were further collapsed into four general categories: alluvial, volcanic, granitic, and sedimentary. Polygon-raster

Table 1.2. Multivariate environmental analysis of watersheds in the NCCCRD.

Data Type	Description	Source	PC 1*	PC 2*	PC 3*
AREA-HA	area in ha			-0.345	-0.2
MEAN-ELEV	mean elevation (m)	DEM (USGS, 2003)	0.211	-0.437	-0.107
MEAN-PPT	Average* mean annual precipitation	PRISM (Daly et al., 1994)	0.408		-0.154
MEAN-TMN	Average mean temperature	PRISM (Daly et al., 1994)	-0.428		0.261
MEAN-TMIN	Average minimum temperature	PRISM (Daly et al., 1994)	-0.248	0.394	
MEAN-TMAX	Average maximum temperature	PRISM (Daly et al., 1994)	-0.35	-0.32	0.246
MEAN-TRNG	Average annual temperature range	PRISM (Daly et al., 1994)	-0.181	-0.473	0.169
PEAK	Peak month of stream flow	EarthInfo (2002)	-0.24	-0.184	
SNWI	Snow index	PRISM (Daly et al., 1994)	0.23	-0.335	-0.269
VOLCAN**	% area volcanic	Jennings (1977)***	-0.264		-0.313
SEDIM†	% area sedimentary	Jennings (1977)***	0.353		0.501
GRANIT††	% area granitic/plutonic	Jennings (1977)***	-0.155	-0.156	
ALLUV†††	% area alluvial	Jennings (1977)***	-0.245	0.151	-0.57

*Loadings with magnitude exceeding 0.1 on each of the first three principle components. **The following lithographic categories were aggregated under VOLCAN: calc-alkaline meta-volcanic, calc-alkaline volcanoclastic, mafic volcanic flow, felsic pyroclastic, felsic volcanic flow, and mafic pyroclastic. ***Information derived from GIS layer based on Jennings (1977). †The following lithographic categories were aggregated under SEDIM: carbonate, conglomerate, interlayered meta-sedimentary, interlayered meta-sedimentary Franciscan, meta-sedimentary phyllite and schist, sandstone, sandstone Franciscan, shale and mudstone, argillite and slate, mixed eugeosynclinal, and siltstone. ††The following lithographic categories were aggregated under GRANIT: calc-alkaline intrusive, granitic gneiss, mafic intrusive, mafic schist and greenstone, ultramafic, alkalic intrusive, and mafic gneiss. †††The following lithographic categories were aggregated under ALLUV: alluvium, dune sand, glacial drift, and landslide.

(PCA) and cluster analysis to the scaled and centered data to discern regional groups of watersheds with similar environmental characteristics. Since we are interested in group structure as well as factors that differentiate watersheds, we used a clustering algorithm based on the on the average (euclidean) distance among members of adjacent clusters rather than a nearest-neighbor analysis.

Table 1.2 lists the data types retained for analysis, and the loadings for each on the first three principal component vectors (see also Plates 4 through 11). The first three principle components explained nearly two-thirds of the variance in the environmental data set. Displaying watersheds in 3-D space defined by the first three components (Figures 1.5 and 1.6) suggests a set of groupings, as well as highlighting important differences among subbasins of the Eel River. Cluster analysis reveals similar groupings, and also captures environmental variability within the Eel River basin and among San Francisco Bay tributaries (Figure 1.7). Apparent groups include:

1. **Northern, large watersheds**: These watersheds penetrate deep inland, drain basins with higher

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joins were used to extract data from DEM and PRISM layers to obtain information on climatic variables and topography. We also obtained or calculated the following characteristics for each watershed: (1) a monthly snow index formed by multiplying total precipitation (in mm) by the proportion of the temperature range that fell below freezing, which were subsequently summed to yield an annual snow index; (2) the month of peak stream flow derived from summaries of USGS gage observations; and (3) planar area. A broader suite of data than reviewed here was considered in preliminary analysis, but a number of variables were dropped due to very tight correlation with variables retained for the final analysis (e.g., mean and maximum elevation.

elevations, and experience cooler (but more variable) temperatures and greater precipitation. This group includes Redwood Creek, Mad River, and major subbasins on the north side of the Eel River.

2. **Northern, small coastal watersheds**: These watersheds tend to be small and restricted to areas very near the coast. Environmental gradients running north-to-south cause gradual differentiation within this group, such that small watersheds from two regions can be observed: (a) small coastal watersheds north of Cape Mendocino, and (b) small coastal watersheds between Cape Mendocino and the Navarro River (exclusive). The environmental characteristics of the lower mainstem Eel River are similar to those of watersheds in this group.

3. **North-central, small coastal watersheds**: Like the preceding group, these watersheds are small and lie near the coast. However, these watersheds tend to be warmer and drier than those to the north. These watersheds lie between the Navarro River and Point Arena.

4. **Northern, intermediate-sized, coastal watersheds**: These watersheds are larger and penetrate further inland than the previous group. As a consequence, these watersheds exhibit more variable, drier climate, and include greater diversity of geology and ecosystems. Since these watersheds span a broader range of conditions, they watersheds fall intermediate to the preceding and following groups, with those in the north more closely resembling the northern, small coastal watersheds and those in the south tending to resemble coastal watersheds in the central part of the NCCCRD. The environmental characteristics of the South Fork Eel River are similar to those of watersheds in this group.

5. **Central, coastal watersheds**: This group includes small to moderately sized, low elevation coastal watersheds south of the Russian River. These watersheds have lower capacity to capture and store water due to their low elevation.

6. **Russian River**: The Russian River stands out as a consequence of its large size and unique climatic traits (e.g., warmer temperatures, yet greater precipitation than the smaller watersheds on the coast and in the San Francisco Bay).

7. **San Francisco Bay tributaries**: This group consists of tributaries that drain into San Francisco and San Pablo bays. Variation within this group is discussed below.

8. **Southern, coastal watersheds**: This group consists of small coastal watersheds south of San Francisco Bay.

Within-basin environmental variability

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 population structure at a finer scale. Four cases exist where this is warranted:

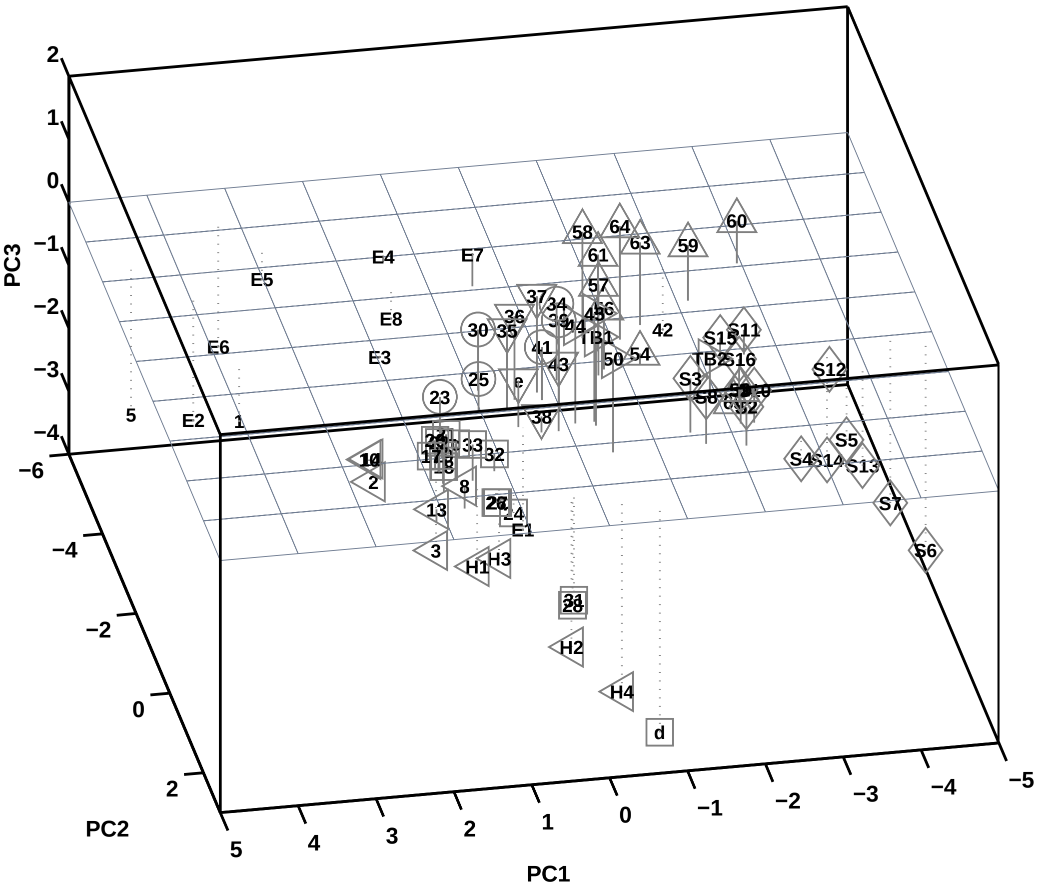

Figure 1.5. Selected NCCCRD watersheds arranged on the first three principle components derived from environmental data aggregated at the watershed scale. Watersheds are identified according to Table 1.1. Large northern basins and the Russian River are indicated solely by their identifiers (i.e., no symbol), and symbols indicate groups of smaller watersheds defined on the basis of geographic proximity and environmental similarity: ◁: coastal basins north of Cape Mendocino; □: small coastal basins between Lost Coast and Mendocino Bay (e.g., Caspar Creek [27]); ○: large coastal basins between Lost Coast and Point Arena (e.g., Navarro River [34]);▽: small coastal basins between Mendocino Bay and Point Arena; ▷: coastal basins between Point Arena and the Golden Gate (sans Russian River); ◊: San Francisco Bay tributaries; △: coastal basins south of San Francisco.

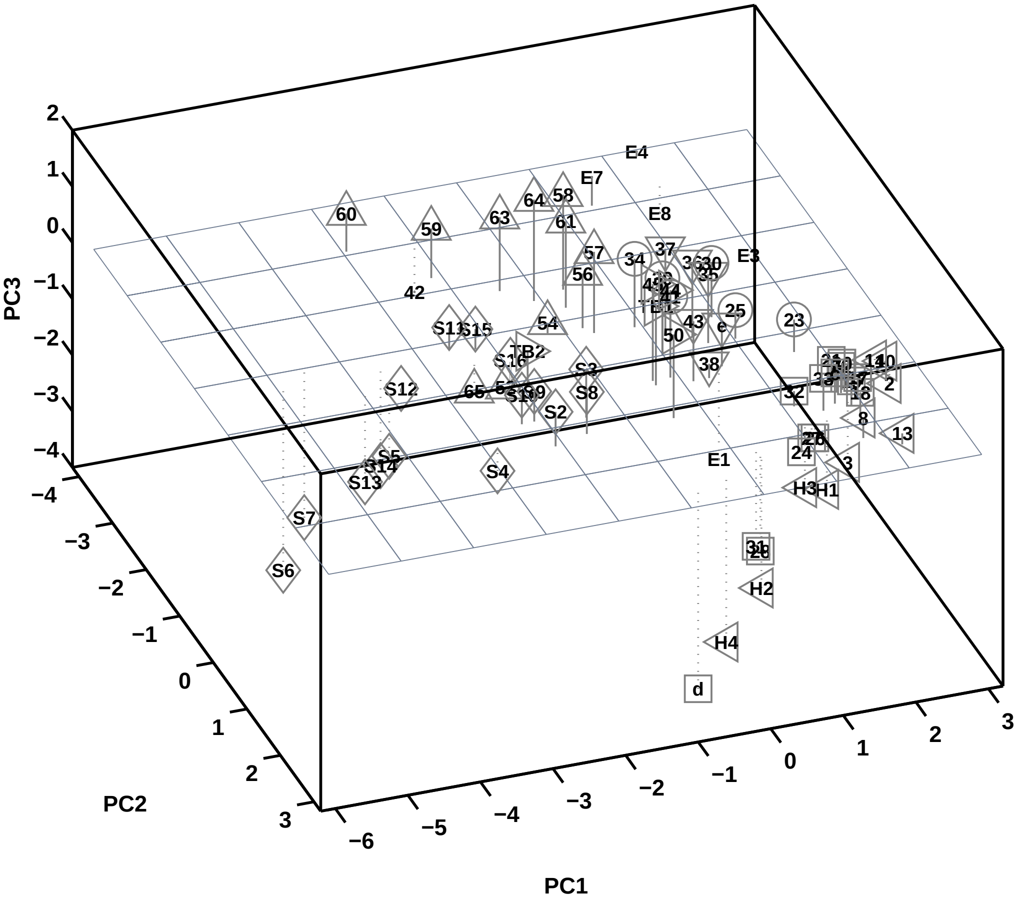

Figure 1.6. Selected NCCCRD watersheds arranged on the first three principle components derived from environmental data aggregated at the watershed scale; zoomed in to focus on dense region from Figure 1.5. Watersheds are identified according to Table 1.1. The Russian River is indicated solely by its identifier (i.e., no symbol), and symbols indicate groups of smaller watersheds defined on the basis of geographic proximity and environmental similarity: ◁: coastal basins north of Cape Mendocino; □: small coastal basins between Lost Coast and Mendocino Bay (e.g., Caspar Creek [27]); ○: large coastal basins between Lost Coast and Point Arena (e.g., Navarro River [34]);▽: small coastal basins between Mendocino Bay and Point Arena; ▷: coastal basins between Point Arena and the Golden Gate (sans Russian River); ◊: San Francisco Bay tributaries; △: coastal basins south of San Francisco.

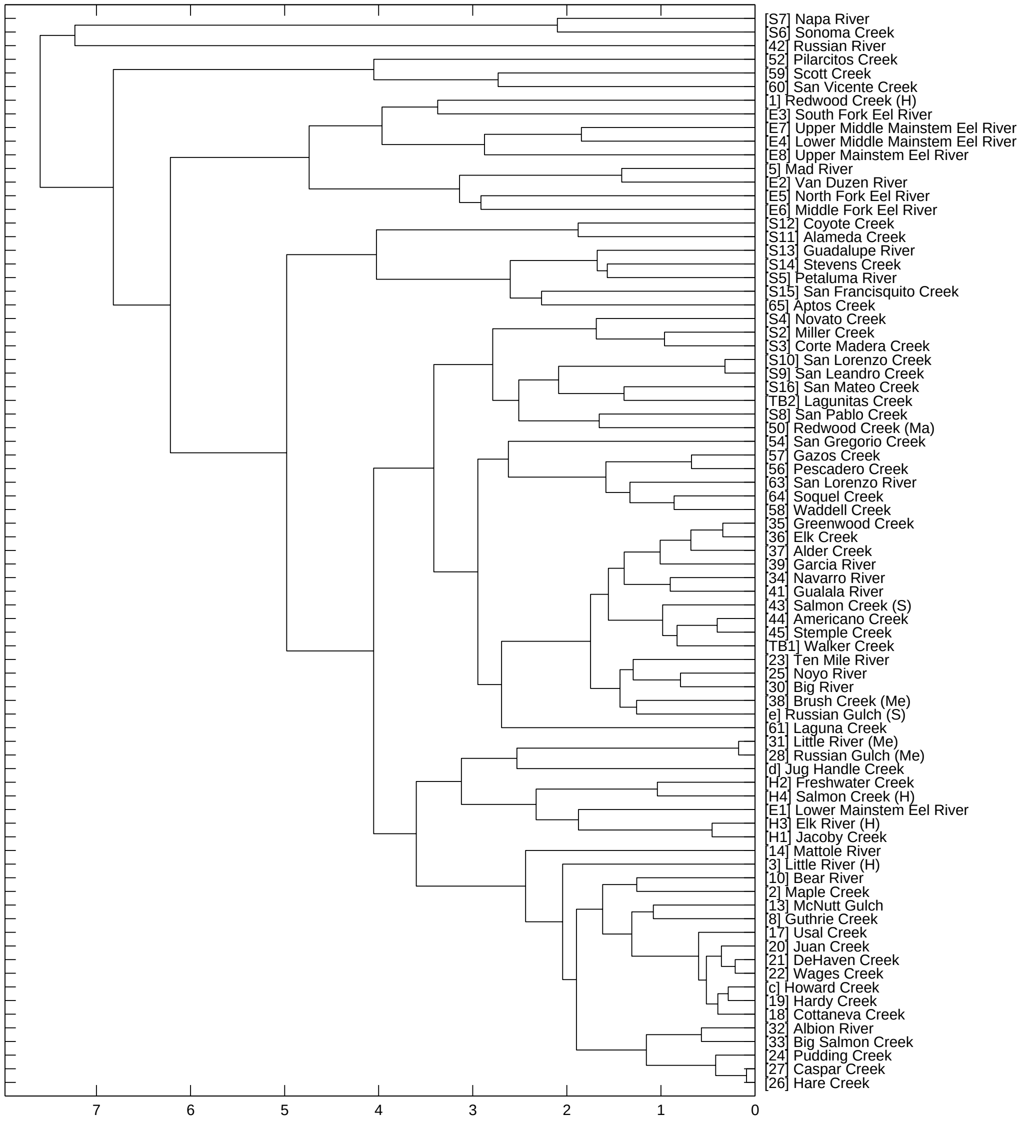

Figure 1.7. Dendrogram based on average-distance clustering algorithm applied to scaled and centered environmental data for watersheds in the North-Central California Coast Recovery Domain. Numbers on branch labels correspond to identifiers in preceding plots. Letters in parentheses distinguish like-named streams by county (“H”, Humboldt;“Me”, Mendocino; “S”, Sonoma; “Ma”, Marin).

Eel River, San Francisco Bay, Humboldt Bay, and Tomales Bay. Cursory examination of environmental conditions across the other large basin of the NCCCRD, the Russian River, suggested that a similar analysis was not warranted.

Humboldt Bay

The four main tributaries to Humboldt Bay (Jacoby Creek [H1], Freshwater Creek [H2], Elk River (Humboldt) [H3], and Salmon Creek (Humboldt) [H4]) all exhibit very similar environmental characteristics (Figures 1.6 and 1.7). There is little support for proposing an environmental hypothesis for population structure among these basins.

Eel River

The Eel River basin includes four major subbasins (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. To account for this variability, we partitioned the Eel River into eight regions (the four major tributaries and four major sections of the mainstem) for inclusion in the multivariate analysis.

Our multivariate analysis highlights substantial environmental variability within the Eel River basin. The South Fork Eel River, in particular, differs substantially from the other parts of the Eel River basin, and save for its size, exhibits environmental characteristics similar to the northern, intermediate-sized and central coastal watersheds. The other major tributaries to the Eel River, i.e., the Van Duzen River, and North Fork and Middle Fork of the Eel River, are affiliated with the large, northern watersheds, i.e., Redwood Creek (H) and Mad River. This latter group drain watersheds that extend to higher elevations and receive part of their precipitation in the form of snow. The Upper Eel River (upstream of the confluence of the Outlet Creek) also resembles the northern large watersheds and northern tributaries of the Eel River, but experiences higher temperatures and less precipitation. The Lower Eel River, which includes mainstem tributaries below the confluence of the South Fork, shares environmental characteristics with Humboldt Bay tributaries. Other portions of the mainstem Eel River do not clearly group with any other watersheds, but this is probably due to the structure of these arbitrarily defined areas, which include minor watersheds, but also lie along the mainstem.

Variation in environmental conditions is reflected in the historical distribution of life history forms of Chinook salmon and steelhead within the Eel River basin. For example, 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 having substantial spring snowmelt. As a contrasting example, only winter steelhead and fall-run Chinook occupy the lower, warmer South Fork Eel River.

San Francisco Bay

Variation within the greater San Francisco Bay basin is apparent in both 3-D space and in the dendrogram (Figures 1.6 and 1.7). In general, variation within the San Francisco Bay basin exists between smaller watersheds draining the eastern slopes of the coastal mountains that share characteristics with coastal watersheds, and the larger, warmer, and drier basins in the northern and southern regions of the Bay. Two watersheds in particular, San Francisquito Creek [S15] and San Mateo Creek [S16], more closely resemble the coastal watersheds they abut than any other watershed tributary to the San Francisco Bay. Watersheds just to the north of the Golden Gate and directly east of the Golden Gate also fall out near coastal watersheds, which reflects the influence of coastal climate in these areas despite substantially lower precipitation in these watersheds. Interior watersheds, i.e., those that lie inland of coastal mountains, do not experience the moderating influence of the ocean as strongly and thus differ more strongly from coastal watersheds. One potentially important characteristic of the San Francisco Bay that is not incorporated in the multivariate analysis is the structure of the Bay itself. The northern part of the Bay is strongly influenced by discharge from the Sacramento-San Joaquin basin, whereas the southern part of the Bay is less so. Environmental variability is considered in more detail in our evaluations of population structure in the CCC-Coho and CCC-Steelhead ESUs.

Tomales Bay

Our environmental analysis suggests that the two main tributaries to Tomales Bay, Walker Creek [TB1] and Lagunitas Creek [TB2], differ sufficiently to warrant separate consideration. Lagunitas Creek [TB2] more closely resembles tributaries to San Francisco Bay, whereas Walker Creek [TB1] more closely resembles the small, coastal basins that lie between Tomales Bay and the Russian River (Figures 1.6 and 1.7). It is possible, however, that homing cues are less effective due to large freshwater inputs during the winter storm season. Winter run-off disrupts the strong longitudinal hydrological structure that develops in Tomales Bay during the dry season, and often results in a freshwater lens covering much of the bay (Largier et al., 1997; Gross and Stacey, 2005). Lagunitas Creek [TB2] contributes approximately one-half of the freshwater inputs to Tomales Bay, and does so at the most inland end of the bay in a region where flows tend to be more or less unidirectional. Walker Creek [TB1] contributes approximately one-quarter of the freshwater input to the bay, and does so in the part of the basin where tidal mixing dominates. Whether these dynamics result in conditions that suffice to reduce the homing ability of salmon and steelhead to the point that population structure can not be maintained is unclear. We therefore treat salmon and steelhead in the two watersheds as separate units, but consider the case for alternative structures in each species-specific analysis.

1.5.7 Synthesizing information on population structure and diversity strata

We have three sorts of information that we can bring to bear to address the task of elucidating historical population structure for each of the ESUs in the NCCCRD: (1) geographical information on the (relative) size of populations and their arrangement in space, (2) information on population genetic structure derived from analysis of putatively neutral molecular markers, and (3) information on basin-scale variation in environmental characteristics that may underlie important differences in the selective environment of salmon and steelhead. These data must be interpreted within the context of the life history and ecological niche of each species.

Of the three types of information listed above, the first two are readily synthesized to develop hypotheses regarding historical population structure. The connectivity-viability model is directly analogous to the models that underlie many of the basic methods of analysis for population genetic data. These two sources of information therefore complement one another quite nicely. Indeed, patterns revealed by analyses of population genetic structure, such as isolation-by-distance, provide rather strong empirical support for adopting a geographic perspective, especially when current observations of population genetic structure are interpreted in the context of historical among-basin and among-ESU transfers. Unfortunately, it is difficult to infer the intensity of demographic processes, such as dispersal, and their effect on population extinction rates from genetic data without substantial ancillary data. In the following chapters, we therefore present genetic data first to evaluate relative scales of population differentiation as an indicator of dispersal among populations. We subsequently draw on these results as support for the assumptions that underlie our initial delineation of demographic units and subsequent application and interpretation of the connectivity-viability model.

We bring environmental information to bear after preliminary hypotheses for historical population structure are developed from the geographic and genetic analyses. According to our second rule for delineating populations, spawning groups within large basins may be partitioned into multiple populations if available evidence indicates a high likelihood that environmental differences suffice to present different homing cues or selective environments, and thus favor the generation of population structure. Population differentiation requires that dispersal among spawning groups be sufficiently low to allow differences in selective regimes to drive local adaptation and population differentiation (Adkison, 1995; Kawecki and Holt, 2002; Lenormand, 2002). We do not have direct information on either of these two factors, and so must consider the plausibility (and any indirect support) for the assumptions necessary to draw a conclusion one way or the other.

Finally, in anticipation of future work focused on ESU viability criteria, we offer results from two additional analyses. First, although we do not use information on specific connections among populations for elucidating population structure, such information is likely to be useful for developing recovery criteria that incorporate the status of dependent populations as a measure of the status of the ESU, and for identifying key populations within the ESU. Therefore, we present the connectivity results in terms of the contribution from source populations (populations identified as functionally or potentially independent) to sink populations (populations identified as potentially independent or dependent). We include potentially independent populations as sources because they exceed the viability-in-isolation threshold and are potentially capable of influencing the dynamics of smaller populations nearby, and as sinks because they are affected by immigration from still larger, often functionally independent populations. Second, we use environmental data to delineate diversity strata that represent important structure at scales intermediate to populations and ESUs. These strata are one basis for incorporating diversity and spatial structure into ESU viability criteria.

Incorporating differences among species: assumptions and implications

This report includes our analysis for three species, two of which include substantially different life-history types. Clearly, a cookie-cutter, one-size-fits-all approach is not appropriate. We therefore take into consideration aspects of each species's (and life-history type's) life history and ecological requirements in our analysis, which can lead to somewhat different results and influence how we incorporate and express uncertainty in our conclusions.

For example, we only conduct connectivity-viability analysis for those life-history types for which we can generate reasonable proxy measures for population carrying capacity, and for the analyses that we can conduct, we develop species-specific thresholds for viability-in-isolation that take into account relevant elements of the species life history. However, we generally lack sufficient information on species-specific homing behaviors (e.g., fidelity rates, precision, spatial variation and scale dependence in these two parameters, etc.) that might allow us to rank (with any confidence) species according to whether populations are more or less likely to exhibit different levels of relative independence measured against some arbitrary absolute threshold. Any such ranking would be based on assumptions that are difficult to test with existing data.

As noted above, we do not have sufficient information from which to draw strong inferences regarding the intensity and variation of selection pressures in freshwater habitats or differences among species with respect to dispersal rates. However, differences among species and major life-history types in how each is distributed in freshwater habitats provides a surrogate measure for potential exchange within a watershed. In particular, we consider how far a species penetrates a watershed, and the scale at which the downstream extent of a species' distribution facilitates connectivity among groups. At one extreme, overlapping distributions allow diffusive exchange to occur even if individuals home relatively precisely and tend to disperse over short spatial scales. At the other extreme, widely separated discrete distributions require rare "long-distance" dispersal events. If we assume, in the absence of information to the contrary, that precision and accuracy of homing behaviors do not vary widely across species[40], then the geographical distribution of spawning groups leads to plausible assumptions about patterns of connectivity. Likewise, differences among species in how long each remains in freshwater (and, as above, where they are generally located), provide a similar surrogate measure for the potential contribution of freshwater environmental characteristics on population differentiation.

Conclusions regarding the scale at which population structure occurs within a basin tend to be very sensitive to the nature of global[41] assumptions made about "effective dispersal", which integrates physical dispersal with a measure of reproductive success, and the geographical structure of the basin as it is used by a particular species. For example, the life history of winter steelhead, which tend to spawn in smaller streams high in a watershed and rear for extended period as juveniles, lead to a set of assump-

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[40] Note that the conclusions that follow rest on an assumption of equal precision and accuracy of homing behaviors across species, but it is likely that natural selection on these two parameters generates positive correlation between the degree of spatial isolation and overall fidelity, particularly if coupled with selection for locally adapted traits (Sultan and Spencer, 2002; Stewart et al., 2003).

[41] We use "global" to describe assumptions that apply consistently across an entire basin or species, in contrast to spatially specific assumptions that have a much more limited scope.

tions (e.g., low potential for exchange, relatively high exposure to selective pressures while in discrete freshwater habitats) that tend to favor conclusions that include relatively fine population structure within a basin. In contrast, assumptions based on the life history of (ocean-type) fall-run Chinook, which tend to spawn in larger mainstem habitats and the lower parts of larger tributaries and migrate to the ocean after a relatively short time in freshwater, tend to favor conclusions in which population structure is apparent at much larger spatial scales within a basin. In the case of steelhead, a relaxation of the assumptions that favor “splitting”, say by assuming that dispersal occurs at greater rates over larger spatial scales, will at some point lead to a relatively rapid transition in the pattern of connectivity that emerges from application of assumptions that favor a “lumped” conclusion. Likewise, decreasing the degree of connectivity among fall-run Chinook salmon in a basin will at some point cause a sharp transition to assumptions that support population structure at a finer scale. Reaching conclusions regarding population structure at an intermediate scale generally requires (spatially) specific assumptions of the form “effective dispersal is greatly reduced across a boundary between tributary X and tributary Y”. In the absence of specific supporting data, such assumptions are difficult to defend and potentially arbitrary.

2 Central California Coast Coho Salmon ESU

2.1 ESU definition

The Central California Coast Coho Salmon (CCC-Coho) ESU includes coho salmon (*Oncorhynchus kisutch*) that spawn and rear in coastal watersheds from Punta Gorda (south of and not including the Mattole River) to the San Lorenzo River, as well as tributaries to the San Francisco and San Pablo bays[1]. The northern boundary of this ESU is defined on the basis of important geological and ecological transitions, as little information is available for coho salmon in the small watersheds along the ∼90 km of coast between the Mattole and Ten Mile rivers (Weitkamp et al., 1995). The current southern extent of the CCC-Coho ESU is the San Lorenzo River; however, any coho salmon that might establish populations watersheds south of the San Lorenzo River by natural colonization are considered part of this ESU[2].

2.2 Life history and general habitat characteristics

The CCC coho salmon ESU constitutes the southernmost portion of the species' North American range. As a consequence, environmental conditions—particularly temperature and flow regimes—faced by coho salmon in streams within this ESU differ from those experienced by more northern populations, a fact reflected in certain unique aspects of their life history.

2.2.1 Life history

In general, coho salmon within California exhibit a three-year life cycle. Entry of adults into natal streams and rivers in the ESU usually occurs from mid-November to January (occasionally extending as late as early March), coincident with the onset of rain-induced freshets in the fall or early winter. Although the correlation between fall freshets and the onset of adult migration is apparent throughout much of the species' range, it is particularly strong in the CCC-Coho ESU because high flows are required to breach sand bars that form across the mouths of many coastal California streams and rivers

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[1] Some historical records suggest that coho salmon occupied Walnut Creek, which enters Suisun Bay, upstream of the Carquinez Strait, and thus lies outside the NCCCRD; wWe therefore consider this watershed in our conclusions, but do not include it in our formal analyses.

[2] Historical records exist to suggest that coho salmon were once present in Soquel Creek and Aptos Creek in Santa Cruz County, so we include these watersheds in our analyses.

during summer. 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 continue to reside in the gravel for an additional 2-8 weeks (Sandercock, 1991). Fry emerge in early spring.

Most juvenile coho salmon in the CCC-Coho ESU undergo smoltification and begin their seaward migration one year after emergence from the redd. Whether this is simply because warmer temperatures in the CCC-Coho ESU allow juvenile coho salmon to reach sufficient size to go to sea or some other cause is not clear. In more northern latitudes, a significant proportion of juveniles may spend a second (or even third) full year in freshwater (Sandercock, 1991). Juveniles that have spent two winters in freshwater have recently been documented in the California portion of the Southern Oregon-Northern California Coast coho salmon (SONCC-Coho) ESU (Bell et al., 2001), and have been observed in Lagunitas Creek and Scott Creek in the CCC-Coho ESU (J. Smith, San Jose State University, *pers. obs.*; S. Hayes, NOAA/NMFS Santa Cruz Laboratory, *pers. obs.*). In the CCC-Coho ESU, smolt outmigration occurs in spring, generally peaking in April or May (Shapovalov and Taft, 1954; Weitkamp et al., 1995; Spence, 1995). The ocean phase of coho salmon typically lasts about 18 months; however, often a substantial 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. (Female “jills” can occur, but are much less common than jacks). Thus, the typical life-span of almost all coho salmon in the CCC-Coho ESU is three years, the exceptions being 2-yr old jacks and occasional 4-yr old adults of both sexes. The relatively rigid life history exhibited by female coho salmon, which limits demographic interactions among brood years, makes them 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 a substantial degree of genetic exchange among brood years within a population.

2.2.2 Typical habitat characteristics and ecological indicators

Following emergence, fry often aggregate along stream margins, within shallow pools, and backwater areas, moving to deeper pools as they increase in size. Compared to other salmonids, juvenile coho salmon have relatively large fins and laterally compressed bodies, both of which are believed to be adaptations to living in the slower-velocity habitats where they most commonly occur. During the summer, juvenile coho salmon generally exhibit preference for pool habitats over runs and riffles (Bisson et al., 1988). During the winter, juvenile coho salmon often move out of the main channel and seek refuge in side channels, alcoves, and other off-channel habitats during periods of high stream discharge (Tschaplinski and Hartman, 1983; Meehan and Bjornn, 1991; Bell et al., 2001). Together, these attributes and behaviors likely explain why juveniles are most abundant in low-gradient (usually $<$2%-3% but occasionally up to 5%), unconstrained reaches than in constrained reaches or steeper headwater streams. Spawning habitats also exhibit these habitat characteristics.

The importance of pool habitat for juvenile coho salmon likely contributes to the strong correlation between the distribution of coho salmon and forests of coastal redwoods or other large conifers. Input of large wood to streams in these ecosystems favors the creation of pool habitats, backwaters and alcoves that are preferred habitats of juvenile coho salmon. For this reason, information on the distribution of such forests, or environmental correlates of such conditions is useful for predicting historically available habitat for coho salmon.

2.3 Historical distribution

We synthesized two complementary data sets to assess the potential distribution of coho salmon in watersheds south of Punta Gorda, and thereby to frame the set of putative populations for subsequent evaluation. One, we used the results from a GIS model to predict the intrinsic potential (IP) for habitat suitable for spawning and rearing of coho salmon to occur in watersheds throughout the range of the CCC-Coho ESU (Burnett et al., 2003; Agrawal et al., 2005). Two, we also used a compilation of historical information on the presence of coho salmon throughout the CCC-Coho ESU (Spence et al., 2005). The results of this synthesis compelled us to incorporate information on summer temperature and ecological indicators in our analysis, particularly in the course of determining which watersheds from the southern portion of the range of the CCC-Coho ESU to include in our analysis (see below).

2.3.1 Recent and historical distribution

Due to the general lack of data on abundance for coho salmon in the CCC-Coho ESU, efforts to assess the status of this ESU have relied heavily on comparisons of current distribution against historical distributions inferred from compilations of historical records of coho salmon in coastal basins (Weitkamp et al., 1995; Spence et al., 2001; West Coast Salmon Biological Review Team, 2005). Spence et al. (2005) have compiled information on historical presence of coho salmon in streams throughout the CCC-Coho ESU, beginning with a foundation assembled from previous efforts by Brown et al. (1994), Adams et al. (1999), and Leidy et al. (2005). In the course of this effort, Spence et al. (2005) identified a substantial number of new streams as potential coho-bearing streams based on information obtained from a broad spectrum of sources, reexamined the historical evidence for the presence of coho salmon in over 80 potential coho-bearing streams within the range of the CCC-Coho ESU, and classified each stream according to the relative strength of available documentation for the presence of coho salmon. For our purposes, we focus our attention most strongly on watersheds that include streams for which Spence et al. (2005) found either (1) direct evidence of coho salmon in the form of documented first-hand observations of coho salmon, or (2) direct assertions by professional fishery biologists familiar with the particular region that indicated a strong likelihood that coho salmon were present in a watershed.

2.3.2 Intrinsic potential

To complement historical information on the distribution of coho salmon throughout the range of the CCC-Coho ESU, we implemented a model developed by Burnett et al. (2003) to predict the intrinsic potential (IP) of stream reaches to exhibit habitat characteristics suitable for juvenile coho salmon; details regarding implementation of the model and assumptions that must be considered in interpreting the model output are provided by Agrawal et al. (2005) and reviewed in the Introduction (§1.5.1). 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 CCC-Coho and SONCC-Coho ESUs where an additional factor, water temperature, is likely to be a major determinant of habitat suitability. We therefore developed a secondary analysis, based on temperature to augment the results from the IP model for coho salmon in the CCC-Coho ESU (see below). To corroborate our interpretation, we also considered the distribution of redwood-conifer forests as an ecological indicator of conditions that favor suitable conditions for coho salmon.

Temperature mask. Summer water temperatures in the interior portions of some larger drainages in the southern part of the range of the CCC-Coho ESU (e.g. Russian River and tributaries to San Francisco Bay) 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 are not available for the NCCCRD. We do not incorporate temperature explicitly in the IP model for this reason, as well as to preserve comparability of the IP model as applied from the NCCCRD through coastal Oregon. 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 climatological threshold air temperature above which coho salmon generally do not occur. This analysis found that coho salmon were very rarely reported as present in watersheds where the lowest mean August air temperature in the basin exceeded 21.5°C (Agrawal et al., 2005). This temperature is comparable to the maximum tolerable water temperature for coho salmon reported by Eaton et al. (1995), and to the temperature for which Welsh et al. (2001) predicted that the likelihood that juvenile coho salmon will be present drops to nearly zero[3]. We therefore used 21.5°C as the threshold to modify results from the IP model by excluding habitat in areas that historically were likely to be consistently too warm for coho salmon (Plate 13).

This mask is intended to identify and eliminate areas that are thought to always be unsuitable for coho salmon. It is likely that areas not eliminated by the temperature mask might experience temperatures that exclude coho salmon in some years but not in others. In any case the suitability of habitats for coho salmon is likely to be degraded at temperatures lower than the threshold developed and implemented here (Hines and Ambrose, 2000; Sullivan et al., 2000; Welsh et al., 2001). However, it is highly likely that the effects of anthropogenic alteration of watershed function and riparian structure affect both stream temperature and the ability of coho salmon to tolerate the full suite of environmental stresses to which they are exposed. For this reason, although temperature might be useful in predicting current

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[3] A similar "exclusion" threshold can not be discerned from the work of Hines and Ambrose (2000) in northern California streams.

distribution, it is not clear how best to bring temperature into an IP model designed to predict the potential for suitable habitat to occur based primarily on geomorphological characteristics of a watershed. Nevertheless, efforts to extend the IP model for coho salmon in California as a predictor of historical distribution will undoubtedly benefit from appropriate inclusion of temperature. For our present purpose, we recognize the potential for our use of an inclusive temperature threshold for IP lead to overestimates of total habitat capacity, and account for this (and other potential biases; see §2.3.2, below) by using a higher threshold for viability-in-isolation to buffer against the error of classifying populations as viable that are not likely to have been so under historical conditions.

Regional variation in hydrology and potential bias in predicted IP for coho salmon. Stream hydrology is strongly influenced by a complex interaction between the amount and timing of precipitation and seasonal temperature patterns, both of which vary considerably over the range of the NCCCRD. We suspect that, despite the use of regional data to fit the simple hydrology model that underlies the IP model, the timing and amount of precipitation throughout the NCCCRD differ sufficiently from conditions observed in coastal Oregon for predictions of IP model to include non-negligible positive bias in at least some parts of the NCCCRD (for greater detail, refer to §1.5.1: Assumptions and the interpretation of the connectivity-viability model). It is not clear how variation in the seasonality of precipitation and temperature influence how IP translates into population carrying capacity, and we are unaware of data sets that would allow such a relation to be estimated. We therefore use a qualitative index of potential bias to guide post-hoc interpretation of analyses based on predictions from the IP model. We use the ratio of mean annual precipitation (MAP) to mean annual temperature (MAT) (each averaged at the watershed scale) as the underlying basis for this index[4], but also consider other information (e.g., finer scale information on MAP/MAT relative to the distribution of areas with high IP and ecological indicators) in evaluating how the IP model might be biased for each watershed (see Plate 6).

For coho salmon, we expect actual IP to be somewhat lower than IP predicted for the warmer, drier interior watersheds such as those tributary to the northern and southern portions of the San Francisco Bay-San Pablo Bay Estuary, and inland tributaries of the Russian River; in some of these areas, however, areas of groundwater discharge along fault-zones might offset this expected bias. The low-elevation coastal watersheds between the Russian River and Tomales Bay are likely to exhibit a similar bias, although in this region, we expect this bias to be of lower magnitude. IP predictions for watersheds draining the Santa Cruz Mountains and coastal watersheds just north of the Russian River are expected to exhibit a relatively small positive bias, and this bias is expected to decline to negligible levels as one moves north from Point Arena to the Lost Coast.

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[4] For watersheds in southern coastal Oregon (e.g., Pistol River, Chetco River, and Elk River), MAP/MAT is approximately 24 mm/°C. In the NCCCRD, this ratio ranges from below 4 mm/°C in the southeastern San Francisco Bay to over 16 mm/°C in northern, coastal watersheds. We use this ratio as the initial basis for assigning a bias index of "severe" ($\text{MAP/MAT} < 6\text{mm}/^\circ\text{C}$), "high" ($6\text{mm}/^\circ\text{C} \leq \text{MAP/MAT} < 9\text{mm}/^\circ\text{C}$), "moderate" ($9\text{mm}/^\circ\text{C} \leq \text{MAP/MAT} < 12\text{mm}/^\circ\text{C}$), or "low" ($12\text{mm}/^\circ\text{C} \leq \text{MAP/MAT} < 16\text{mm}/^\circ\text{C}$) to each watershed.

Ecological Indicators. One symptom of high temperatures and other factors that reduce the suitability of stream habitats for coho salmon is differences in the vegetation: coho salmon typically occur in coastal redwood and conifer forests rather than the oak savannahs that dominate some portions of the NCCCRD (Plate 2). For this reason, we also consider ecological indicators such as evidence for the presence of coastal redwoods or similar conifer forests as a measure of the likelihood that of coho salmon could persist in a given watershed, and as evidence that the environmental conditions do not deviate too far from those in coastal Oregon for the IP model to be entirely invalid. We also draw on results from our multivariate analysis of environmental characteristics to compare watersheds for which we have poor historical records pertaining to coho salmon to those for which we have good evidence that coho salmon occurred historically or currently.

Over much of the potential historical range of the CCC-Coho ESU, such indicators give us reasonable confidence that the predictions from the IP model, corrected by the temperature mask, adequately capture the historical distribution of coho salmon. For example, watersheds tributary to the western San Pablo and San Francisco bays that drain the eastern slopes of the coastal mountains (e.g., Corte Madera Creek in the north and San Francisquito Creek in the south), and watersheds that drain the hills directly opposite the Golden Gate (e.g., San Pablo, San Leandro, and Strawberry creeks.) exhibit environmental characteristics similar to those of watersheds along the open coast, and appear to have harbored historical populations of coho salmon. Many basins for which we have less compelling evidence for historical presence of coho salmon tend to be dominated by by vegetation consistent with drier, warmer conditions that we expect are less likely to provide consistently favorable conditions for coho salmon, and that are potentially more likely to exhibit conditions entirely unfavorable to coho salmon during drought conditions. However, some of these basins, such as the Napa River, also include areas where conditions appear favorable for coho salmon, including upper reaches of watersheds dominated by redwood/conifer forests, or have areas of groundwater discharge along fault zones that might maintain suitable juvenile habitat over a limited area. Note that coho salmon have been reported from a number of the watersheds that we conclude are unlikely to have exhibited environmental characteristics consistent with populations of coho salmon likely to have been viable-in-isolation (e.g., tributaries to the southern San Francisco Bay Leidy et al., 2005; Spence et al., 2005). None of these records provides strong evidence of consistent historical presence of or successful reproduction by coho salmon in these watersheds; however, historical records on the distribution of coho salmon are generally not available for periods prior to substantial anthropogenic disturbance in the San Francisco Bay region.

2.3.3 Synthesis of historical information and GIS model predictions

We combined information from historical records and predictions from the IP model (modified by the temperature mask) to develop a working list of putative populations for further consideration and analysis. Primarily this consisted of (1) using predictions of IP to offset the lack of records of historical presence or absence of coho salmon in many small coastal watersheds in which ecological conditions appear to be favorable for coho salmon, and (2) recognizing that assumptions of the IP model are likely to be violated in areas where overall ecological conditions are generally unfavorable for coho salmon.

We did not include in this set all of the smaller watersheds where coho salmon might be or once have been. Rather, we limited this set to those with $\geq$ 3.2 IP-km, or one-tenth the amount of habitat thought necessary to support a population that would be viable-in-isolation (see below). A few watersheds smaller than this threshold for which historical evidence of coho salmon is available are listed in Table 1.1 but were excluded from subsequent consideration.

Our greatest uncertainty regarding the historical distribution of coho salmon concerns the historical occupancy of San Francisco Bay tributaries and to a lesser degree, the historical presence of coho salmon in the upper portion of the Russian River basin. It is in these locations that we most strongly depend on a synthetic view of historical information and predictions of IP in the context of ecological indicators. Historical records for most San Francisco Bay tributaries are generally inconclusive regarding whether coho salmon were consistently observed, whether abundance at any one time was sufficiently high to suggest the existence of a persistent population, or whether coho salmon reproduced successfully. We are most certain that coho salmon historically occupied streams for which observations or museum collections of juvenile coho salmon strongly suggest successful reproduction (e.g., Arroyo Corte Madera del Presidio [S1], Corte Madera Creek [S2], and San Mateo Creek [S16]), and are less confident of historical presence in streams where historical use is based on the capture or observation of few adults.

Fortunately, the streams for which we have the strongest evidence for historical presence of coho salmon are those with environmental characteristics that most closely resemble conditions observed for coastal basins, which gives us some confidence that this set of streams did indeed offer habitats suitable for supporting persistent populations of coho salmon under historical conditions. These basins occur in three locations: (1) the coastal mountains of Marin County that drain into the northwest corner of San Francisco Bay estuary, (2) basins in a small region directly east of the Golden Gate that are more exposed to coastal conditions than other areas on the eastern shore of San Francisco Bay, and (3) basins draining the east side of Santa Cruz Mountains that separate San Francisco Bay from the Pacific Ocean. We emphasize, however, that because this area has experienced profound environmental changes since the arrival of Europeans, the extent of which was not rigorously documented, it is difficult to determine the true historical extent of environmental conditions that are consistently favorable to coho salmon. This uncertainty is further compounded by the fact that what early reports are available are compromised by the fact that, at the time, the taxonomy of Pacific salmon was still very much unsettled. Lacking further information, we simply discount the potential for habitat suitable for juvenile coho salmon in San Francisco Bay tributaries that do not belong to the set of basins with evidence of successful reproduction by coho salmon or environmental conditions that closely resemble those of coastal watersheds.

2.4 Population genetic structure of the CCC-Coho ESU

For coho salmon, we have available for our consideration three data sets based on neutral molecular markers that include multiple samples from the CCC-Coho ESU, each of which is reviewed below. Such data provide insight to the current population structure of the ESU, and so we must consider the effect that recent events—in particular, basin-to-basin transfers—might have had in causing the current pattern to deviate from the general characteristics the historical state. Therefore, we first review available information on artificial propagation of coho salmon with a focus on among-basin and among-ESU transfers to set the context for interpreting available genetic data to draw inference regarding the the historical structure of the ESU. In doing so, we look to genetic data to provide insight to population structure directly, and as a means of evaluating the validity of geographic analyses that follow.

2.4.1 Historical artificial propagation

Artificial propagation of coho salmon and out-of-basin stock transfers have occurred in California since the early 1900s. Records of these hatchery activities are incomplete for a number of reasons. First, many plantings of hatchery fish undoubtedly went unrecorded. Second, fish distribution records for many hatcheries have been lost or destroyed, leaving the US Bureau of Fisheries annual reports and California Fish and Game Fish Commission biennial reports as the primary sources of hatchery activities from the late 1800s to around 1950. These reports often fail to identify broodstock used at hatcheries around the state and typically report releases by county, rather than detailing specific interbasin transfers that occurred.

Despite these limitations to the historical record, it is evident that the history of artificial propagation and out-of-basin stock transfers of coho salmon in California differs in several ways from that of either Chinook salmon or steelhead. Whereas Chinook salmon were reared in large numbers in California for more than 25 years before the turn of the 20th century, there were no known releases of coho salmon into coastal waters within the CCC-Coho ESU (or elsewhere in California) until 1906, and stocking of coho salmon in the CCC-Coho ESU was infrequent prior to 1929. The numbers of hatchery coho salmon distributed within the state have been relatively small, but in many cases, the receiving population has been small or strongly depressed. Most of the major watersheds in the CCC-Coho ESU have received some out-of-basin or out-of-ESU transfers at some time in the past, however, with few exceptions, these introductions have been of short duration. Thus, the potential for lasting genetic consequences is uncertain as these two factors–the small size of the receiving population and the short duration of stocking activities–have opposing implications for the effect of among-basin transfers on population genetic structure.

Previous studies have reviewed, in more or less detail, historical information on artificial propagation and releases of juveniles originating from from out-of-basin or out-of-ESU broodstock, including transfers within or to populations in the CCC-Coho ESU (e.g., Brown et al., 1994; Weitkamp et al., 1995; CDFG, 2004). We conducted a similar review, from which we collated information focused solely on out-of-basin or out-of-ESU transfers to populations in the CCC-Coho ESU. Results of this review are summarized in Table 2.1. Rather than review this information here in detail, we note where it is relevant to interpreting available genetic data.

2.4.2 Genetic data sets and analyses

Allozyme data: Bartley et al. (1992)

Bartley et al. (1992) provided the only genetic data for the CCC-Coho ESU that was considered in

Table 2.1. Known out-of-basin and out-of-ESU releases of coho salmon fry and fingerlings into rivers and streams of the CCC-Coho ESU.

Basin*	**Period (Years)****	**Egg Source (Hatchery)*****	**Numbers****	**Reference**
Coastal streams	1969 (1)	unknown	10,000	CDFG Reg. 3
N. of Ten Mile River	1985 (1)	***Klamath R (via MRH)***	***6,000***	NRC (1996)
	1988 (1)	Noyo R (via MRH/WSH)	130,250	NRC (1996)
	1996-1998 (3)	Noyo R (most likely via MRH)	119,579	Harris (2001)
Ten Mile River	1955 (1)	unknown	892	CDFG Reg. 3
	1964,1975 (2)	***Alsea R, OR (via DSH/MSH)***	***242,860***	CDFG Reg. 3
	1965-1967 (3)	***Klatskanine R, OR (via DSH)***	***100,174***	CDFG Reg. 3
	1967, 1978 (2)	***Green R, WA (via DSH/MRH)***	84,344	CDFG Reg. 3
	1971-1976 (5)	Noyo R (via MRH/DSH)	180,598	NRC (1996) ; CDFG Reg. 3
	1975 (1)	unknown (poss. Klamath)	68,000	NRC (1996)
	1974-1979 (4)	***Trinity R (via MRH/TRH/MSH/DSH)***	***796,561***	NRC (1996) ; CDFG Reg. 3
	1976 (1)	***Skagit R (via MRH)***	***166,800***	CDFG Reg. 3
	1978 (1)	unknown (possibly WA; via CLH)	9,988	CDFG Reg. 3
	1983 (1)	Wisconsin (via TMH)	75,000	CDFG Reg. 3
	1983 (1)	***Hollow Tree, Eel R (via TMH)***	10,000	NRC (1996)
Pudding Cr	1959 (1)	unknown	43,192	CDFG Reg. 3
	1967 (1)	Noyo R (via MSH)	81,395	CDFG Reg. 3
Noyo River	1959 (1)	unknown	44,520	CDFG Reg. 3
	1962 (1)	Pudding Cr (via DSH	99,604	CDFG Reg. 3
	1963-1964 (2)	***Alsea R, OR (via DSH)***	***242,808***	CDFG Reg. 3
	1966 (1)	***Klatskianine R, OR (via DSH)***	100,033	CDFG Reg. 3
	1975 (1)	***Trinity R (via DSH)***	60,022	CDFG Reg. 3
	1980 (1)	unknown (via MRH)	103,668	NRC (1996)
	1981 (1)	***Mad R (via MRH)***	***40,970***	NRC (1996)
Big River	1959-1963 (2)	unknown (via DSH)	58,750	CDFG Reg. 3
	1965 (1)	Klatskanine R, OR (via DSH)	38,025	CDFG Reg. 3
	1974-1975 (2)	***Trinity R (via MSH/DSH)***	111,085	CDFG Reg. 3
	1970-1976 (6)	Noyo R (via DSH)	110,054	CDFG Reg. 3
	1963-1975 (3)	***Alsea R OR (via MSH/CCH/DSH***	***191,310***	CDFG Reg. 3
	1976 (1)	***Skagit R, WA (via MRH)***	***89,964***	CDFG Reg. 3
	1979 (1)	unknown (possibly WA; via CLH)	9,988	CDFG Reg. 3
	1981 (1)	***Hollow Tree, Eel R (via SRANC)***	***12,500 (E)***	NRC (1996)
Albion River	1969-1970 (2)	Noyo R (via DSH)	60,004	CDFG Reg. 3
Navarro River	1962 (1)	***Alsea R, OR (via DSH)***	20,020	CDFG Reg. 3
	1967 (1)	***Green R, WA (via DSH)***	40,014	CDFG Reg. 3
	1968-1976 (3)	Noyo R (via DSH/MRH)	143,812	NRC (1996) ; CDFG Reg. 3
	1979 (1)	unknown (poss. WA*; via CLH)	30,000	CDFG Reg. 3
Garcia River	1976 (1)	***Skagit R WA (via MRH/SOSHG)***	***75,375***	CDFG Reg. 3
	1976 (1)	unknown (via SOSGP)	38,000	NRC (1996)
	1977 (1)	***Trinity R (via MRH)***	***75,000***	CDFG Reg. 3
	1978 (1)	unknown (poss. Noyo or Soos Cr, WA)*	134,335	CDFG Reg. 3
	1978 (1)	***Soos Cr WA***	***2,800***	CDFG Reg. 3
	1979 (1)	unknown (poss. WA)*	43,400	CDFG Reg. 3

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Basin[*]	**Period (Years)**[**]	**Egg Source (Hatchery)**[***]	**Numbers**[**]	**Reference**
Garcia River	1981 (1)	unknown	6,000	CDFG Reg. 3
	1982-1988 (5)	Noyo R (via SOSGP/WSH/SFB)	183,153	NRC (1996) ; CDFG Reg. 3
Gualala River	1969-1973 (5)	Noyo R (via DSH)	135,030	CDFG Reg. 3
	1975 (1)	***Trinity R (via DSH)***	***10,005***	CDFG Reg. 3
	1988 (1)	Noyo R (via WSH)	54,000	NRC (1996)
	1996-1998 (3)	Noyo R (via MRH?)	45,280	Harris (2001)
Russian River[†]	1970 (1)	Noyo R (via MRH)	20,448	NRC (1996)
	1980-1989 (5)	***Klamath R/Iron Gate (via WSH)***	***415,730***	NRC (1996)
	1983-1988 (5)	unknown (via WSH)	359,349	NRC (1996)
	1984-1998 (7)	Noyo R (via WSH)	247,270	CDFG Reg. 3; CDFG HR
	1990 (1)	***Hollow Tree Cr, Eel R***	***7,998***	NRC (1996)
	1990-1991 (2)	Mixed stock[††] (via WSH)	31,650	NRC (1996)
	1991 (1)	Mixed stock[†††] (via WSH)	8,295	NRC (1996)
Tomales Bay and tribs (Lagunitas and Walker creeks)	1960 (1)	unknown	14,144	Seymour (2003)
	1962 (1)	***Alsea R, OR***	20,001	Seymour (2003)
	1963-1987 (11)	Noyo R (via ???/DSH/CCTU)	305,421	NRC (1996) ; Seymour (2003)
	1967 (1)	***Green R, WA***	***55,326***	Seymour (2003)
	1973 (1)	***Klaskanine R, OR***	***5,760***	Seymour (2003)
	1973 (1)	unknown (via DSH)	40,018	Seymour (2003)
	1977 (1)	***Skagit R, WA (via MRH)***	***15,411***	NRC (1996)
	1977 (1)	unknown (via CLH)	40,114	Seymour (2003)
	1979 (1)	unknown (via MRH)	35,000	Seymour (2003)
	1980 (1)	***Trinity R (via MRH)***	***49,603***	NRC (1996)
SF Bay and tribs	1930-1938 (5)	Scott Cr[‡] (via BRH/BCH)	8,200	Snyder (1932, 1934, 1936); Taft (1938, 1941)
	1974 (1)	Unknown	9,940	NRC (1996)
	1975 (1)	Noyo R (via MRH)	1,993	NRC (1996)
	1977 (1)	***Skagit R, WA (via MRH)***	***30,500***	NRC (1996)
Coastal tributaries south of SF Bay (Gazos, Waddell, Scott creeks)	1932 (1)	***Eel R (via FSH/BRH)***	15,000	Strieg (1991); CDFG (1998)
	1933-1935 (2)	***Prairie Cr (via BRH)***	44,597	Strieg (1991); CDFG (1998)
	1964 (1)	Noyo R	15,008	CDFG (1998)
	1977-1986 (10)	***Multiple stocks***[‡‡]	1,454,552	NRC (1996)
San Lorenzo River[‡‡‡]	1906-1910 (4)	Birdsview Station, WA (via BRH)	***400,000 (E)***[§]	Bowers (1906, 1907, 1908); Bowers (1909, 1910)
	1930-1932 (2)	***Eel R (via FSH/BRH)***	***60,500***	Strieg (1991); CDFG (1998)
	1933-1938 (5)	***Prairie Cr (via BRH)***	***145,960***	Strieg (1991); CDFG (1998)
	1963-1964 (2)	***Alsea R***	***48,225***	CDFG (1998)
	1964 (1)	unknown	32,000	CDFG (1998)
	1964-1976 (10)	Noyo R (CDFG)	230,385	CDFG (1998)
	1983 (1)	***Klamath R (via MRH)***	***19,770***[§§]	CDFG (1998)
	1984 (1)	Russian R (via MBSTP)	17,160	CDFG (1998)
	1986-1989 (3)	Noyo R (via MBSTP)	62,044[§§§]	CDFG (1998)
	1986-1994 (4)	Scott Cr/Big Cr (via MBSTP)	45,951	NRC (1996)
	1990 (1)	***Prairie Cr (via MBSTP)***	***34,500***	NRC (1996) ; CDFG (1998)
Aptos Cr./Soquel Cr.	1934, 1938 (2)	***Prairie Cr (via BRH)***	68,590	Strieg (1991); CDFG (1998)
	1963 (1)	unknown	10,500	CDFG (1998)

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Basin[*]	Period (Years)[**]	Egg Source (Hatchery)[***]	Numbers[**]	Reference
Unknown[¶]	1962-1973 (12)	unknown (via DSH)	6,162,445	NRC (1996)
	1968-1972 (5)	unknown (Via PCH)	685,820	NRC (1996)

[*]Blocks indicate distinct individual coastal basins or regional groups of small watersheds; streams named parenthetically are tributaries known to have received specified transfers. [**]Records from 1950 to the present. Plantings of fewer than 500 fish not listed. “(E)” indicates eggs delivered. [***]Hatchery abbreviations are as follows: BRH=Brookdale; BCH=Big Creek Hatchery; CCH=Cedar Creek; CCTU=CA Council of Trout Unlimited; CLH=Crystal Lake; DSH=Darrah Springs; MRH=Mad River; MSH=Mt. Shasta Hatchery; SFB=unknown; SOSGP=Save Our Salmon Garcia Ponds; SOSHG=Save Our Salmon Hutton Gulch; SRANC=Salmon Restoration Association of Northern California; TMH=Ten Mile; TRH=Trinity River; WSH=Warm Springs. [†]Warm Springs hatchery also released 609,351 fish identified as “Dry Creek” stock between 1982 and 1990 (11 years); these fish are likely progeny of Noyo R, Klamath R, and other stocks released into the basin. [††]Mixed stock included fish from Dry Creek (Russian River), Noyo River, and Hollow Tree Creek (Eel River). [†††]Mixed stock included fish from Dry Creek (Russian River) and Noyo River. [‡]Fish are presumed to be from Scott Creek; however, fish from Prairie Creek were also reared at BRH during this time, so fish released may have included fish from Prairie Creek. [‡‡]Releases from ocean salmon ranching operations near Davenport Landing. Egg sources included a variety of stocks from WA (Skagit, White Salmon, Cowlitz, Toutle, and U. of Washington), OR (Ore-Aqua, Alsea River), and CA (Klamath, Noyo). SSHAG (2003) reports that fish from BC and AK were also released.
[‡‡‡]San Lorenzo River also received 33,329 fish identified as San Lorenzo stock between 1988 and 1994 (via MBTSP). These fish are likely the result of previous stocking on out-of-basin fish. [§]Total is eggs delivered to Brookdale Hatchery; distribution information is unavailable, but it is probable that many fish were released into the San Lorenzo River. As this was a county-owned facility at the time, fry were most likely released into local waters. [§§]NRC (1996) reports this total as 11,650. [§§§]Reported as Russian River fish; however, fish are likely from Warm Springs Hatchery, which was using Noyo River coho for broodstock at the time. [¶]Release location listed as California coastal basins, Klamath River to Sacramento River. Some unknown proportion of fish likely released into rivers within the CCC ESU. Sources of fish not documented.

[‡‡‡]San Lorenzo River also received 33,329 fish identified as San Lorenzo stock between 1988 and 1994 (via MBTSP). These fish are likely the result of previous stocking on out-of-basin fish. [§]Total is eggs delivered to Brookdale Hatchery; distribution information is unavailable, but it is probable that many fish were released into the San Lorenzo River. As this was a county-owned facility at the time, fry were most likely released into local waters. [§§]NRC (1996) reports this total as 11,650. [§§§]Reported as Russian River fish; however, fish are likely from Warm Springs Hatchery, which was using Noyo River coho for broodstock at the time. [¶]Release location listed as California coastal basins, Klamath River to Sacramento River. Some unknown proportion of fish likely released into rivers within the CCC ESU. Sources of fish not documented.

the initial coastwide status review of the species (Weitkamp et al., 1995). These data consist of 23 polymorphic allozyme loci sampled from 27 locations in northern and central California, 18 of which are in the CCC-Coho ESU. A phylogeographic tree constructed by Bartley et al. (1992) showed little evidence for concordance between geographic and genetic structure in the CCC-Coho ESU; however, Bartley et al. (1992) noted that the data were limited by small sample sizes, that much of the information contained in the data was associated with rare or unique alleles, and that the history of inter-basin transfers might have obscured historical patterns[5]. These data, as a consequence of small sample sizes and a general lack of polymorphic loci, have limited power to differentiate among populations.

Microsatellite data: Hedgecock (2002)

Hedgecock (2002) report relationships among 33 pooled[6] samples of coho salmon based on genetic data collected for 7 microsatellite loci. Of these samples, those from Green Valley Creek (Russian River) and

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[5] Weitkamp et al. (1995) analyzed an expanded data set that included data from Bartley et al. (1992), but also found no strong evidence for concordance between geography and genetic population structure in the CCC-Coho ESU.

[6] These 33 samples were developed by pooling samples from an original total of 49 based on analyses of admixture, family structure, and homogeneity of samples within watersheds and sites. Please refer to Hedgecock (2002) for details regarding how pooling decisions were made.

Redwood Creek (Marin) were identified as genetic outliers on the basis of their extreme genetic distance from other samples in the data set, including samples from the SONCC-Coho ESU. Figure 2.1 presents results from analysis of the data sans these outlier samples. These results include some evidence of congruence between geography and population structure, such as robust distinction between the CCC-Coho ESU and the SONCC-Coho ESU and the distinct clusters of samples from streams north and south of San Francisco. However, evidence for concordance between genetic population structure and geography at smaller scales is less compelling among samples from basins north of San Francisco, and is not apparent within the group of samples from basins south of San Francisco (Figure 2.1).

Microsatellite data: Santa Cruz Laboratory

Recent work at the NOAA Santa Cruz Laboratory provides additional genetic data for evaluation of population structure of coho salmon in the CCC-Coho ESU (L. Gilbert-Horvath, et al., *unpublished data*). Population structure was examined with 18 microsatellite loci genotyped in approximately 4000 coho salmon comprising 41 samples, in which each sample represents a specific cohort sampled in a specific watershed. The data include samples from 17 basins, of which 14 span almost the entire range of the CCC-Coho ESU and include all known extant coho salmon populations south of the Russian River. The data set is based on samples of adult and juvenile coho salmon collected from 1998 to 2003 that vary with respect to cohort, life stage, and collection method. Therefore, genetic distances calculated from these data may include a component of variance due to sampling scheme or temporal and spatial variation in allele frequencies. Fortunately, the data set includes samples from multiple cohorts in the same watershed, which supports evaluation of year-to-year variation in genetic composition. The data set also includes samples collected from different tributaries of the same basin which provide insight to structure within a basin and to relative levels of temporal and spatial genetic variation in the ESU.

Initial examination of the population sample data found that several of the samples exhibit evidence of violations of the assumption of constant population size, such as substantially lower levels of variation and evidence of recent population bottlenecks, indicating that they were derived from just a few breeding individuals. The samples exhibiting these characteristics are those from Green Valley[7] and Dutch Bill creeks (tributaries to the Russian River), Pine Gulch[8], and a sample from Redwood Creek (Humboldt) that consists of individuals exhibiting unusual coloration. Non-equilibrium samples are included in some of the analyses below, but are excluded from other analyses (e.g., isolation-by-distance) in which departure from equilibrium confers the samples with undue leverage and obscures patterns apparent in the rest of the data set. Note that although the sample from Redwood Creek (Marin) also has a large genetic distance with respect to most samples in the data set, it does not exhibit strong evidence of a recent bottleneck.

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[7] In particular, samples from Green Valley Creek are noted for their highly divergent allele frequencies and significantly lower number of alleles. Numerous alleles observed at high frequencies in samples from Green Valley Creek are observed at very low frequencies in populations in which they do occur and not at all in others, and the set of populations with which the Green Valley samples share alleles is highly variable across loci. The genesis of these patterns is highly uncertain.

[8] Coho salmon in Pine Gulch represent a very recent recolonization event, with available evidence suggesting Redwood Creek (Marin) as the most likely source of colonists, so the status of this sample as an outlier is not surprising.

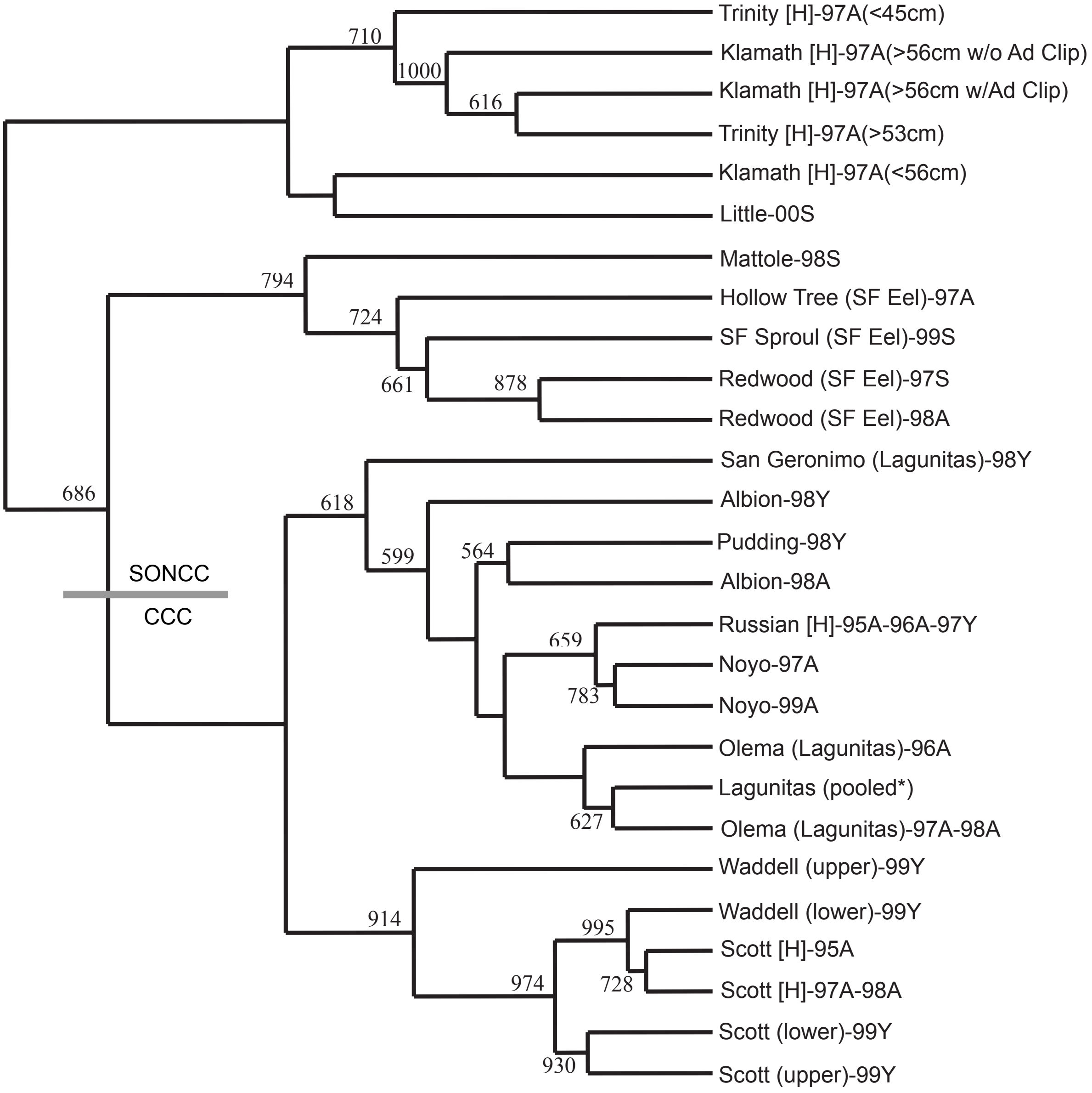

Figure 2.1. Unrooted UPGMA phylogram based on CSE Chord distances among 27 pooled populations of coho salmon from California after removal of outliers from Green Valley Creek (Russian River) and Redwood Creek (Marin). Numbers indicate nodes that occurred in more than 500 of 1000 bootstrap iterations. Redrawn from Figure 8 in Hedgecock (2002). The pooled Lagunitas sample includes all samples from the basin above the confluence of Olema Creek, save Arroyo San Geromino-98Y, which is included separately in the analysis.

All of the exact tests for population differentiation (Raymond and Rousset, 1995) proved significant, which provides evidence of substantial genetic structure within the CCC-Coho ESU.

Phylogeographic trees. Phylogeographic trees clearly distinguish the CCC-Coho ESU from the SONCC-Coho ESU (e.g., Figure 2.2), and analyses that exclude non-equilibrium outlier samples resolve this separation even more clearly (results not shown). Although the internal branches among clusters of samples from the CCC-Coho ESU (sans the outlier samples from the Russian River and Redwood Creek (Marin)) have low bootstrap support, the general structure of the tree is consistent across tree building methods. In most basins, including those on the Mendocino coast and Lagunitas Creek, all samples, regardless of cohort, form robust clusters with high bootstrap support. Samples from watersheds south of the Golden Gate (Scott, Waddell, Gazos, and San Vicente creeks) do not fit this pattern, however, nor do they disrupt the general concordance between geographical and population genetic structure apparent in Figure 2.2. The cluster of Redwood Creek (Marin) and Pine Gulch reflects the recent colonization of Pine Gulch by strays from Redwood Creek (Marin). We do not read much into the placement of samples from the Russian River and Redwood Creek (Marin)/Pine Gulch on this tree, as these samples are all very distant from one another and the rest of the data set[9].

Inferences regarding the role and structure of dispersal. The distribution of pairwise F_{ST} indicates hierarchical genetic population structure within the CCC-Coho ESU (Figure 2.3). Mean pairwise F_{ST} between samples from the same location but different cohorts is 0.0248. Among samples from different locations, however, mean pairwise F_{ST} between samples from different tributaries within the same basin is 0.0564, which is about half that observed between samples from different basins (0.1079). Since F_{ST} is inversely related to dispersal rate, these results suggest that temporal dispersal among broodyears, which is driven by variation in age-at-reproduction (most probably due to jacks), occurs at a greater frequency than dispersal within a basin, which is in turn more common than dispersal among basins.

Regression of pairwise F_{ST} on geographic distance yields a highly significant relationship between genetic and geographic distance that explains approximately 35% of the variation in the data (Figure 2.4). Such a pattern of isolation-by-distance supports the hypothesis that dispersal is a driving force underlying population structure of coho salmon in California and suggests that an equilibrium between dispersal and genetic drift, which maintains genetic variability, has developed over a long period of time[10].

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[9] Preliminary analyses of samples recently collected from Redwood Creek (Marin) offer a different result, in that the sample from Redwood Creek (Marin) falls squarely where it would be expected to on the basis of geography: between samples from Lagunitas Creek and Scott Creek. In any case, the grouping formed by the sample from Dutch Bill Creek in the Russian River basin with the samples from Redwood Creek (Marin) and Pine Gulch is not strongly supported by the bootstrap analysis. Indeed, although samples from Redwood Creek (Marin) cluster and from the Russian River are genetic distant from one another other, they also exhibit high genetic distances from from other samples, which can lead to spurious grouping near the base of long branches, a phenomenon known as long branch attraction (Felsenstein, 2003).

[10] Since isolation-by-distance is based on an assumption of equilibrium between dispersal and drift, we excluded samples identified as genetic outliers from this analysis. (Analyses for the complete data set still yield a significant isolation-by-distance relationship, but the percentage of variance explained by this relationship is substantially reduced.) Inferences regarding the role of migration may not hold for the populations represented by samples that show evidence of strongly violating equilibrium

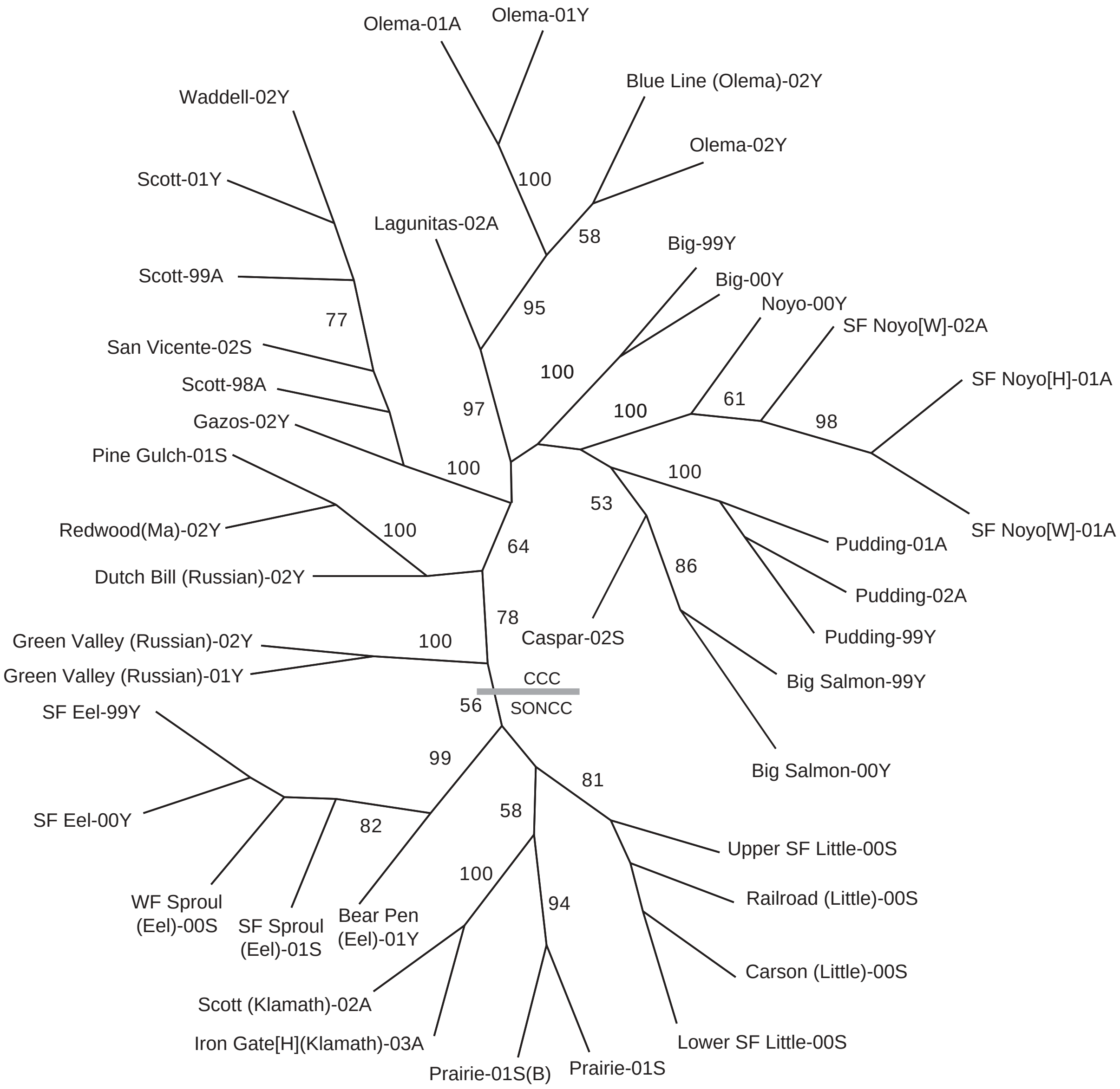

Figure 2.2. Bootstrap consensus tree for coho salmon in California. Consensus tree is based on trees constructed with a neighbor-joining algorithm (Saitou and Nei, 1987) using Cavalli-Sforza and Edwards (1967) chord distances calculated for 5000 data sets generated by bootstrap resampling from data for 18 microsatellite loci. Numbers on internal branches indicate the proportion (>50%) of trees in which the indicated node appeared. Samples are identified by stream, brood year, life stage (“A” indicates adult; “S” indicates smolt or outmigrating juvenile; “Y” indicates young-of-year juvenile), and where appropriate, as being collected from hatchery “[H]” or wild “[W]” populations. Parenthetical information indicates tributary basin (where relevant) or county.

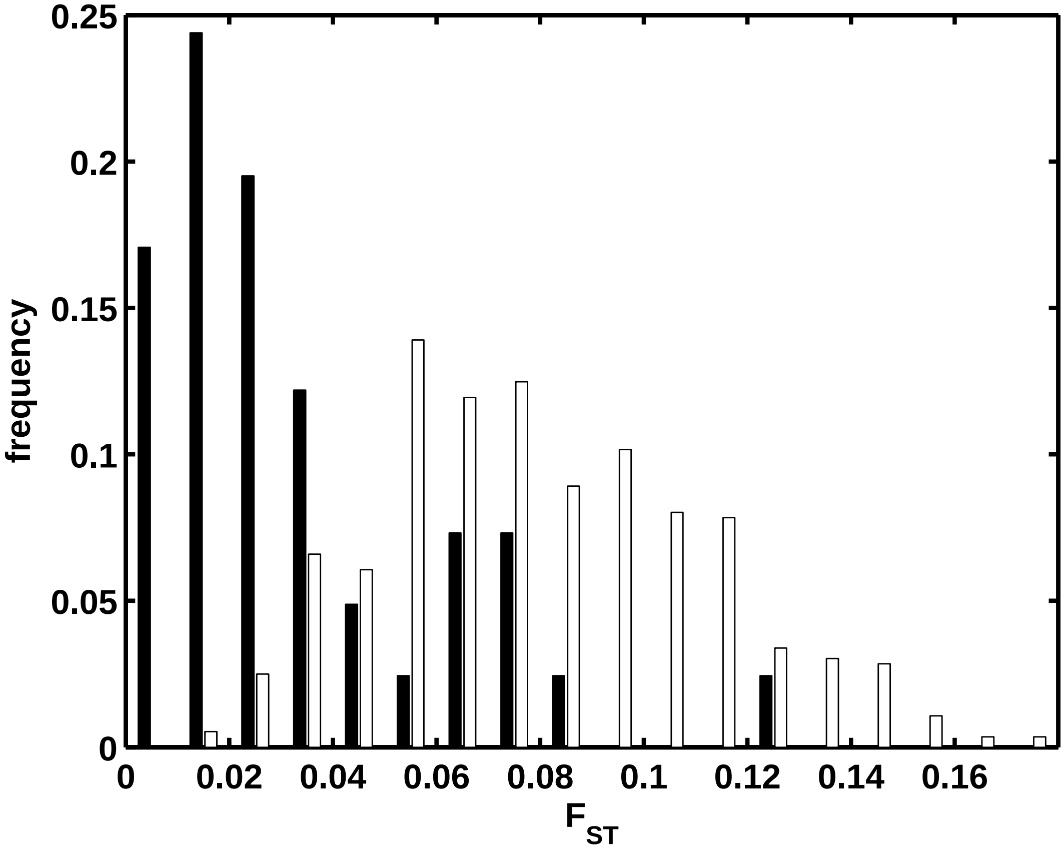

Figure 2.3. Frequency distributions of estimated pairwise F_{ST} among sites within the same basin (dark bars) and among sites in different basins (white bars) for coho salmon in coastal California.

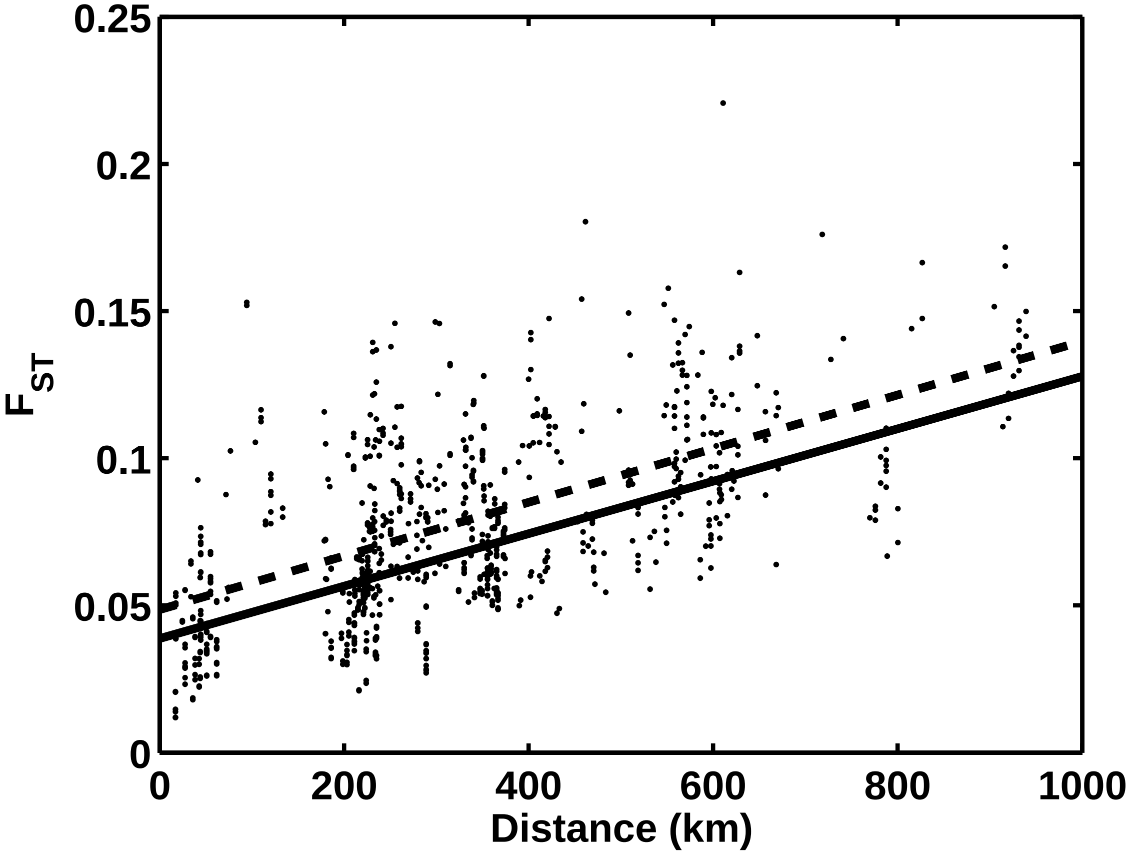

Figure 2.4. Isolation-by-distance in coho salmon based on pairwise F_{ST} and geographic distance for samples from the CCC-Coho ESU (solid line) and throughout coastal California (dashed line). For samples from different basins, geographic distance is calculated as the sum of the length of the coastal contour (omitting major bays such as the San Francisco Bay) between stream mouths and the upstream distance of each sample location. For samples from within the same basin, geographic distance is calculated as the distance "as-the-fish-swims" within the stream network.

Results of assignment tests are consistent with the other analyses in that they indicate a highly structured set of populations. The analysis correctly assigned most (>98%) individuals to their basin of origin, and also performed very well in assigning individuals to the correct tributary or cohort where such samples are available. Of those fish that were not correctly assigned to the population sample of origin, most misassignments (75%) were to other population samples from the same basin, either a different tributary or cohort. Of the 72 misassignments between basins, 72% occurred between Waddell, Scott, and San Vicente creeks, all of which are small streams adjacent to one another south of the Golden Gate.

Assignment tests were also used to determine the most likely source of a handful of juvenile coho salmon sampled in two tributaries of the Russian River for which a larger sample is not available (Mark West Creek and Redwood Creek, a tributary to Maacama Creek). These tests assigned each of these fish to the Green Valley population. Although it is difficult to infer much from such a small sample, these results suggest that dispersal of coho salmon within the Russian River can occur over substantial distances.

2.4.3 Synthesis of information on population genetic structure

Available genetic data describe a current population structure within the CCC-Coho ESU that is consistent with a plausible hypothesis for historical population structure. In particular, two analyses—the construction of phylogeographic trees (Figure 2.2) and examination of isolation-by-distance (Figure 2.4)–offer strong support for the role of dispersal among populations in generating concordance between geographical and population genetic structure. Among-basin transfers are likely to have altered the population genetic structure of coho salmon in the CCC-Coho ESU from its historical state, but it is not clear how strong an influence such transfers have had. In some cases, however, weak differentiation among populations suggests that such transfers have had some effect.

For example, inter-basin transfers are likely to have had at least some effect on population genetic structure of coho salmon south of the Golden Gate. Estimates of pairwise F_{ST}, which is inversely related to the rate of gene flow among populations, are substantially smaller among basins south of the Golden Gate than elsewhere in the CCC-Coho ESU, and a lack of strong differentiation among these populations underlies the apparently weak concordance between geographical and genetic structure in this region (Table 2.1 and Figures 2.1 and 2.2). These results are consistent with the potential effects of recent transfers of coho salmon from Scott Creek to other nearby small basins. Inter-basin transfers might have had a large effect in this area, since populations of coho salmon occupy small basins and have been at substantially depressed levels for much of the recent past. However, it is also quite likely that natural dispersal among populations contributes substantially to the relatively weak genetic structure observed in this region. Indeed, uniquely high rates of dispersal have been reported among populations of coho salmon in this area by Shapovalov and Taft (1954). Nevertheless, given the intensity of recent outplanting activities relative to the size of the recipient populations, it is difficult to conclude that the degree of connectivity implied by the genetic data is solely a consequence of naturally high rates of

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assumptions.

migration.

Likewise, genetic data suggest that coho salmon in basins along the Mendocino coast form a set of closely related populations, for which strong evidence of concordance between geography and genetic structure is lacking. This, too, probably reflects some effect of extensive basin-to-basin transfers of coho salmon in this area (with the primary source being Noyo River fish; Table 2.1). Although one data set includes patterns consistent with the plausible effects of inter-basin transfers (e.g., intermingling of samples from different basins apparent in Figure 2.1, Hedgecock, 2002), the data set expected to have greater resolving power consistently finds that samples from a basin group together within the regional cluster of samples from the Mendocino Coast (Figure 2.2). Therefore, it appears that historical inter-basin transfers have not entirely homogenized population genetic structure of coho salmon along the Mendocino coast, but the degree to which such transfers have reduced differentiation among populations is less clear.

In considering how to use genetic data to inform our analysis of population structure, we have placed less emphasis on samples taken from tributaries of the Russian River. These samples are outliers within the broader data set, and exhibit both strong departures from genetic equilibrium and evidence of recent, severe population bottlenecks. Coho salmon in the Russian River have been at extremely depressed levels for decades, so it is possible that the samples simply reflect a plausible outcome of a population bottleneck imposed on historical levels of genetic diversity. However, the basin has also received substantial transfers from numerous out-of-basin sources, large proportions of which are known to have originated in the Klamath River and Noyo River (Table 2.1). Such conditions greatly increase the potential for out-of-basin transfers to have a strong effect on the genetic composition of the receiving population. Thus, the mechanism or mechanisms that gave rise to these samples' characteristics is highly uncertain, and in any case, the utility of these samples for inferring the place of the Russian River in population genetic structure of the CCC-Coho ESU is highly suspect.

To summarize, we conclude that the isolation-by-distance relationship and overall concordance between geographic and population genetic structure over the range of the CCC-Coho ESU support the use of geographic structure as a template for interpreting population structure throughout the CCC-Coho ESU. We are less confident that recent genetic information resolves fine-scale historical structure, particularly given the potential effects of among-basin transfers and evidence for the consequences of such transfers in some areas (e.g., south of San Francisco). However, regions where known transfers appear to have blurred historical structure are insufficient to undermine our general conclusion regarding the utility of geography for evaluating historical population structure of coho salmon.

2.5 Geographical structure of the CCC-Coho ESU

Insight gained from the analyses of available genetic data generally support the assumptions of the geographic model for historical population structure in the CCC-Coho ESU. Therefore, we use the connectivity-viability model, which is outlined in general terms in the Introduction, to synthesize information on the relative size of historical populations of coho salmon and their distribution along the coast. In this section, we develop the inputs for the connectivity-viability model for populations in the

CCC-Coho ESU, and review results of the analysis in the context of the assumptions that underlie the model.

Translating IP-km into a proxy measure of population size

We use predictions from the IP model excluding areas with mean August air temperatures exceeding 21.5°C as the basis for our habitat-based population proxy, and (following the reasoning outlined in the Introduction) assume that carrying capacity of coho salmon populations is linearly proportional to the integrated length of accessible habitat within a watershed weighted by the intrinsic potential for habitat suitable for juvenile rearing (IP-km).

Viability-in-isolation threshold

We used a threshold value of 32 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 in Nickelson (Nickelson), and has been selected for consistency with the TRTs responsible for the Oregon Coast Coho Salmon ESU (Lawson et al., 2004) and Southern Oregon/Northern California Coast Coho Salmon ESU. Briefly, Nickelson (Nickelson) 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[11]. The model provides quantitative predictions of extinction probabilities, but such predictions of absolute extinction risk are highly sensitive to model parameters. In contrast, extinction probabilities consistently begin to rise sharply as available high quality habitat decreases below 24 km (Nickelson, Nickelson; Lawson et al., 2004). Recall that IP is the potential for habitat to be suitable, and does not explicitly predict the location of or potential for "high quality" or "low quality" habitat. Therefore, rather than attempt to define "high quality habitat" in terms of IP, we chose to set the threshold at 32 IP-km under the assumption that watersheds that satisfy this integrated measure of habitat potential will also include sufficient high quality habitat to satisfy the model-based criterion for viability-in-isolation, even in the face of potential temperature effects. Note that our selection of this threshold reflects a precautionary approach, in which we choose to err on the high side of a range of watershed sizes likely to span the actual average threshold[12] and to account in part

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[11] "High quality" habitat is defined as habitat capable of sustaining populations above a "critical threshold" (2.4 fish km^{-1}) through periods of poor marine survival (i.e., a smolt-to-adult survival rate of 3%) (Nickelson and Lawson, 1998).

[12] For context and in anticipation of how our population designations will comport with subsequent viability analysis, it is useful to consider what our habitat proxy might mean in terms of numbers of fish. Based on genetic arguments, (Allendorf et al., 1997) suggested a threshold of 2500 spawners per generation to avoid deleterious evolutionary dynamics within a population. Given the dominant life history of coho salmon in the CCC-Coho ESU, this leads to an approximate abundance of 833 spawners per year. Lawson et al. (2004) developed predictions of the capacity of Oregon Coast watersheds for smolt production as a function of IP and empirical maximum habitat capacities for juvenile coho salmon. These predictions compare very favorably to maximum adult abundance estimates based on historical catch records (Lawson et al., 2004). Based on the relation between abundance and IP, this viability-in-isolation threshold suggests that historically independent populations in coastal Oregon were capable of producing on the order 15,000 adults under extremely favorable conditions for ocean survival (e.g., a smolt-to-adult survival rate of 10%), and 1,500 adults under extremely poor conditions for ocean survival (e.g., a

for the effects of possible biases in our IP model[13]. By doing so, we concentrate on populations most central to ESU structure and persistence, and greatly reduce the likelihood that subsequent analysis and conclusions regarding ESU viability criteria will rest on populations that are not truly viable-in-isolation.

Note that populations occupying watersheds with less than 32 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 100s of years.

Consequences of hydrological bias in IP

Violations of the assumptions that underlie the IP model are expected to yield a latitudinal gradient of bias in the predictions of the IP model, largely as a consequence of regional differences in hydrology[14]. Such bias is expected to have its strongest influence on the position of a population along the viability-in-isolation axis, and a weaker effect on predictions of self-recruitment to a population. We consider these consequences below in our interpretation of results from the connectivity-viability model.

Connectivity-viability analysis

We used the connectivity-viability model outlined introductory chapter (§1.5.1) to examine how watershed size and location contribute to population structure in the CCC-Coho ESU. IP km calculated for areas not excluded by a temperature mask of mean August temperature ≥21.5°C, was used as a proxy for population size in the analysis[15]. We include all direct tributaries to the Pacific Ocean with ≥ 3.2 IP-km (10% of the viability-in-isolation threshold) in the connectivity-viability analysis for the CCC-Coho ESU, and treated the San Francisco Bay as a single population with a proxy size based on IP predictions for only those watersheds for which we concluded that the historical persistence of coho salmon has a reasonably strong likelihood (Table 1.1). Assuming that all populations within San Francisco Bay err in returning through the Golden Gate at the same rate, treating the tributaries of San Francisco Bay as a composite population has no effect on dispersal to nearby populations. We assume that migration from watersheds to the north of Punta Gorda can safely be neglected, and allow both northern and southern

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smolt-to-adult survival rate of 1%). Therefore, under the worst conditions, we conservatively expect spawner abundance to be approximately double that necessary to satisfy the criteria proposed by Allendorf et al. (1997). Note, however, that these predictions are relevant only during periods when the watershed characteristics are optimal for coho salmon, and are not expected to hold following a substantial disturbance to the watershed (Reeves et al., 1995). Furthermore, conversions between IP-km and abundance for the CCC-Coho ESU analogous to those developed for the Oregon Coast Coho Salmon ESU are likely to be confounded by hydrological bias as it affects predictions from the IP model. We therefore believe that our threshold as proposed, although intentionally conservative and precautionary, is consistent with likely conclusions from and application of viability analyses.

[13] See §2.3.2 and §2.3.2 regarding possible consequences of environmental differences between the NCCCRD and coastal watersheds to the north.

[14] For greater detail, refer to §2.3.2: 'Regional variation in hydrology and potential bias in predicted IP for coho salmon', above, and §1.5.1: 'Assumptions and the interpretation of the connectivity-viability model' in the Introduction

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

frontiers of the ESU's range to be open boundaries to emigration. As a measure of population independence, we compare self-recruitment against the fidelity rate to separate source from sink populations.

Figure 2.5 illustrates the position of coho salmon populations in viability-independence space for a range of dispersal functions. Thirteen populations fall robustly in the functionally independent quadrant of viability–self-recruitment space, and most other populations fall out as dependent populations. For the most part, these results are consistent with an intuitive assessment of the role of various populations in the ESU. For example, the importance of populations in the Russian River [42], the larger watersheds along the Mendocino and Sonoma county coasts (Ten Mile [23], Noyo [25], Big [30], Albion [32] and Navarro [34] rivers), and the larger watersheds south of San Francisco (San Gregorio Creek [54], Pescadero Creek [56] and San Lorenzo River [63]) is clear. However, given the likelihood that predictions from the IP model exhibit a positive bias in various regions of the CCC-Coho ESU, there are a few populations for which it is likely that the true historical status lies closer to the dependent quadrant than is predicted in this analysis. For example, it is likely that predictions from the IP model for moderately-sized watersheds between the Russian River and the Golden Gate (e.g., populations in Salmon Creek (S) [43], Americano Creek [45], Stemple Creek [46], and tributaries to Tomales Bay [47]) include significant potential bias, and these populations are therefore likely to have been more clearly in the potentially independent quadrant, at best. The habitat proxy for Soquel Creek [64] is also likely to be somewhat too large, although the bias in this case is expected to be smaller than for the previous group. More importantly, self-recruitment to the population of coho salmon in Soquel Creek [64] is inflated as a consequence of its position near the edge of the range of the CCC-Coho ESU; it receives few immigrants from the south, yet dispersal from the San Lorenzo River [63] is not constrained by the ESU boundary. Thus, Soquel Creek [64] population is more likely to have been smaller and received more immigration than predicted in this analysis, which would place it in the dependent quadrant of Figure 2.5. Note that results from this analysis are not strongly sensitive to variation in the size of the San Francisco Bay population within the range of IP-km associated with plausible scenarios of historical occupancy.

Figure 2.6 provides an example of model results for the contribution of source populations to sink populations within the ESU[16]. The dominant role of the Russian River as a source population is apparent south of Point Arena, whereas there is no single dominant source population north of Point Arena, or south of San Francisco (Figure 2.6).

2.6 Abundance and Population Dynamics

Spence et al. (2001) and Spence and Bjorkstedt (2005) summarize available information on abundance and distribution of coho salmon in the CCC-Coho ESU. No rigorous abundance estimates are available to support analysis of demographic correlation among putative populations in this ESU.

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[16] We consider potentially independent populations as sources as well as sinks in this analysis because they exceed the viability-in-isolation threshold and are potentially capable of influencing the dynamics of smaller populations nearby, and as sinks because they are affected by immigration from still larger, functionally independent populations.

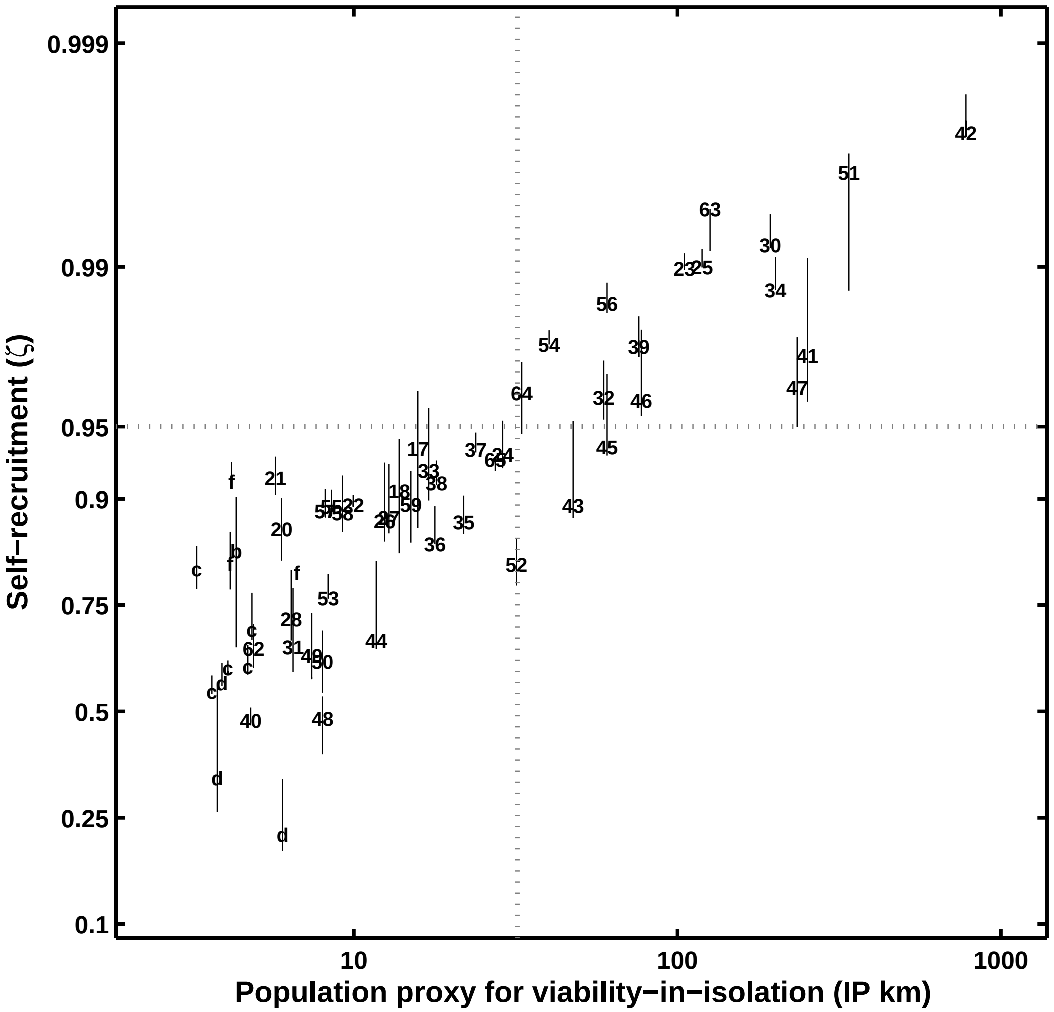

Figure 2.5. Structure of CCC-Coho ESU based on predictions of viability-in-isolation (based on predictions from the IP model, excluding areas where mean August air temperature exceeds 21.5 °C, and self-recruitment. Viability-in-isolation is based on a population proxy derived from a GIS model for habitat potential that accounts for areas from which coho salmon are likely to be excluded by high summer temperatures (see text). Self-recruitment is a function of relative population size, spatial arrangement of ocean-entry points, and width of the dispersal function. Populations are identified by number. 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 -0.10 km; identification numbers indicate self-recruitment for δ = -0.05 km. Horizontal grey 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 grey dotted line indicates threshold for viability-in-isolation at 32 IP-km (see text for details). The San Francisco Bay population [51] includes only those watersheds for which the historical presence of coho salmon is highly probable.

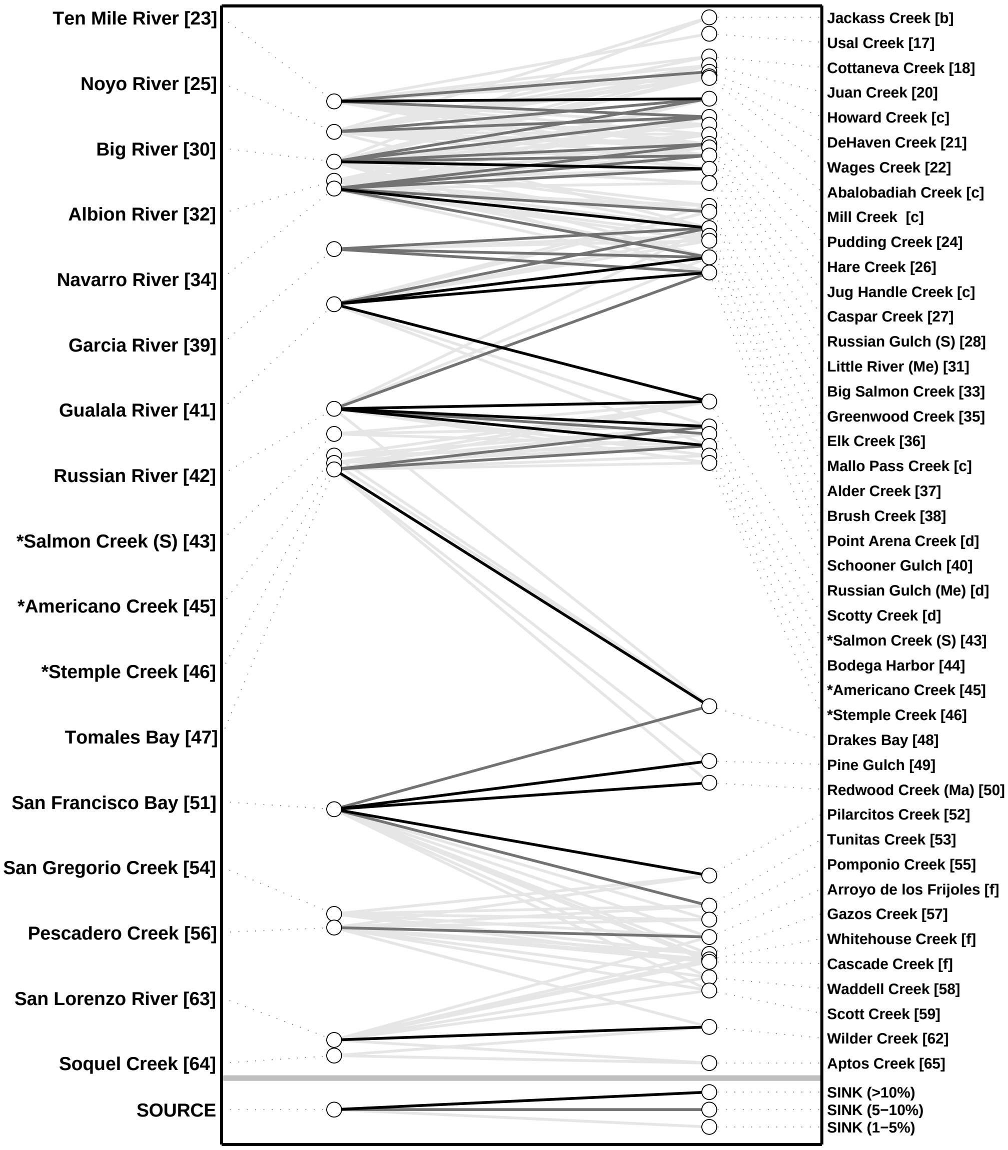

Figure 2.6. Connectivity within the CCC-Coho ESU, as measured by the contribution of source populations (on the left) to sink populations (on the right) as a function of the proportion (in excess of 1%) of the spawning run to a sink population contributed by each source population. Connectivity based on an exponential dispersal function with the decay parameter set to -0.05 km. Distribution of populations reflects distance along the coastline. Assignment of populations as source (functionally and potentially independent) or sink (potentially independent and dependent) populations is based solely on comparison of IP-km (excluding areas where mean August air temperature exceeds 21.5 °C) to our viability-in-isolation threshold of 32 IP-km. Potentially independent populations are indicated by an asterisk and included as source populations and sink populations. (Self-recruitment for potentially independent populations is not displayed.)

2.7 Life history variation

We examined life history information summarized in previous Status Reviews (Weitkamp et al., 1995; Spence et al., 2001; Spence and Bjorkstedt, 2005), an concluded that none of this information was useful for discerning population structure in the CCC-Coho ESU.

2.8 Historical population structure of the CCC-Coho ESU

Table 2.2 summarizes our conclusions regarding the historical population structure of coho salmon within the CCC-Coho ESU. These conclusions depend almost entirely on (1) results from the connectivity-viability analysis to putative populations, interpreted in light of potential biases in the IP model for juvenile coho salmon, and (2) analyses of available genetic data. In combining insights from these two sources of information, it is important to recognize where the two approaches potentially diverge. In particular, while we typically assume a consistent pattern of dispersal in generating predictions of self-recruitment, the genetic data offer some indication that rates of exchange may vary along the coast. Whether this is a consequence of artificial propagation and inter-basin transfers is not clear.

Russian River

We conclude that coho salmon in the Russian River existed in two populations: a functionally independent population that spawned in watersheds in the lower basin where coastal climate moderated summer temperatures, and a dependent population that occupied tributaries in the northwest corner of the basin. Coho salmon in the Russian River [41] were once sufficiently abundant to support a commercial in-river fishery, which is consistent with the extent of areas with high IP for spawning and rearing habitat in the lower basin (Steiner Environmental Consulting, 1996, Plate 13). Thus, despite the potential for positive bias in our interpretation of IP, we are confident that the historical population of coho salmon in the Russian River was sufficiently large to have been viable-in-isolation. Historical records include observations of coho salmon in the upper Russian River basin, particularly tributaries of of the mainstem Russian River (above the confluence of the East Fork Russian River) that drain the east slope of the coastal mountains; however, IP-km for these areas do not satisfy our threshold for viability-in-isolation. Although evidence is available regarding the existence distinct “long-run” and “short-run” coho populations in other large basins elsewhere in California (e.g., the Eel and Klamath rivers), we think it unlikely that a coho salmon consistently occupied the upper part of the Russian River. Such a population would have been almost entirely dependent on immigrants from much lower in the basin and it is highly likely that tributaries in the upper Russian River basin frequently were too warm or dry for coho salmon, and thus did not offer reliably favorable conditions for completion of the coho salmon life cycle. Thus, we think that tributaries in the upper Russian River basin might have harbored an ephemeral population of coho salmon: a population that was occasionally recolonized by dispersal from the lower basin during periods of exceptionally favorable conditions, but that was incapable of consistently enduring intervening periods of less favorable conditions.

Table 2.2. Historical population structure of coho salmon in the CCC-Coho ESU.

Population	IP km	IP Bias Index	Self-recruitment	Historical Population Status
Jackass Creek [b]	4.33	low	0.840	dependent
Usal Creek [17]	15.77	low	0.938	dependent
Cottaneva Creek [18]	13.80	low	0.907	dependent
Juan Creek [20]	5.98	low	0.868	dependent
Howard Creek [c]	3.27	moderate	0.814	dependent
DeHaven Creek [21]	5.72	moderate	0.918	dependent
Wages Creek [22]	9.95	low	0.894	dependent
Abalobadiah Creek [c]	4.08	low	0.611	dependent
Ten Mile River [23]	105.14	moderate	0.990	**Functionally Independent**
Mill Creek [c]	4.70	low	0.615	dependent
Pudding Creek [24]	28.86	moderate	0.935	dependent
Noyo River [25]	119.27	moderate	0.990	**Functionally Independent**
Hare Creek [26]	12.44	moderate	0.878	dependent
Jug Handle Creek [c]	4.84	moderate	0.701	dependent
Caspar Creek [27]	12.84	moderate	0.881	dependent
Russian Gulch (Me) [28]	6.40	moderate	0.723	dependent
Big River [30]	193.66 (194.76)	high	0.992	**Functionally Independent**
Little River (M) [31]	6.49	moderate	0.661	dependent
Albion River [32]	59.18	high	0.963	**Functionally Independent**
Big Salmon Creek [33]	17.04	high	0.923	dependent
Navarro River [34]	201.04 (232.51)	high	0.987	**Functionally Independent**
Greenwood Creek [35]	21.85	high	0.876	dependent
Elk Creek [36]	17.82	high	0.849	dependent
Mallo Pass Creek [c]	3.64	high	0.551	dependent
Alder Creek [37]	23.81 (23.87)	high	0.937	dependent
Brush Creek [38]	18.00	high	0.914	dependent
Garcia River [39]	76.04 (105.25)	high	0.978	**Functionally Independent**
Point Arena Creek [d]	3.91	high	0.573	dependent
Schooner Gulch [40]	4.80	high	0.476	dependent
Gualala River [41]	252.18 (277.90)	high	0.975	**Functionally Independent**
Russian Gulch (S) [d]	6.02	moderate	0.219	dependent
Russian River [42]	779.41 (1661.99)	high	0.997	**Functionally Independent**
Scotty Creek [d]	3.78	high	0.334	dependent
Salmon Creek (S) [43]	47.60	high	0.894	dependent
Bodega Harbor [44]	11.72	high	0.676	dependent
Americano Creek [45]	60.63	high	0.939	dependent
Stemple Creek [46]	77.36	high	0.961	dependent
Tomales Bay [47]	234.52		0.966	
Walker Creek [TB1]	103.68	high		***Potentially Independent******
Lagunitas Creek [TB2]	114.83	high		**Functionally Independent**
Drakes Bay [48]	8.00	high	0.4.83	dependent
Pine Gulch [49]	7.41	high	0.640	dependent
Redwood Creek (M) [50]	7.99	high	0.626	dependent
San Francisco Bay [51]	339.18** (669.26)		0.996	

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Population	IP km	IP Bias Index	Self-recruitment	Historical Population Status
Arroyo Corte Madera del Presidio[S1]	10.55	high		dependent
Corte Madera Creek [S2]	35.18	high		dependent
Miller Creek [S3]	31.02	high		dependent
Novato Creek [S4]	73.98	severe		dependent
Petaluma River [S5]	233.01	severe		dependent
Sonoma Creek [S6]	227.10	high		dependent
Napa River [S7]	491.76 (500.04)	severe		dependent
San Pablo Creek [S8]	18.40	severe		dependent
San Leandro Creek [S9]	21.56	severe		dependent
San Lorenzo Creek [S10]	58.94	severe		dependent
Alameda Creek [S11]	105.52 (435.60)	severe		dependent
Coyote Creek [S12]	182.84 (338.98)	severe		dependent
Guadalupe River [S13]	153.64	severe		dependent
Stevens Creek [S14]	23.28	severe		dependent
San Francisquito Creek [S15]	46.94	severe		dependent
San Mateo Creek [S16]	42.09	severe		dependent
Pilarcitos Creek [52]	31.79	high	0.820	dependent
Tunitas Creek [53]	8.33	high	0.763	dependent
San Gregorio Creek [54]	40.12	high	0.978	dependent
Pomponio Creek [55]	8.52	high	0.893	dependent
Pescadero Creek [56]	60.62	high	0.985	**Functionally Independent**
Arroyo de los Frijoles [e]	6.67	high	0.808	dependent
Gazos Creek [57]	8.16	high	0.888	dependent
Whitehouse Creek [e]	4.19	high	0.915	dependent
Cascade Creek [e]	4.15	high	0.822	dependent
Waddell Creek [58]	9.23	high	0.886	dependent
Scott Creek [59]	15.00	high	0.895	dependent
San Vicente Creek [60]	3.12	high	—	dependent
Wilder Creek [62]	4.90	high	0.657	dependent
San Lorenzo River [63]	126.19	high	0.994	**Functionally Independent**
Soquel Creek [64]	33.03	high	0.964	dependent
Aptos Creek [65]	27.35	high	0.931	dependent

[*] Status of historical population in Walker Creek is especially uncertain due to environmental and ecological conditions; this population might have been dependent (mostly on the population of coho salmon in Lagunitas Creek) under historical conditions. [**]IP km for San Francisco Bay is conservative, and includes only those watersheds for which there is reasonable support for persistent presence of coho salmon.

Variation in environmental conditions within the lower Russian River basin, especially between tributaries near the coast (e.g., Austin Creek) and those further inland (e.g. Mark West and Maacama creeks), raises the possibility that coho salmon might have existed in multiple populations in the Russian River under historical conditions. However, without better information on where coho salmon occurred, it is difficult to determine whether (1) distributions were sufficiently discontinuous to allow for differentiation, or (2) spawning groups occupied areas that varied substantially in their environmental characteristics. Furthermore, we have little information with which to evaluate historical patterns of dispersal of coho salmon within the Russian River[17]. Given this level of uncertainty, it is essentially impossible to differentiate between single- and multiple-population hypotheses. Rather than exacerbate this uncertainty by making assumptions regarding where breaks between putative populations are located, we choose to treat coho salmon in the lower Russian River basin as a single, functionally independent population and to highlight the role of spatial structure and diversity within this population.

San Francisco Bay

Evaluating the historical population structure of coho salmon in tributaries of San Francisco Bay is especially difficult due to a lack of information on historical conditions. At the most basic level, despite extensive efforts to compile historical records, (e.g., Leidy et al., 2005; Spence et al., 2005), our understanding of the historical distribution of coho salmon in these watersheds is somewhat limited, and for a number of watersheds, observations of coho salmon are such that whether they indicate a self-sustaining population or a chance occurrence remains ambiguous. This situation is further exacerbated by uncertainty regarding the pristine condition of the watersheds themselves, and uncertainty regarding the influence of environmental conditions on the distribution of coho salmon in these watersheds, which lie inland from the southern part of the species's coastal range.

Results from our IP model are of limited use in offsetting these uncertainties. Predictions from the IP model are likely to include substantial positive bias relative to the actual historical potential for habitat suitable for juvenile coho salmon. This bias is likely to vary within the Bay area in ways that are not captured by the temperature mask, with relatively lower bias expected in the Santa Cruz Mountains and relatively stronger bias expected in the northern and southeastern tributaries to the San Francisco Bay-San Pablo Bay estuary. However, although we must consider the predictions of the IP model to be biased on the basis of model structure and inputs, we must be equally cautious in assuming that (informally) “bias-corrected” IP is a better predictor of historical reality. Groundwater discharge associated with geological fault zones (a mechanism not accounted for in the IP model) might have been sufficient to maintain cool summer flows in extensive parts of some watersheds that might otherwise appear unsuitable for coho salmon when examined at a coarse scale (Leidy et al., 2005, and see below).

The original (historical) distribution of coho salmon is a central basis for evaluating historical population structure. We therefore first present our conclusions regarding the likely historical distribution of coho salmon in the region. With these conclusions serving as the template, we subsequently discuss our reasoning and conclusions regarding historical population structure.

Historical distribution of coho salmon in tributaries of San Francisco Bay We are most confident that, under historical conditions, coho salmon were consistently present in watersheds in three relatively small areas around the estuary: (1) small watersheds in Marin County just north of the Golden Gate,

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[17] Samples from two locations in the Russian River (Dutch Bill Creek and Green Valley Creek) are very different from one another, but the nature of these samples and the recent history of coho salmon in the basin prevents us from drawing too much from these data. In contrast, assignment tests showed that a handful of juvenile coho salmon sampled in Mark West Creek and Redwood Creek, a tributary to Maacama Creek, were most similar to coho salmon in Green Valley. Although it is difficult to infer much from such a small sample, these results suggest that dispersal of coho salmon within the Russian River can occur over substantial distances.

(2) watersheds that drain the Berkeley and Oakland hills along the eastern shore of the Bay directly across and north from the Golden Gate, and (3) watersheds draining the eastern slopes of the Santa Cruz Mountains south of what is now San Francisco. In all three cases, recent evidence of successful reproduction by coho salmon supports the conclusion that coho salmon were historically present in these areas. Moreover, the environmental characteristics of these three areas, especially the eastern slope of the Santa Cruz Mountains, are more or less similar to those of coastal basins, and we can therefore have somewhat greater confidence in the validity of IP predictions in these areas. Of these three areas, however, we are less certain that populations of coho salmon in the Berkeley/Oakland hills would have been able to persist through periods of extended drought, as these watersheds are lower in elevation and receive less precipitation than the watersheds that drain the coastal mountains.

We are also reasonably confident that persistent populations of coho salmon were not present in watersheds that drain into the southeastern portion of San Francisco Bay (e.g., Alameda Creek and Coyote Creek). Adult coho salmon have been captured in these watersheds (Leidy et al., 2005; Spence et al., 2005). Leidy et al. (2005) report that habitat suitable for juvenile rearing occurs in these basins, including areas influenced by groundwater discharge. However, these watersheds differ substantially from coastal watersheds where persistent populations of coho salmon are known to have existed, and in particular are warmer and receive less precipitation. We believe that these watersheds are likely to have supported coho salmon only intermittently, and that such populations would have been highly susceptible to extended periods of drought. Consequently, we are hesitant to accept reports of adult coho salmon being captured in these streams as evidence of persistent populations.

In contrast to these two extremes, we are somewhat less confident in drawing conclusions regarding the historical presence and status of coho salmon in the northern tributaries to San Pablo Bay (e.g., Petaluma River, Sonoma Creek, and Napa River) and in Guadalupe River, a tributary to southern San Francisco Bay. Historical records of coho salmon in these three basins are ambiguous as to whether persistent populations of coho salmon occupied these watersheds (Leidy et al., 2005; Spence et al., 2005). Leidy et al. (2005) report that habitats apparently suitable for coho salmon exist in the Napa River and Sonoma Creek basins, and corroborate this conclusion with evidence that in some areas, vegetation communities commonly associated with coho salmon are present as well as microclimates and extensive zones of groundwater discharge that might suffice to maintain cool water temperatures. Similar surveys in Guadalupe River also identify areas in the eastern Santa Cruz Mountains with habitat conditions that appear suitable for coho salmon Leidy et al. (2005); however, the current vegetation community is less similar to that commonly associated with coho salmon in coastal basins. The Napa River, Sonoma Creek, and Guadalupe River watersheds all include areas that receive average amounts of precipitation similar to those observed in tributaries with a more coastal character (e.g. San Mateo Creek) and greater than observed in the drier watersheds in the southeastern San Francisco Bay (e.g., Alameda Creek) (Leidy et al., 2005, and see Plate 4). These characteristics suggest that these watersheds would therefore continue to provide suitable habitat for juvenile coho salmon over a broader range of climatic variation than would Alameda and Coyote creeks, although the northern watersheds would show greater variability as a consequence of being that are further removed from direct influence of maritime climates.

Evaluation of historical population structure. We believe that the scale and environmental heterogeneity of the San Francisco-San Pablo Bay provide a reasonable basis for assuming that dispersal among historical populations of coho salmon was sufficiently limited to allow for population differentiation. Dispersal among such populations was probably greater than among analogous coastal populations for a number of reasons: (1) these populations enter and leave the ocean at a more-or-less common location, (2) substantial freshwater inputs consistently covered the Estuary with a substantial layer of freshwater, and (3) adjacent watersheds exhibit similar environmental characteristics and in some cases, drained through common wetlands. Environmental similarities at a regional scale also appear in coastal regions where populations enter and exit the ocean along the open coast. We therefore conclude that it is likely that coho salmon exhibited sufficient fidelity to natal watersheds to maintain distinct populations such that coho salmon in separate tributaries to the Estuary constitute separate populations, and we consider historical population structure accordingly[18]

In this framework, synthesis of available historical information and environmental data suggests a plausible model for the historical status of coho salmon in tributaries to San Francisco Bay and San Pablo Bay that is consistent with the position of the estuary along the coastal-inland boundary of the species' range. Under this model, we expect that relatively that relatively few watersheds consistently provided conditions that would support successful reproduction by coho salmon. We are most confident that four watersheds, Arroyo Corte Madera del Presidio [S1], Corte Madera Creek [S2], San Francisquito Creek [S15], and San Mateo Creek [S16], supported persistent populations of coho salmon, but remain very uncertain whether any of these watersheds provided sufficient habitat to support a population likely to have been viable-in-isolation. All four of these watersheds drain the eastern slope of coastal mountains, and are among the most likely to receive immigrants from populations of coho salmon in watersheds along the open coast.

In contrast, other tributaries to the San Francisco-San Pablo Bay estuary are likely to have provided extensive areas of suitable habitat for coho salmon on a less consistent basis. This is not to say that coho salmon did not occupy these basins or that these watersheds lacked the capacity to support a sizeable population coho salmon during periods of favorable conditions. However, populations of coho salmon in these watersheds are likely to have been more susceptible to environmental variation, particularly in the form of drought. Even if environmental variability, in contrast to mean conditions, were relatively constant over space, these populations would have experienced unfavorable conditions with greater frequency, duration and intensity. Thus, we conclude that populations of coho in watersheds other than the four western tributaries mentioned above were especially dependent on immigration for continued persistence, and possibly for recolonization. Within this general conclusion, we note that (1) Napa River [S7], Sonoma Creek [S6], and Guadalupe River [S13] are perhaps more likely than other basins to maintain a cool water refugium for coho salmon due to watershed structure (east-west running tributaries) or fault-related groundwater discharge, and (2) watersheds east of the Golden Gate might also have been more resilient to drought conditions due to more direct exposure to maritime climates.

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[18] If the assumptions that underlie treatment of coho salmon in each watershed as a distinct population is not correct, then our analysis should be interpreted in terms of more-or-less distinct units within regional populations, with subsequent consideration of how spatial structure contributes to population viability.

Even under historical conditions, we think it unlikely that coho salmon would have persisted over long time scales in San Francisco Bay without immigration from coastal populations. However, it is possible that dispersal among tributaries of San Francisco Bay–particularly among the four tributaries that drain the coastal mountains–yielded a degree of mutual dependence that rendered coho salmon in San Francisco Bay, as a whole, somewhat less dependent on dispersal from coastal populations that would have been expected were these four tributaries each more isolated. In part this conjecture is motivated by the lack of evidence of large populations in coastal watersheds in close proximity to the Golden Gate, and the prediction that immigration from the four largest potential source populations (Russian River, Pescadero Creek, San Lorenzo River, and perhaps the populations in Tomales Bay) is not likely to have had a strong influence on the dynamics of coho salmon populations in tributaries of San Francisco and San Pablo bays. The hypothesis of mutual dependence is also motivated by the fact that we are unable to identify unambiguously a tributary to San Francisco Bay or San Pablo Bay capable of supporting a functionally independent population of coho salmon. Moreover, under our assumption that dispersal among populations within the Estuary is higher than among similar populations along the coast, we expect that it is less likely for individual populations of coho salmon in San Francisco Bay tributaries satisfied an absolute threshold for independence. Note that we do not suggest that coho salmon in San Francisco Bay functioned as a classic metapopulation in which populations randomly go extinct and empty patches are randomly recolonized. Rather, it seems most plausible that (1) populations in tributaries draining the coastal mountains west of San Francisco and San Pablo bay exhibited a substantial degree of mutual dependence, which increased their ability to persist despite the lack of a dominant population (i.e., coho salmon might have existed as a "patchy population" *sensu* Harrison and Taylor (1997), and (2) this set of populations acted as the major source of immigrants or colonists for tributaries in less favorable regions of the San Francisco Bay basin.

As a final note, while we believe that the preceding conclusions are plausible and do not depart substantially from historical reality, we strongly emphasize the uncertainty that underlies our conclusions and the information on which they rest.

Coastal basins: Lost Coast to Point Arena

Based on the information and analyses discussed above, we conclude that the historical population structure of coho salmon along this stretch of coast included a series of functionally independent populations in the larger watersheds (Ten Mile [23], Noyo [25], Big [30], Albion [32], Navarro [34], and Garcia [39] rivers) nested among a set of mostly dependent populations in smaller watersheds (Table 2.2)[19] Our conclusions reflect the geography of this stretch of coastline, as synthesized in the connectivity-viability model (Figure 2.5). Despite the potential effects of inter-basin transfers (primarily of Noyo River fish), available genetic data support the hypothesis that dispersal among historical populations of

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[19] Given the uncertainty associated with our selection of 32 IP-km as the threshold for viability, and our interpretation of potential bias in the IP model as applied to watersheds in California, it is possible that coho salmon in Pudding Creek (28.86 IP-km) might have also been viable-in-isolation under historical conditions. If this were the case, however, coho salmon in Pudding Creek would have constituted a potentially independent population, due to immigration from larger watersheds nearby.

coho salmon followed patterns consistent with the assumptions of the connectivity-viability model, and thus support the population structure proposed in Table 2.2.

Coastal basins: Point Arena to the Golden Gate

The Gualala River [40] is the only sizeable watershed to enter the Pacific Ocean between Point Arena and the mouth of the Russian River. As a consequence, it is isolated from sizeable populations to the north and south by stretches of coastline drained by very small watersheds. We conclude that coho salmon in the Gualala River [40] comprise a functionally independent population (Table 2.2). We base our conclusion on the extent of the watershed with high IP for spawning and rearing habitat (Plate 13) and conclusive historical evidence that much of the watershed was used by coho salmon (Spence et al., 2001, 2005).

Our connectivity-viability model predicts that Salmon Creek [42], Americano Creek (Estero Americano) [43], Stemple Creek (Estero de San Antonio) [45], and the tributaries of Tomales Bay [47] harbored potentially independent populations of coho salmon[20]. Of these basins, however, strong evidence of historical occupancy by coho salmon exists only for Salmon Creek [43], and both tributaries to Tomales Bay [47] (Spence et al., 2005). Americano Creek (Estero Americano) [45] and Stemple Creek (Estero de San Antonio) [46] drain low elevation basins (among the lowest in the NCCCRD) and thus are likely to deviate significantly from the hydrological model that underlies our IP model (Plates 1 and 4). Thus, we have concerns similar to those outlined in our discussion of coho salmon in San Francisco Bay tributaries regarding the use of predictions from the IP model for Americano Creek (Estero Americano) [46] and Stemple Creek (Estero de San Antonio) [45]. Given the high likelihood that the IP model yields positively biased predictions for these two streams, we conclude that coho salmon spawning in Americano Creek (Estero Americano) [45] and Stemple Creek (Estero de San Antonio) [46] comprise dependent populations (Table 2.2). Likewise, although the watershed of Salmon Creek [43] is dominated by the Coast Range ecoregion, it is not clear that areas of predicted high IP occurred in areas where the IP model can be expected to hold. Therefore, we conclude that the historical population of coho salmon that occupied Salmon Creek [43] was a dependent population.

We conclude that coho salmon in the tributaries of Tomales Bay historically existed as a potentially independent population in Walker Creek [TB1] and a functionally independent population in Lagunitas Creek [TB2][21]. In reaching this conclusion, we note that the two watersheds are similar in size, but that predictions from the IP model are likely to include somewhat greater bias for Walker Creek [TB1] than for Lagunitas Creek [TB2], and thus for the disparity in potential carrying capacity to be somewhat larger than that suggested by the predictions of the IP model[22].

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[20] Despite the potential for substantial dispersal between the major tributaries of Tomales Bay, Walker Creek [TB1] and Lagunitas Creek [TB2], we consider coho salmon in these watersheds as separate populations based on the physical separation of the mouths and environmental differences between the watersheds.

[21] If dispersal among these two watersheds was historically greater than we have assumed, an alternative conclusion might be reached in which coho salmon in Tomales Bay existed as a single population, with substantial spatial structure and environmental diversity represented by the two major watersheds.

[22] The Lagunitas Creek watershed reaches higher elevations than the Walker Creek watershed, which tends to increase

Coastal basins: south of the Golden Gate

We conclude that under historical conditions, coho salmon existed as functionally independent populations in San Gregorio Creek [54], Pescadero Creek [56] and San Lorenzo River [63], and as dependent populations in the numerous smaller watersheds that drain this stretch of coastline (Table 2.2). These conclusions are based almost entirely on the predictions of the connectivity-viability analysis, as other relevant sources of information (e.g., genetic data and estimates of migration rate) appear to be confounded by the effects of among-basin transfers, and in any case are drawn from what we conclude are historically dependent populations.

2.9 Diversity strata

Figure 2.7 summarizes assignments of populations to diversity strata within the CCC-Coho ESU. Our conclusions regarding these assignments derive largely from our multivariate analysis of basin-scale environmental and ecological characteristics for the NCCCRD, tempered with consideration of the geographical arrangement of populations. We initially divided the ESU among three broad strata, however, sufficient geographically coherent environmental variability remained within two of these strata to suggest further subdivision. Subdivision of the Lost Coast-Point Arena "super-stratum" is based on the north-to-south gradient in precipitation and temperature, which causes a shift in the characteristics of the larger basins in particular to exhibit increasing similarity to basins to the south. Note, however, that this shift is largely due to changes in the conditions found in the interior portions of the larger basins, while conditions in more coastal areas do not differ strongly from conditions observed in basins to the north. Subdivision of the Point Arena-Golden Gate "super-stratum" is based entirely on the substantial differences between the migration routes of coastal populations and those of populations that enter San Francisco Bay. Again, environmental conditions are generally similar within this stratum–particularly in the parts of larger watersheds in which persistent, self-sustaining coho salmon populations are likely to have existed under historical conditions–and we expect to focus our attention on the overarching stratum in the course of developing ESU viability criteria. The Santa Cruz Mountains diversity stratum consists of watersheds that are generally similar environmentally, and does not exhibit any clear basis for further subdivision. Note that the South Bay [51C] population of coho salmon occupies watersheds that also drain the Santa Cruz Mountains, and have environmental characteristics similar to those of coastal watersheds in the Santa Cruz Mountains diversity stratum. We do not include the South Bay population in this diversity stratum based on geographic separation of ocean entry points and expected differences in migration routes; however, the alternative case (e.g., including the South Bay population with coastal basins south of the Golden Gate) also has some merit.

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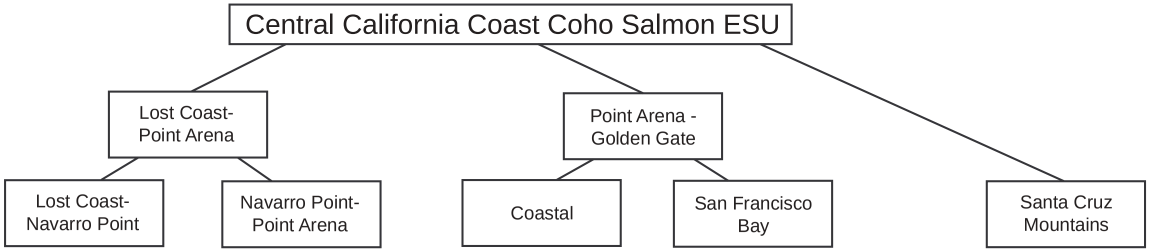
precipitation and cool temperatures, and Lagunitas Creek is known to include areas of groundwater discharge associated with fault zones.



Jackass Creek [b]
Usal Creek [17]
Cottaneva Creek [18]
Juan Creek [20]
Howard Creek [c]
DeHaven Creek [21]
Wages Creek [22]
Abalobadiah Creek [c]
Ten Mile River [23]
Mill Creek [c]
Pudding Creek [24]
Noyo River [25]
Hare Creek [26]
Jug Handle Creek [c]
Caspar Creek [27]
Russian Gulch (Me) [28]
Big River [30]
Little River (Me) [31]
Albion River [32]
Big Salmon Creek [33]

Navarro River [34]
Greenwood Creek [35]
Elk Creek [36]
Mallo Pass Creek [c]
Alder Creek [37]
Brush Creek [38]
Garcia River [39]

Gualala River [41]
Russian Gulch (S) [d]
Russian River [42]
Scotty Creek [d]
Salmon Creek (S) [43]
Bodega Harbor [44]
Americano Creek [45]
Stemple Creek [46]
Walker Creek [TB1]
Lagunitas Creek [TB2]
Drakes Bay [48]
Pine Gulch [49]
Redwood Creek(Ma) [50]

A. Corte Madera d. Presidio [S1]
Corte Madera Creek [S2]
Miller Creek [S3]
Sonoma Creek [S6]
Napa River [S7]
San Pablo Creek [S8]
Strawberry Creek [e]
San Leandro Creek [S9]
San Lorenzo Creek [S10]
Guadalupe River [S13]
San Francisquito Creek [S15]
San Mateo Creek [S16]

Pilarcitos Creek [52]
Tunitas Creek [53]
San Gregorio Creek [54]
Pomponio Creek [55]
Pescadero Creek [56]
Gazos Creek [57]
Whitehouse Creek [e]
Cascade Creek [e]
Waddell Creek [58]
Scott Creek [59]
Wilder Creek [62]
San Lorenzo River [63]
Soquel Creek [64]
Aptos Creek [65]

Figure 2.7. Arrangement of historical populations of the CCC-Coho ESU into diversity strata. Functionally independent populations are listed in bold font. Potentially independent populations are listed in italic font. Dependent populations are listed in regular font.

3 California Coast Chinook Salmon ESU

3.1 ESU definition

The California Coast Chinook salmon (CC-Chinook) ESU includes Chinook salmon (*Oncorhynchus tshawytscha*) that spawn in coastal watersheds from Redwood Creek (Humboldt County) in the north to the Russian River in the south, inclusive (Myers et al., 1998; West Coast Chinook Salmon Biological Review Team, 1999). Any Chinook salmon found in coastal basins south of this range are considered to be part of this ESU (Myers et al., 1998). The ESU historically included fall-run Chinook salmon and spring-run Chinook salmon; however, we currently lack substantive information for either run. Therefore, analysis of population structure is especially constrained by the lack of data for this ESU.

3.2 Life history and general habitat characteristics

The CC-Chinook ESU constitutes the southernmost coastal portion of the species' range in North America. Environmental conditions faced by Chinook salmon in this ESU differ from those experienced in coastal ESUs to the north and to ESUs of Chinook salmon that occupy interior basins of the Central Valley, Klamath River, and other large basins to the north.

3.2.1 Life history

As a species, Chinook salmon exhibit considerable diversity in their life histories (see Myers et al., 1998, for a thorough review). This diversity underlies traditional classifications of Chinook salmon stocks based on aspects of both adult and juvenile life histories; however, such distinctions are rarely without ambiguity. The major distinction between stocks is based on adult run-timing, in which populations are classified according to the season of peak migration. Most populations are designated as either spring-run or fall-run stocks, both of which historically occurred in the CC-Chinook ESU. Juveniles are classified based on period of freshwater residence, with "ocean-type" fish moving to sea in the first year of life and "stream-type" juveniles residing in streams for a full year or more. In general, spring-run Chinook salmon produce offspring that exhibit the stream-type juvenile life history, whereas fall-run Chinook salmon produce ocean-type juveniles. The correlation between adult and juvenile life history characteristics is not perfect; for example, small numbers of apparent "stream-type" juveniles have been observed recently in Redwood Creek and Mad River where only fall-run populations are known to be extant (Sparkman, 2002a,b).

Throughout their range, fall-run Chinook salmon generally return to freshwater from September to October or early November and spawn shortly thereafter; however, along the central coast of California, fall-run Chinook may only gain access to rivers following the arrival of large winter storms in November through January, and might time their return migrations accordingly. This is especially true in watersheds that bar over during the summer. In contrast, adult spring-run Chinook salmon migrate upstream during the period of peak snowmelt and stream discharge–usually April to July or August in California–and then hold in deep pools, before moving into natal areas to spawn in the fall. The peak spawning period for populations in the Smith, Klamath, and Trinity rivers is generally between September and December; we lack similar data for spring-run Chinook salmon populations in the CC-Chinook ESU. Fry subsequently emerge from the gravel in late winter or spring. Ocean-type juveniles may begin migrating toward sea within a few weeks to a few months of emergence, but some individuals may reside in rivers through the summer months, before moving to estuaries during the fall or winter (Reimers, 1973; Healy, 1991; Moyle, 2002). Stream-type juveniles typically spend just over a year in freshwater and migrate to sea in spring or early summer. Chinook salmon reside in the ocean for one to five years, but some males (so-called “jacks”) may return after 6-18 months at sea at a total age of two years. In California populations, most adults return after two or three years at sea. The most common ages-at-maturity for Chinook salmon in the CC-Chinook ESU are three and four years, with five-year-olds constituting a small proportion of some populations (Myers et al., 1998); however, this age-distribution may be truncated or compressed towards earlier ages-at-maturation relative to historical patterns by the selective effects of intensive troll fisheries over the past century (Ricker, 1981; Hankin and Healy, 1986).

3.2.2 Evolutionary relationships between fall- and spring-run Chinook in the CC-Chinook ESU

An extensive analysis of evolutionary relationships among Chinook salmon throughout California and the Pacific Northwest shows that in coastal basins, spring-run Chinook salmon are more closely related to fall-run Chinook salmon in the same basin than to spring-run Chinook salmon in other coastal regions (e.g., coastal Oregon and Washington, lower tributaries of the Columbia and Fraser rivers Waples et al., 2004). These results provide evidence for independent evolution of spring-run Chinook salmon from fall-run Chinook salmon in coastal basins (Waples et al., 2004). In contrast, genetic data indicate deep divergence between spring-run and fall-run Chinook salmon in interior basins, such as the interior Columbia River and the Central Valley, so much so that Chinook salmon exhibiting different run-timing are considered to be separate ESUs (Myers et al., 1998; Waples et al., 2004). The lack of extant populations of spring-run Chinook salmon prevents direct evaluation on such relationships in the CC-Chinook ESU. We assume that the evolutionary relationship between fall- and spring-run Chinook salmon in the CC-Chinook ESU was similar to that found in other coastal ESUs.

3.2.3 Typical habitat characteristics and ecological indicators

Fall-run Chinook salmon occur in rain-dominated systems or the lower portions of systems with both rain and snowmelt influence. Ocean-type juveniles may begin migrating toward sea within a few weeks to a few months of emergence, but some individuals may reside in streams in rivers through the summer months, before moving to estuaries during the fall or winter (Reimers, 1973; Healy, 1991; Moyle, 2002). Juvenile Chinook, especially ocean-type juveniles, appear to use estuary habitats more than any of the other five Pacific salmon species and may reside in estuaries for several months[1]. In contrast, spring-run Chinook salmon occur in watersheds or portions of watersheds where snowmelt constitutes a significant contribution to the annual hydrograph, and provides both access to the system, and a source of cold water relatively late into the summer. Unlike fall Chinook, which enter freshwater just prior to spawning, adult spring Chinook require deep pools where cool temperatures are maintained throughout the summer to survive the period between entering freshwater and spawning. Likewise, the stream-type juveniles typical of spring-run populations are restricted in their distributions to streams where water temperatures remain sufficiently cool to allow fish to survive over the summer (although this is not necessarily limited to systems dominated by snowmelt). Although spring- and fall-run Chinook may both occur in the same watershed, spring-run Chinook tend to spawn higher in the watershed than fall-run Chinook, as a consequence of differences between life history types with respect to where each stages for the final stages of migration to spawning grounds and the timing of spawning.

3.3 Historical distribution

We synthesized two complementary data sets to assess the potential distribution of Chinook salmon in coastal watersheds south of the Klamath River as means to frame the set of putative populations for subsequent evaluation. One, we compiled information, both historical and recent, on the distribution of Chinook salmon throughout the range of the CC-Chinook ESU (Agrawal et al., 2005). Two, we developed a simple model in GIS to predict the intrinsic potential (IP) for habitat suitable for spawning by fall-run Chinook salmon (Agrawal et al., 2005). We do not explicitly predict IP for spring-run Chinook salmon because available geographic data and the underlying hydrological model does not predict the potential for special habitat requirements of spring-run Chinook salmon (e.g., summer resting pools). In evaluating the potential historical extent of suitable habitat, we also consider ancillary information on environmental characteristics, such as the potential for drought and sandbars to limit access to freshwater habitats for fall-run Chinook salmon.

3.3.1 Recent and historical distribution

Only fall-run Chinook salmon currently occur in the CC-Chinook ESU. Spring-run stocks no longer occur in the NCCCRD; however, historical information indicates that spring-run Chinook salmon historically existed in the Mad River and the North Fork and Middle Fork of the Eel River (Keter, 1995; Myers et al., 1998; Moyle, 2002).

Recent information on the distribution and status of fall-run Chinook salmon in the NCCCRD is quite limited, and what information is available is concentrated in watersheds that enter the Pacific Ocean north of Punta Gorda (i.e., north of the Mattole River, inclusive) and the Russian River (Agrawal

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[1] Estuary use appears to be inversely related to the length of time spent in freshwater (Healy, 1991).

et al., 2005)[2]. Historical accounts are also sparse and do little to reduce our uncertainty regarding whether populations of fall-run Chinook salmon persisted in coastal watersheds between of Cape Mendocino and the Russian River. Moreover, populations of salmon in the Russian River were known to be in dramatic decline in the 1880s (Steiner Environmental Consulting, 1996), and it is quite possible that Chinook salmon had been effectively extirpated from the Russian River before the turn of the 20th century (Myers et al., 1998), all of which limits our ability to evaluate the historical structure of Chinook salmon in the southern range of the CC-Chinook ESU. Most historical accounts correspond to watersheds for which we have evidence of Chinook salmon from relatively recent spawner surveys; however, sparse historical evidence and recent angler reports suggest that Chinook salmon at least occasionally enter the Ten Mile, Noyo, Big, Albion, Navarro, Garcia, and Gualala rivers. Following Myers et al. (1998) and subsequent evaluations, we believe it highly unlikely that Chinook salmon consistently occupied coastal basins south of the Russian River. This conclusion is based in part on the environmental conditions and topological characteristics of these basins (discussed in more detail below), and in part on the nature of available historical observations, none of which provide evidence for persistent reproductive success[3].

Chinook salmon in San Francisco Bay tributaries. We do not formally consider population structure of Chinook salmon in tributaries of San Francisco Bay in this report. As noted above, Biological Review Teams for Chinook salmon reached the conclusion that the southernmost persistent population of Chinook salmon in a coastal watershed occupied the Russian River (Myers et al., 1998; West Coast Chinook Salmon Biological Review Team, 1999). Available historical and archaeological evidence suggests that Chinook salmon were present in tributaries to San Francisco and San Pablo bays, but these data do not indicate that populations of Chinook salmon were either large or persistent in these watersheds (Leidy et al., 2003; Gobalet et al., 2004). Recent observations of successful reproduction by Chinook salmon[4] in some San Francisco Bay tributaries suggest that historical conditions did allow Chinook salmon to occupy at least some basins. However, given the size and location of the water-

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[2] The information compiled by Agrawal et al. (2005) does not comprise a systematic or consistent survey of all potential spawning habitat for Chinook salmon, and is limited by the fact that absence, particularly historical absence, is very difficult to demonstrate without ancillary data, such as the location of a demonstrable barrier to access. Thus, this information provides a minimum estimate of the current spawning distribution of Chinook salmon in the CC-Chinook ESU. Notable gaps regarding the distribution of Chinook salmon include watersheds along the Mendocino and Sonoma county coasts and the mainstem Eel River. Survey efforts in this area generally focus on coho salmon, which due to differences in run-timing reduces the likelihood of detecting Chinook salmon, particularly when Chinook salmon are rare.

[3] One of the observations that offers what appears to be compelling evidence for successful reproduction in a coastal basin south of the Russian River is a set of museum collections from Lagunitas Creek in 1897 and subsequent observations of adult Chinook salmon in 1900 and 1901. These samples and observations are directly linked to unsuccessful stocking attempts in which fry derived from Battle Creek (Central Valley) stock were planted in 1897 and 1899 (Rutter, 1904). The current population of Chinook salmon in Lagunitas Creek is a result of a recent colonization event from an unknown source, and dam-regulated flow intended to support coho salmon in this watershed is likely to be contributing to the persistence of this population.

[4] These recent observations represent “colonizations” derived from hatchery strays from the Central Valley and their progeny.

sheds tributary to the San Francisco and San Pablo bays, it is very possible that populations Chinook salmon in these tributaries were strongly influenced by immigration from the massive Central Valley stocks of Chinook salmon. This possibility is especially relevant for the northern watersheds, which lie directly on the path between the Golden Gate and the Sacramento-San Joaquin delta. Moreover, the nearest basin likely to harbor a persistent population of Chinook salmon (the Russian River) is over 90 km from the Golden Gate (well over 120 km as the fish swims). Such a combination of immigration and isolation greatly reduces the potential for populations of Chinook salmon in tributaries to San Francisco and San Pablo bays to maintain a "coastal" character. Unfortunately, off-site releases from Central Valley hatcheries have increased straying rates such that Chinook salmon that currently spawn in San Francisco Bay tributaries are heavily impacted by, if not entirely derived from, Central Valley hatchery stocks. Therefore, genetic analysis is expected to be of little assistance in evaluating the historical status of these populations.

3.3.2 Intrinsic potential

To complement available information on the distribution of spawning habitat, we generated a simple model to predict the potential for spawning habitat for fall-run Chinook salmon to occur at the scale of stream reaches throughout the NCCCRD. The approach is identical to that used for coho salmon and steelhead (Burnett et al., 2003; Agrawal et al., 2005), except that we used habitat suitability curves designed to capture the characteristics of areas in which fall-run Chinook salmon typically spawn. To reflect current spawning distributions, we examined analyses based on two suitability curves relating mean annual discharge to habitat potential: one which did not limit the potential for Chinook salmon spawning habitat for any stream or river with average flow above some minimum threshold, and another for which the potential for Chinook salmon spawning habitat was reduced in rivers with average flow exceeding 50 $m^3\ s^{-1}$. Plate 12 illustrates results predicted under this more conservative model; the model in which IP is not limited in areas of high annual discharge predicts high IP for the entire length of the Eel River mainstem below the confluence of the Middle Fork. While the conservative model better describes what we know about current spawning distributions, it is unknown how well the current distribution reflects historical patterns or whether historical conditions in the mainstem Eel and Russian rivers were substantially more favorable than is currently observed. We emphasize strongly that this exercise essentially is a simple mapping of literature values and expert opinion regarding the characteristics of spawning areas used by Chinook salmon in terms of geomorphological and hydrological characteristics of a stream reach, and is not explicitly based on empirical data collected for the CC-Chinook ESU. Thus, the results of this modeling exercise offer only preliminary predictions for the extent and distribution of spawning habitat for fall-run Chinook salmon.

Regional variation in seasonal precipitation and potential bias in predicted IP for fall-run Chinook salmon. Fall-run Chinook salmon occupy freshwater habitats during the time of year coincident with the onset of winter storms and high stream flows. The specific timing of early storms can strongly affect when fall-run Chinook salmon can enter streams, particularly streams of moderate or small size.

Nicholas and Hankin (1988) report that fall-run Chinook salmon in coastal watersheds of Oregon exhibit substantial flexibility with respect to the timing of freshwater-entry and are capable of delaying the final stages of maturation while they wait for access to freshwater habitats. Fall-run Chinook salmon in coastal California are likely to exhibit similar plasticity, which reduces the potential for temporal variation in the onset of winter storms to have a critical influence on the suitability of watersheds to support persistent populations.

Despite such life history flexibility, southward declining trends in the reliability and extent of access to freshwater habitats and the realized capacity of a watershed to support fall-run Chinook salmon are likely to have been and remain an important constraint on the southern range of the CC-Chinook ESU. We therefore considered regional patterns in recent climatological averages of October[5] precipitation, in terms of both the overall spatial pattern and total precipitation integrated at the watershed scale, as a crude qualitative index of potential bias in our IP model. In combination with historical records, patterns in October precipitation suggest that small to moderate size watersheds south of the Russian River are substantially less likely to have supported persistent populations of Chinook salmon. Two of these watersheds, Salmon Creek [43] and Lagunitas Creek [TB2], have greater potential to have provided suitable access and habitat at least occasionally, but we have no historical evidence for natural Chinook salmon populations in either of these watersheds[6].

Estuarine habitats. Estuaries can be an important habitat for juvenile Chinook salmon; however, quantitative inclusion of estuarine habitats in our analysis is constrained by two factors. First, the spatial extent and dynamics of estuarine habitats in the NCCCRD has not been well documented and available information includes substantial uncertainty. Second, the contribution of such habitats to population dynamics and the consistency with which they present favorable conditions is not well understood. Nevertheless, we consider evidence for historical presence of estuarine habitats in reaching our conclusions regarding each population's historical status and potential role in the ESU.

3.3.3 Synthesis of historical information and GIS model predictions

Table 1.1 summarizes the set of watersheds included in our analysis of historical population structure of the CC-Chinook ESU. This set includes all basins for which we have historical or recent observations, as well as any intervening watersheds for which the habitat model predicted at least 2.0 IP-km, or one-tenth the amount of habitat thought necessary to support a population that would be viable-in-isolation (see below). We recognize that this threshold (2.0 IP-km) is likely to be overly inclusive, particularly

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[5] Geographical patterns in relative mean precipitation are very similar from September through December; areas that receive more precipitation than other areas do so consistently throughout the fall and winter. Therefore, any given month can serve as a suitable index of spatial patterns in the precipitation climatology. Mean October precipitation patterns were chosen as the basis for the bias index as these patterns reflects both differences in the magnitude of precipitation and the effects of variation in the onset of winter storm season.

[6] Chinook salmon currently spawn in Lagunitas Creek; however, this population is a result of a recent colonization event from an unknown source, and dam-regulated flow intended to support coho salmon in this watershed is likely to be contributing to the persistence of this population.

towards the southern end of the NCCCRD. Based on environmental considerations and sparse historical evidence we believe it highly unlikely that Chinook salmon consistently occupied coastal basins south of the Russian River (Myers et al., 1998). Based on the historical record and recent observations of successful reproduction by Chinook salmon in some San Francisco Bay tributaries, we include selected San Francisco Bay tributaries in our analysis (e.g., Napa River, Leidy et al., 2003). However, it is very likely that any historical populations of Chinook salmon in these tributaries were strongly influenced by dispersal from populations from the Sacramento-San Joaquin basin. Indeed, we believe that the ability of populations in tributaries to San Francisco Bay to maintain a "coastal" character is likely to have been limited in the face of such immigration pressure, and we therefore suggest that the decision to include populations of Chinook salmon that historically spawned in San Francisco Bay tributaries in the CC-Chinook ESU brings with it substantial uncertainty. For continuity, we include watersheds between the Russian River and the Golden Gate in our analyses to consider these hypotheses more fully, but exclude coastal basins south of the Golden Gate from formal analysis.

3.4 Population Genetic Structure of the CC-Chinook ESU

For Chinook salmon, we have available for our consideration four data sets based on neutral molecular markers that include multiple samples from within the CC-Chinook ESU, each of which is reviewed below. Such data provide insight to the current population structure of the ESU, and so we must consider the effect that recent events—in particular, basin-to-basin transfers—might have had in causing the current pattern to deviate from the general characteristics the historical state. Therefore, we first review available information on artificial propagation of coho salmon with a focus on among-basin and among-ESU transfers to set the context for interpreting available genetic data to draw inference regarding the the historical structure of the ESU. In doing so, we look to genetic data to provide insight to population structure directly, and as a means of evaluating the validity of geographic analyses that follow.

3.4.1 Historical artificial propagation

Interpretation of modern genetic data bearing on the question of population structure requires some appreciation of the potential effects of artificial propagation and among-basin and among-ESU stock transfers. Therefore, to provide context for evaluating the genetic data available to us, we summarized available information on among-basin and among-ESU transfers of Chinook salmon within the CC-Chinook ESU (Table 3.1). Two points bear general emphasis. First, early records are likely to overstate the potential impact of releases on native stocks. Most early records document movement of eggs among facilities rather than the number of fry or fingerlings released. In many cases, fry were released unfed shortly after yolk-sac absorption and are likely to have suffered very high mortality rates. Later releases of fed fry and fingerlings are more likely to have had an effect on population genetic structure in the CC-Chinook ESU. Second, widespread among-basin and among-ESU transfers in the CC-Chinook ESU generally ceased in the mid- to late-1980s, and most recent and ongoing artificial propagation efforts in the CC-Chinook ESU are small in scale and restricted to supplementing depressed populations with progeny of local broodstock (Table 3.1). Some among-basin and among-ESU transfers continued as late as the mid-1990s, particularly in the Russian River (Table 3.1).

As mentioned previously, populations of salmon in the Russian River were known to be in dramatic decline in the 1880s, and it is quite possible that Chinook salmon had been effectively extirpated from the Russian River before the turn of the 20th century (Steiner Environmental Consulting, 1996). The degree to which Chinook salmon that currently spawn in the Russian River are related to the original native stock is essentially impossible to establish. It is possible, and perhaps likely, that the intensive stocking with fish derived from other basins and ESUs (see below) has contributed in some way to the re-establishment of Chinook salmon in the Russian River, and that as a consequence, the current composition of Chinook salmon in the Russian River might bear little resemblance to that of the original population.

Among-basin and among-ESU transfers are certainly mechanisms for altering the population genetic structure of an ESU. In the case of the CC-Chinook ESU, we are also concerned that large-scale releases of hatchery-reared Chinook salmon derived from putatively local stocks has substantially altered the population genetic structure of the ESU. For example, between 1973 and 1994, the Eel River received over 2.1 million juvenile Chinook salmon derived from spawners collected in a broad range of tributaries, reared at numerous hatcheries (including some located in other basins, such as the Mad and Russian rivers) and released at numerous locations that often were different than the location from which the adults were collected. Such practices are likely to reduce the precision of the homing response in those fish that survive to adulthood, and thus increase rates of dispersal (Pascual and Quinn, 1995). The Mad River received more juveniles (approximately 3.6 million between 1972 and 1993 NRC, 1996), but there is less evidence that fish were moved throughout the basin. Stocking from local sources in the Russian River (approximately 450,000 fish between 1986 and 1993), consisted entirely of fish previously derived from out-of-basin or out-of-ESU transfers.

3.4.2 Genetic data sets and analyses

Genetic data that bear on the identification of independent populations of Chinook salmon in the Coastal California Chinook ESU include data reported by Bartley and colleagues (Bartley and Gall, 1990; Bartley et al., 1992), Hedgecock (2002), and recent analyses conducted by scientists at the Santa Cruz Laboratory (S. Blankenship, et al., *unpublished data*).

Allozyme data: Bartley and Gall (1990); Bartley et al. (1992)

Bartley and Gall (1990) present data for 22 polymorphic allozyme loci for 25 naturally spawning populations and 10 hatchery stocks of Chinook salmon in California, of which nine naturally spawning populations and three hatchery stocks are within the CC-Chinook ESU. Of the 22 loci, one is monomorphic in the CC-Chinook ESU, and an additional 8 are monomorphic in all but 1 population. These data suffer from a number of technical issues that limit their utility for analysis of population structure: (1) the samples were collected in downstream migrant traps, and thus each sample might represent an admixture of populations, (2) the data were collected over a four year period, and thus include varia-

Table 3.1. Known out-of-basin and out-of-ESU releases of Chinook salmon fry and fingerlings into rivers and streams of the CC-Chinook ESU.

Basin[*]	**Period (Years)**[**]	**Egg Source (Hatchery)**[***]	**Numbers**[**]	**Reference**
Redwood Creek (H)	1890-1898 (?)	***Trinity River (via FGH/RCHS)***	***unknown***	Snyder (1931)
	1964-68 (4)	unknown	1,978,059	Myers et al. (1998)
	1985 (1)	Eel R (via PCFFA)	1,416	NRC (1996)
	1992 (1)	SF Eel R (via PCFFA)	69,201	NRC (1996)
(Prairie Creek)	1965, 1987 (2)	unknown	67,187	Myers et al. (1998)
	1969-1972 (3)	unknown	1,946,591	NRC (1996)
Strawberry Creek	1993 (1)	Freshwater Creek (via PLC)	10,000	Myers et al. (1998)
Mad River	1912-1915 (4)	***McCloud R, Battle Cr, Mill Cr (via PCH)***	***775,000***	Shebley (1914, 1916)
	1916 (1)	***McCloud R, Battle Cr, Mill Cr (via UKH)***	***550,000***[†]	Myers et al. (1998)
	1971 (1)	***Minter Creek (WA)***	***648,120***	Myers et al. (1998)
	1974 (1)	Freshwater Cr	139,887	Myers et al. (1998)
	1983 (1)	unknown	51,654	Myers et al. (1998)
Humboldt Bay*	1969-1972 (4)	unknown (via CP)	584,000	Myers et al. (1998)
	1985 (1)	***Rowdy Cr (Smith R)***	1,027	NRC (1996)
	1987 (1)	Cochran Pond	14,139	Myers et al. (1998)
	1988 (1)	MRH	4,088	Myers et al. (1998)
Eel River	1898-1919 (19)	***Sacramento R (via BDS/BAC/MCH)***	***84,479,810 (E)***	Cobb (1931)
(Mainstem Eel River)	1920-1922 (3)	***Klamath R (via FSH)***	***unknown***	Hederley (1923, 1924)
(Upper Eel River?)	1923 (1)	***Klamath R (via KECS/FSH)***	***250,000 (E)***	Hederley (1923)
	1972-77 (6)	***Klamath R (via IGH)***	***625,853***	Myers et al. (1998)
	1979 (1)	***Trinity R (via TRH)***	***5,000***	NRC (1996)
(South Fork Eel River/	1985 (1)	SF Eel R (via RCE)	14,791	NRC (1996)
Van Duzen River/	1984 (1)	Outlet Cr (mainstem Eel R.; via RCE)	41,206	NRC (1996)
(Lower Eel?))	1985, 1988 (2)	Redwood Cr (H) (unknown hatchery)	20,986	Myers et al. (1998)
	1992-1993 (2)	Freshwater Cr (via PLC)	75,500	Myers et al. (1998)
Ten Mile River	1979 (1)	***Trinity R (TRH)***	***400,418***[††]	NRC (1996)
	1980-1982 (2)	***Hollow Tree Cr (SF Eel R)***	300,000[†††]	Maahs (1999)
	1983 (1)	***Wisconsin***	100,000[‡]	Maahs (1999)
	1985-1987 (3)	***Composite***[‡‡]	16,000	Maahs (1999)
Big River	1949-1952 (4)	Mad R	615,000	CDFG 1955
Russian River	1881 (1)	***Sacramento R (via BDS)***	***30,000***	Cobb (1931)
	1956-1964 (3)	***Battle Cr, Sacramento R (via CNFH)***	***1,999,400***	Myers et al. (1998)
	1969-1970 (2)	unknown	879,885	Myers et al. (1998)
	1975 (1)	***Iron Gate Hatchery***	***73,800***	Myers et al. (1998)
	1981-1993 (7)	***Outlet Cr, Hollow Tree Cr (Eel R; via WSH)***	***185,326***	NRC (1996)
	1982-1994 (6)	***Feather River (via FRH)***	***1,154,161***	Myers et al. (1998)
	1982 (1)	unknown (via Ocean King)	58,500	Myers et al. (1998)
	1982-1986 (5)	***Wisconsin***	***1,173,077***	Myers et al. (1998)
	1983 (1)	MRH	9,250	Myers et al. (1998)
	1983 (1)	unknown (via Silver King)	11,500	Myers et al. (1998)
	1985 (1)	***Warm Springs/Wisconsin***	***98,400***	Myers et al. (1998)
	1986-1993 (6)	Russian R./Dry Cr. (WSH composite)[‡‡‡]	450,562	NRC (1996)
	1990-1994 (5)	***Nimbus Hatchery (via NH)***	***648,242***	Myers et al. (1998)

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[*]Blocks indicate coastal basins; streams named parenthetically are tributaries known to have received specified transfers. [**]Most thorough coverage is from the 1950's to the present, although some earlier records are included. "(E)" indicates eggs delivered. [***]Hatchery abbreviations are as follows: BDS=Baird Station, McCloud River; BAC=Battle Creek; BRH=Brookdale; BCH=Big Creek; FGH=Fort Gaston Hatchery; FSH=Fort Seward; KECS=Klamathon Egg Collecting Station; PLC=Pacific Lumber Co.; RCH=Redwood Creek substation of Fort Gaston Hatchery; RCE=Redwood Creek on South Fork Eel River; IGH=Iron Gate; MCH=Mill Creek; MRH=Mad River; NH=Nimbus, American River; PCFFA=Pacific Coast Federation of Fisherman's Association; PCH=Price Creek; PLC=Pacific Lumber Company, Scotia; SRANC=Salmon Restoration Association of Northern California; TMH=Ten Mile; TRH=Trinity River; WSH=Warm Springs. [†]The CFGC biennial report indicates that 550,000 fish were distributed to Humboldt County; it is likely that these were released into the Mad River, as was done in the preceding four years. [††]It is unclear how many of these Trinity River Hatchery fish were ultimately planted into the Ten Mile River. See text for explanation. [†††]Number of fish delivered to Ten Mile Ponds from Hollow Tree Creek for rearing purposes only. Fish were released into Ten Mile River accidentally. [‡]Total is number of fish delivered. Actual number of fish released appears closer to 75,000. An additional 20,000 fish from Wisconsin were delivered in 1982, but the majority of these are believed to have died from disease. [‡‡]These fish were progeny from previous plantings of both Eel River and Wisconsin fish. [‡‡‡]Although listed as within-basin stocks, these fish are likely derived from various nonnative stocks, particularly Eel River and Sacramento River Chinook salmon, planted in previous years.

tion due to differences in cohorts represented in each sample, and (3) in some cases, sample sizes are sufficiently small to affect the accuracy of estimates of allele frequencies, which reduces the power of any analysis based on allele frequencies. Furthermore, Bartley et al. (1992) compared allele frequencies estimated from the Bartley and Gall (1990) samples collected in 1983-1986 and a more rigorously collected sample in 1987-1988 for seven of the same naturally-spawning populations and found statistically significant changes in allele frequencies at 19% of the loci. While these may represent real biological differences, Bartley et al. (1992) state that some of the earlier data may have been "artefactual". We do not consider these data further.

Bartley et al. (1992) present data for 47 polymorphic allozyme loci in 37 collections of Chinook salmon from the entire range of the species in California, 11 of which were drawn from the CC-Chinook ESU. (These data were included in analyses conducted in the course of coastwide status review for Chinook salmon (Myers et al., 1998).) Of the 47 loci, 11 are monomorphic in samples from the CC-Chinook ESU, another 11 are variable in one sample only, and of the latter 11, 9 were found to be variable only in the sample from Redwood Creek. Like the samples in the Bartley and Gall (1990) data set, these samples were also collected in downstream migrant traps, and thus each sample might represent an admixture of populations. However, these data were collected over a shorter period of time, which should reduce the effect of differences in cohort composition.

Bartley et al. (1992) examined phylogeographic structure in their data, and drew several conclusions from their analysis. First, samples in the region cluster together to the exclusion of those from other regions; these data, in part, form the basis for ESU delineation (Myers et al., 1998). Second, within the CC-Chinook ESU, the populations in the Mattole and Mad rivers were the most distant from other samples within the region. Third, samples from naturally spawning populations in the Eel River and Redwood Creek cluster into a single group, and appear to be more closely related than any other California or Oregon populations surveyed in this study. Within this group, however, samples did not cluster according to the geographic structure of the Eel River basin. Myers et al. (1998) also analyzed these data, as part of a coastwide analysis, and obtained a tree that suggests slightly different conclusions, in that only the Mattole River sample stands out as strongly separated from the rest of the group. This analysis also finds that concordance between the arrangement of samples from the Eel River and the structure of the basin is tenuous at best.

To determine whether the allozyme data presented in Bartley et al. (1992) might provide insight to the population structure of CC-Chinook ESU, we re-analyzed these data to examine the sensitivity of tree structure to choice of tree building algorithm (Neighbor Joining (NJ) *versus* Unweighted Pair Group with Arithmetic Mean (UPGMA)) and genetic distance (Cavalli-Sforza and Edward's Chord (CSE) *versus* Nei's D) and used the bootstrap to examine uncertainty in tree topology for all cases. For all analyses, data from the Smith River sample was used as an outgroup. We found that only one of the groupings identified by Bartley et al. (1992), that between the Van Duzen River and the South Fork Eel River (Benbow), occurs consistently with high bootstrap support (results not shown). In contrast, samples from elsewhere in the Eel River, the Mad River, Mattole River, and Redwood Creek (Humboldt) did not form robust groups or exhibit consistently large separation from other samples across tree-building methods. It is likely that differences in outgroups contributed to differences in tree topology in Bartley et al. (1992), Myers et al. (1998), and our reanalysis. However, the strong sensitivity of the results to this factor and to the choice of tree building algorithm and genetic distance simply reflects the low information content of the data regarding structure within the ESU.

Microsatellite data: Hedgecock (2002)

This data set is based on 7 microsatellite loci collected for samples of Chinook salmon from the Russian River and Eel River, as well as a number of populations from outside the geographic range of the CC-Chinook ESU. Samples from the Russian River and Eel River group together to the exclusion of all other populations, yet differ sufficiently to indicate separation between Chinook salmon in the these two basins (Hedgecock, 2002, Figure 3.1). Few conclusions can be drawn from these results regarding population structure, as there are no other within-ESU comparisons.

Microsatellite data: Santa Cruz Laboratory

Recent work at the NOAA Santa Cruz Laboratory provides additional genetic data for evaluation of genetic population structure of Chinook salmon in the CC-Chinook ESU (S. Blankenship et al. *unpublished data*). These data were collected from 19 microsatellite loci for 526 chinook salmon collected from 5 basins in the ESU: the Russian, Noyo, Mad and Eel rivers and Wages Creek. Two samples were collected from the Russian River, and multiple sites were examined in the Eel, including at least one site from three of the main tributaries: the South Fork, Middle Fork and upper main stem. Genetic data from populations in two Central Valley Chinook ESUs and one population from the Klamath River are included as outgroups. Adults comprise all of the samples save those from the lower Russian River (Healdsburg), Noyo River, and Wages Creek, which are based on collections of juveniles from downstream migrant traps, and thus might represent an admixture of spawning groups. Samples were collected from the 2000-2003 brood years, which means that they likely contain different proportions

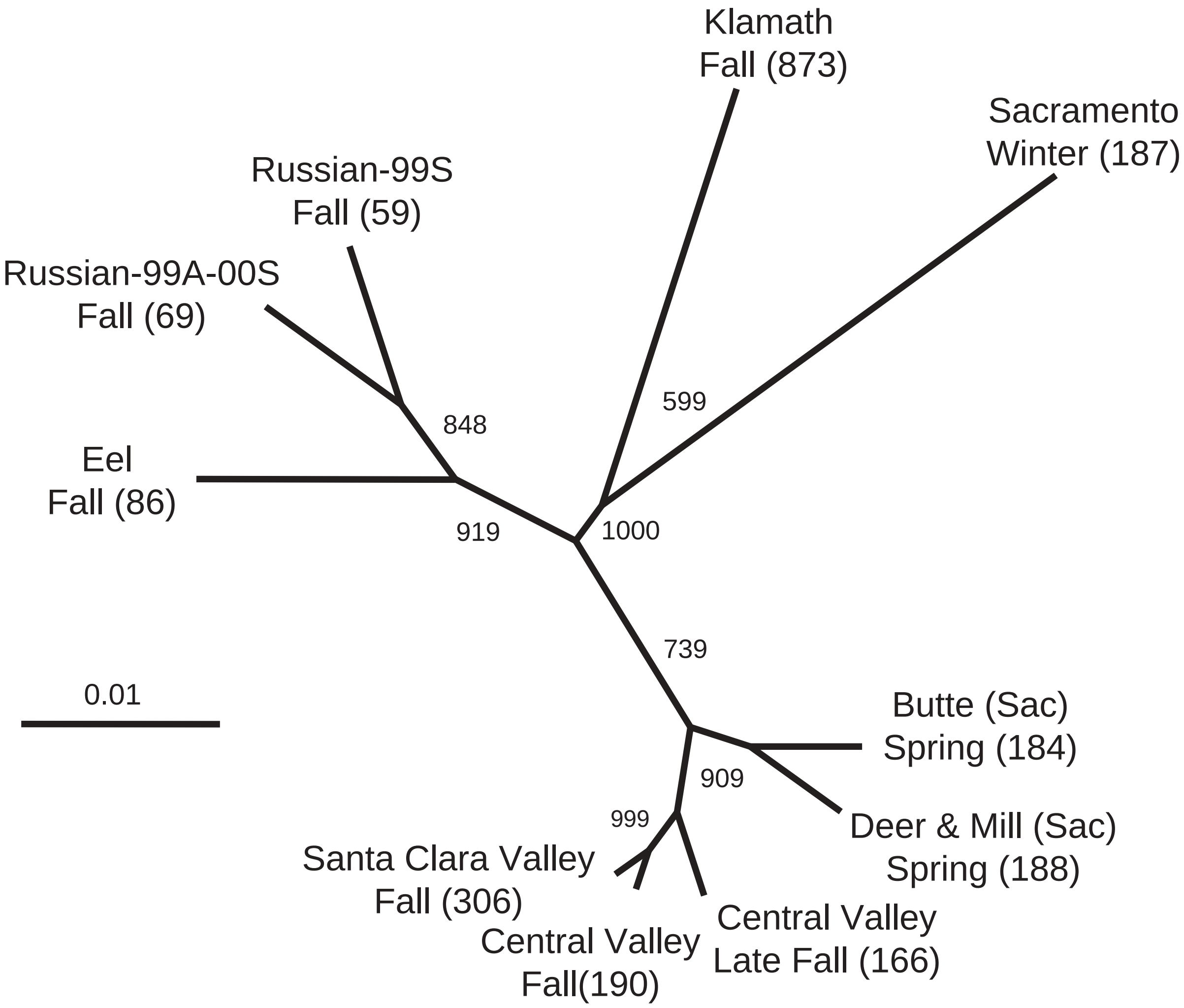

Figure 3.1. Unrooted UPGMA phylogram based on CSE chord distances calculated from data for 7 microsatellite loci, with all Eel River samples pooled. Central Valley data from Banks et al. 2000. Numbers in parentheses indicate sample size. Branch length is scaled to genetic distance (see scale in figure), and numbers at nodes indicate number of bootstrap iterations out of 1000 in which the node occurs. (Redrawn from Figure 9 in Hedgecock (2002)).

of individuals from specific cohorts, but are probably influenced largely by the same cohorts.

Initial analysis of these data with exact tests of population differentiation (cf. Raymond and Rousset, 1995) found significant differences in all interbasin sample comparisons. However, differentiation amongst samples from within the Eel River basin was minimal. The data did not reject the hypothesis that the sample from Cahto Creek (tributary to the South Fork Eel) was drawn from the same population as either the sample from Outlet Creek in the upper Eel basin or one of the tributaries to Outlet Creek (Baechtel Creek), and differentiation between the samples taken in Outlet Creek and another one of its tributaries (Long Valley Creek) was only marginally significant ($p = 0.047$). It should be noted that this test is very sensitive with microsatellite data, frequently finding significant differences on small temporal and spatial scales, and that p-values were not corrected for multiple tests. Therefore, although these tests indicate that gene flow between Eel river tributaries is high, they do not rule out the possibility that there is some differentiation among different subpopulations in the Eel, or that it existed historically.

Phylogeographic trees. Phylogeographic trees indicate rough correspondence between genetic structure and geography, including clear separation between populations from the CC-Chinook ESU and those from the Central Valley and upper Klamath River (Figure 3.2). Within the CC-Chinook ESU, all of the Eel River population samples form a cluster that also includes the Mad River sample, and the two samples from the Russian River, although they do not form a group supported by high bootstrap values, are indeed similar to one another. Differentiation between the two samples collected from the Russian River is likely due in part to differences in how the samples were collected: the sample from the upper Russian River is from adults that migrated upstream to the Coyote Valley Fish Facility, while the sample from the lower Russian River is from outmigrating juveniles and is might include contributions from a broader group of spawning adults[7]. The samples from Wages Creek and the Noyo River have significantly longer branch lengths than all other samples, which is probably a consequence of substantially lower effective population sizes in these samples compared to others in the data set[8], which might reflect the effect of recent population bottlenecks or recolonization events, or might simply reflect a disproportionate number of siblings in the sample.

Inferences regarding the role and structure of dispersal in the CC-Chinook ESU. The distribution of pairwise F_{ST} values indicates hierarchical structure within the CC-Chinook ESU (Figure 3.3). Mean pairwise F_{ST} value for all interbasin comparisons in the ESU was 0.0278 (±0.0156), which is over twice the mean value for intrabasin comparisons (0.0114 ±0.0058). Since F_{ST} is an inverse function of the number of migrants exchanged per generation between two populations, these results are consistent with our assumption that dispersal (straying) between tributaries within a basin (in this case mainly the Eel River) is much greater than between river basins.

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[7] Evidence that this sample does not represent the progeny of few adults is provided by the high allelic richness (an estimate of the average number of alleles per locus, corrected for sample size), which is a correlate of effective population size.

[8] Estimates of allelic richness, which is the mean number of alleles per locus and correlates with effective population size, for Wages Creek (3.30) and Noyo River (4.78) are substantially lower than the average for the remaining samples in the CC-Chinook ESU (5.96 ± 0.23).

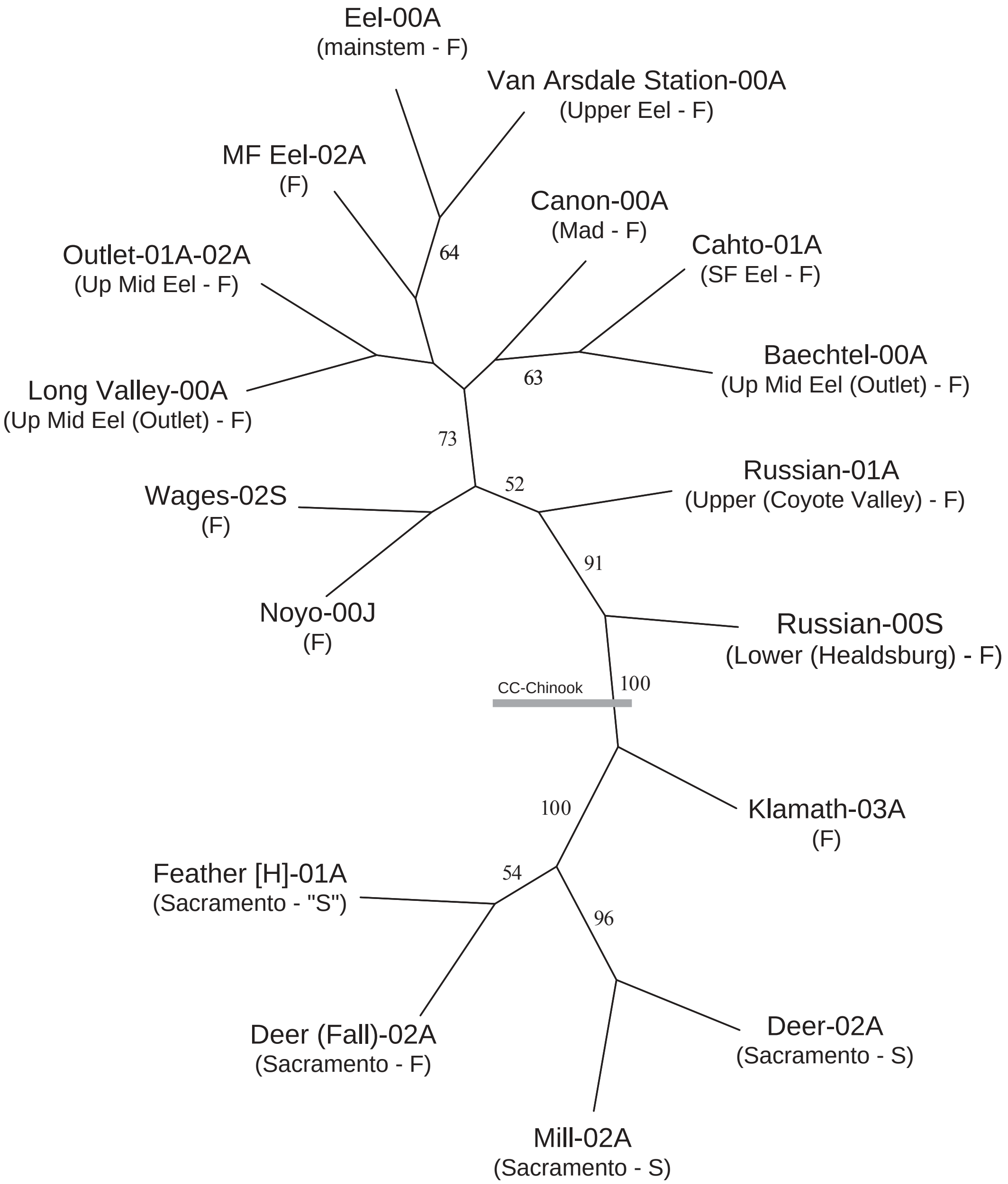

Figure 3.2. Bootstrap consensus tree for Chinook salmon in California. Consensus tree is based on trees constructed with a neighbor-joining algorithm (Saitou and Nei, 1987) using Cavalli-Sforza and Edwards (1967) chord distances calculated for 1000 data sets generated by bootstrap resampling from data for 19 microsatellite loci. Numbers on internal branches indicate the proportion ($>$50%) of trees in which the indicated note appeared. Samples are identified by stream, brood year, and life stage ("A" indicates adult; "S" smolt or outmigrating juvenile). Parenthetical information indicates river or stream to which the stream from which the sample was collected is tributary and run-timing of population represented by sample (F: fall-run, S: spring-run, "S": "spring-run" fish produced at Feather River Hatchery).

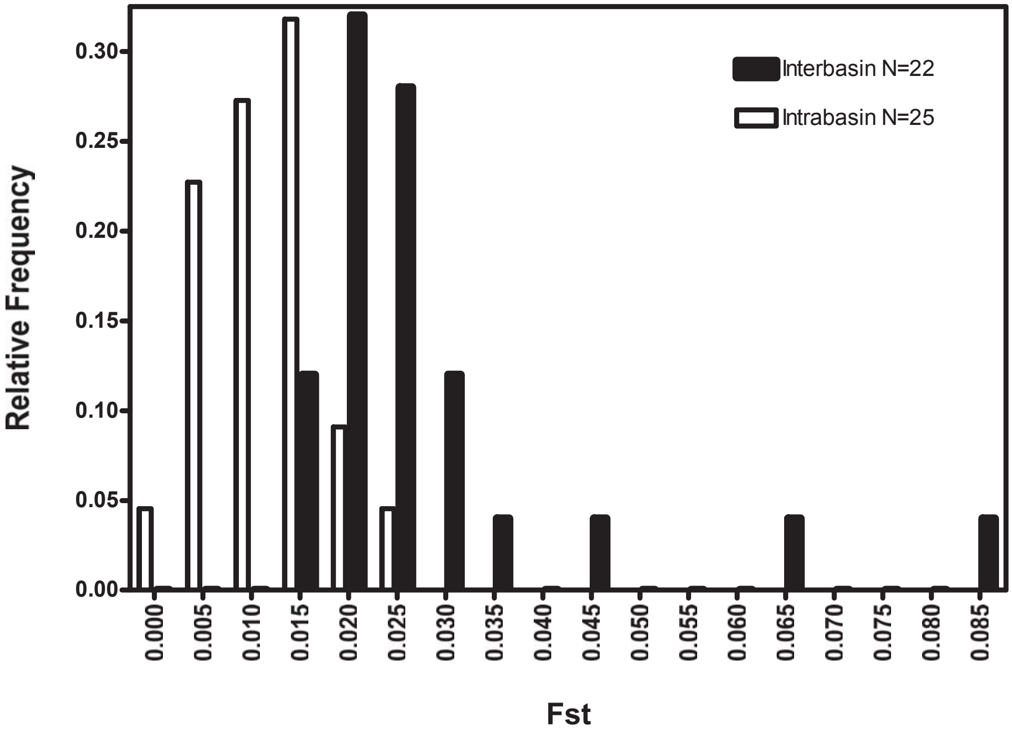

Figure 3.3. Frequency distributions of estimated pairwise F_{ST} for Chinook salmon from the CC-Chinook ESU, partitioned among intrabasin (white bars) and interbasin (dark bars) comparisons. All but one of the intrabasin comparisons are between samples from the Eel River basin.

Regression of pairwise F_{ST} on geographic distance revealed a weak, but marginally significant, signal of isolation-by-distance (results not shown). This is not entirely surprising given the geographic structure of the data set: samples from within the two large basins are separated by distances on the same order as distances between basin mouths, and few samples are available from intervening watersheds.

Assignment tests correctly assigned approximately 95% of fish to their basin of origin. Substantial rates of cross-basin misassignment occurred only from the Mad River to the Eel River (5 of 35 fish; 14.3%) and the Noyo River to the Eel River (2 of 19 fish; 10.5%). A few Russian River fish were misassigned to the Eel River (8 of 111 fish; 7.2%) or to Central Valley populations (5 of 111 fish; 4.5%). Within the Eel River basin, rates of cross-assignment between samples were substantial, with almost half (120 of 257 fish; 46.7%) of the individuals assigned to population samples other than those from which they were drawn.

3.4.3 Synthesis of information on population genetic structure

Biological structure inferred from available genetic data is consistent with the ESU structure of Chinook salmon (Figures 3.1 and 3.2, Myers et al., 1998; West Coast Chinook Salmon Biological Review Team, 1999); however, available genetic data are less informative regarding historical population structure within the CC-Chinook ESU. In part, this is because of the lack of samples from many of the watersheds in the NCCCRD, but the substantial uncertainty associated with the influence of artificial propagation on population genetic structure also contributes to the lack of definitive conclusions regarding genetic signals of historical population structure. Artificial production has occurred over a long time, during which a general decline in abundance of Chinook salmon is likely to have exacerbated the potential for stocked fish to have significant effect. Moreover, hatchery-reared fish were commonly transferred among basins directly or, where putatively local stocks were used, were reared according to practices that are now thought likely to inflate the dispersal rate of hatchery-reared fish. Indeed, the most critical uncertainty is not whether artificial propagation has influenced population genetic structure—it almost certainly has—but rather whether the effect of stocking within and across basins has been to mildly blur historically weak population structure or to eliminate initially strong signals of population structure.

With these limitations in mind, we note that the strongest signal within the ESU is the least surprising: that Chinook salmon from the Eel River and other northern watersheds differ from those from watersheds along the Mendocino coast and from those in the Russian River (Figures 3.1 and 3.2). This is not surprising, given the geographical distance between the various basins. However, we are not able to state with any certainty whether the degree of separation among populations apparent in the data reflects historical structure within the ESU or is is an artefact based on differences between the Eel River and a population of Chinook salmon in the Russian River that has been strongly influenced by out-of-basin transfers. Moreover, we can say little about the historical status of populations of Chinook salmon along the Mendocino Coast. Elsewhere in the CC-Chinook ESU, genetic data do not offer clear signals of population structure within and among northern basins of the NCCCRD. Microsatellite data suggest weak separation between samples collected in the upper and lower parts of the Eel River basin (Figure 3.2), but this pattern is not consistently apparent in other, less powerful data sets (Bartley et al., 1992). Likewise, while both microsatellite and allozyme data suggest that samples from low in the Eel River basin (e.g., the South Fork Eel River and the Van Duzen River) tend to group with samples from other coastal basins (e.g., the Mad and Mattole rivers), there are clear exceptions to this pattern in both data sets.

Given the high uncertainty inherent in the available genetic data and the additional uncertainty regarding the influence of stocking of hatchery fish on the population genetic structure of the CC-Chinook ESU, we consider the results of genetic analyses with great caution. Apparent signals of hierarchical structure within the data are consistent with expectations from parsimonious models of ESU structure, but the degree to which the population genetic structure of the CC-Chinook ESU is likely to have been disrupted from its historical state prevents us from straightforwardly drawing from these data strong support for the assumptions of our geographic model of ESU structure. Instead, we draw on the strength of patterns inferred for other species and observations of isolation-by-distance apparent in Chinook salmon elsewhere in the North Pacific (e.g., Guthrie and Wilmot, 2004) as support for our assumptions regarding dispersal that underlie our geographic model.

3.5 Geographical structure of the CC-Chinook ESU

Insight gained from analyses of genetic data generally support the assumptions of the geographic model for historical population structure in the CC-Chinook ESU, although with markedly more uncertainty than for ESUs of coho salmon and steelhead considered in this report. Nevertheless, we use the connectivity-viability model, which is outlined in general terms in the Introduction, to synthesize information on the relative size of historical populations of Chinook salmon and their distribution along the coast. In this section, we develop the inputs for the connectivity-viability model for populations of fall-run Chinook salmon in the CC-Chinook ESU, and review results of the analysis in the context of the assumptions that underlie the model. Again, our focus is solely on fall-run Chinook salmon, as we believe that our model for habitat potential is most appropriate for this life history type, and may be entirely inadequate for spring-run Chinook.

Translating IP-km into a proxy measure of population size

We use predictions from our IP model for spawning habitat of Chinook salmon as the basis for our habitat-based population proxy for fall-run Chinook salmon. Following the reasoning outlined in the Introduction, we assume that carrying capacity of populations of fall-run Chinook salmon is linearly proportional to the integrated length of accessible habitat within a watershed weighted by the intrinsic potential for habitat suitable for spawning (IP-km).

Viability-in-isolation threshold for Chinook salmon

To develop a preliminary threshold for viability-in-isolation for Chinook salmon, we make the following assumptions:

1. **An IP score of 1.0 corresponds to a maximum density of 20 redds per linear stream km.** We base this assumption on a review of available information on redd densities throughout northern California and the Pacific Northwest, taking into account (a) differences in the size of the rivers from which these estimates are taken, and (b) potential effects of variability in spawner density due to variation in ocean survival. This value is on the high end of the typical range of densities observed for watersheds in coastal Oregon (Riggers et al., 2003), and is comparable to values from large systems such as the Upper Columbia River (Hanrahan et al., 2004), and Klamath-Trinity basin (Quihillalt, 1999; Grove, 2003). Although more than 20 females can spawn in a given reach over the course of a spawning season, we assume that redd superposition effectively caps production at a level equivalent to 20 undisturbed redds per linear stream km. Other assumptions implicit in this assumption are discussed in greater detail below.

2. **A Chinook salmon population requires an average abundance of 2500 spawners per generation to be at negligible risk of extinction.** We chose 2500 spawners as a preliminary abundance corresponding to population viability following Allendorf et al. (1997). If we assume that the typical generation time for a typical Chinook salmon population in the CC-Chinook ESU is 4 years,

an average of 625 spawners per year will return to a population that is viable-in-isolation. Using a purely demographic model developed for a coastal population of Chinook salmon (spring-run Chinook in the South Fork Umpqua River), Ratner et al. (1997) found that an average abundance of 200-250 spawners per year appears to be consistent with long-term persistence. This number is substantially lower than the threshold presented here, which is based on the genetic concerns outlined in Allendorf et al. (1997); however, we choose to use the higher value as our threshold for viability-in-isolation to reduce the likelihood of erring by identifying populations as viable-in-isolation that are not. Choosing a higher threshold also buffers our analysis against having chosen too great a density of spawners per linear kilometer as a measure of the typical average capacity of streams of moderate size in the range of the CC-Chinook ESU.

3. **Chinook salmon exhibit a 1:1 sex ratio.**

Under these assumptions, we arrive at viability-in-isolation threshold of approximately 15.6 IP-km for fall-run Chinook salmon. We emphasize that this threshold depends strongly on the assumptions outlined above. Further, the assumptions are based on data from watersheds that are not part of the NCCCRD and ESUs other than the CC-Chinook ESU. Therefore, although we believe a threshold of 15.6 IP-km to be plausible, we adopt a precautionary stance and use a slightly higher threshold (20 IP-km) to account for uncertainty in the IP model used to predict potential for spawning habitat, and in the assumptions used to translate these predictions into population size as a proxy for population viability. We still assume that a population of fall-run Chinook salmon typically requires approximately 625 spawners per year to be viable, and our choice to adopt a threshold of 20 IP-km is intended solely to reflect uncertainty regarding our prediction of the habitat necessary to support a population of this size. By adopting this precautionary approach, we reduce the likelihood that populations that are not viable-in-isolation are treated in subsequent analyses as if they are.

By selecting this threshold for viability-in-isolation, we do not imply that populations occupying watersheds with less than 20 IP-km will 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 100s of years.

Consequences of assumptions underlying the viability-in-isolation threshold

Changing our general assumptions regarding typical maximum density of redds or the total number of spawners required for a population to persist will, of course, alter the threshold for viability-in-isolation. This is more a matter for sensitivity analysis than a structural consequence of our assumptions.

Our general assumption regarding maximum density of redds requires an implicit assumption or assumptions regarding the size of typical stream reaches or how redds are distributed within a stream reach. The simplest assumption—that the maximum density of redds in a stream reach is independent of the size of a stream reach—is generally untenable[9]. Therefore, more completely stated, our assumption is

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[9] One might assume that as the *area* of the typical stream reach increases with stream width, the proportion of that area that

that the maximum redd density of 20 redds per linear km applies to a typical stream reach in the smallest watershed that can support a population of Chinook salmon that satisfies our definition of viability-in-isolation. Since the average width (area) of a stream reach is expected to increase with some measure of watershed size, e.g., total mean annual discharge at the mouth, it might be expected that the typical reach of larger watersheds can potentially accommodate more spawning Chinook salmon than can the typical reach of a smaller watershed. If this is so, carrying capacity of a watershed will increase as some power (greater than one) of watershed size measured as IP-km, and thus violate our assumption that population carrying capacity is linearly proportional to IP-km. By accepting the implicit assumption—that the maximum redd density applies to the minimum watershed—the location of the viability-in-isolation threshold is fixed according to the assumptions listed above. However, if population carrying capacity increases as some power (greater than one) of IP-km, then we expect populations populations to shift towards the extremes of the diagonal distribution in viability–self-recruitment space: populations in watersheds smaller than the viability-in-isolation threshold will actually be smaller than predicted and have lower self-recruitment, and conversely, populations watersheds smaller than the viability-in-isolation threshold will be larger than predicted and have higher self-recruitment. Note that this implicit assumption does not undermine the qualitative results of the connectivity-viability analysis, which derive from a monotonic ranking of populations according to size on one axis (viability-in-isolation) and a function of relative size on the other (self-recruitment).

Connectivity-viability analysis

We conducted self-recruitment analyses for fall-run Chinook salmon for the set of watersheds that exceeded 2.0 IP-km for Chinook salmon, following our typical practice of setting the threshold for including a watershed at 10% of the viable-in-isolation threshold. We examined a case in which the full Eel River basin was included, and also a case in which exchanges between the Eel River and other basins were limited to the South Fork Eel River, Van Duzen River and tributaries of the Lower Eel River. The latter analysis is intended to reflect a potential difference in rates at which Chinook salmon that spawn in interior, high elevation subbasins and those that spawn in tributaries closer to the coast disperse to other basins along the coast. We assume that immigration from the Klamath River is negligible; genetic evidence used to delineate ESUs suggests that this assumption is reasonably robust (Myers et al., 1998; West Coast Chinook Salmon Biological Review Team, 1999). We include a San Francisco Bay population as a (small) proxy for Central Valley stocks. We treat the southern boundary as open to emigration, but include no potential populations south of the Golden Gate.

Figure 3.4 illustrates the results from analyses with sources of emigration from the Eel River limited to the lower Eel River basin. Predictions of IP for Chinook salmon suggest that a number of watersheds in the NCCCRD are sufficiently large to support independent populations of Chinook salmon, and among these, many consistently appear as functionally independent according to the connectivity-

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is suitable as spawning habitat declines. While this appears to be somewhat consistent with the observation that in large rivers, a large proportion of the streambed lies in areas where the water is too deep and the stream flows too slowly for spawning habitat to occur (e.g., Hanrahan et al., 2004), the likelihood that such a relationship is exactly compensating is very low.

viability analysis (i.e., Redwood Creek (Humboldt) [1], Mad River [5], Eel River [7], Mattole River [14], Ten Mile River [23], Noyo River [25], Big River [30], Navarro River [34], and Russian River [42]). Predictions of self-recruitment to populations in the Mad River [5] and Mattole River [14] are sensitive to the assumption regarding sources of immigration from the Eel River–including the entire Eel River as a whole reduces self-recruitment to these populations so that the Mad River [5] population falls in the "potentially independent" quadrant of viability-independence space[10] and the status of the Mattole River [14] population becomes more dependent on the details of the dispersal model. Self-recruitment to Redwood Creek (Humboldt) [1] is less sensitive to our assumptions regarding the Eel River, but is sensitive to the assumption that immigration from the Klamath River is negligible. The connectivity-viability analysis predicts that populations in tributaries to Humboldt Bay [6], Bear River [10], Garcia River [39], and Gualala River [41] were potentially independent under historical conditions. All other historical populations are likely to have been dependent on one or more of the larger populations.

Figure 3.5 illustrates the contribution of immigration from source populations to sink populations predicted by the connectivity-viability model. Not surprisingly, historically large populations of Chinook salmon in the Eel [7] and Russian [42] rivers would be predicted to have strong influence in the northern and southern parts of the CC-Chinook ESU, respectively. Immigration from the source populations occupying moderately sized watersheds along the Mendocino Coast plays a more local role, but appears to be important in linking the structure of the ESU. The apparently high rate of dispersal from the Mattole River [14] to Usal Creek [17] is an artefact of the structure of the model: half of the individual dispersing from the Mattole River [14] (or from any population, for that matter) are assumed to disperse to the south, and the first suitable watershed south of the extensive Lost Coast is Usal Creek, which therefore receives the bulk of these dispersers. Note, however, that if the level of immigration from north of the Lost Coast (i.e., the Mattole River [5], Eel River [7], Bear River [10], etc.) to Usal Creek [17] is reduced substantially or even eliminated, the population of Chinook salmon in Usal Creek [17] remains a dependent population, due to immigration from sources to the south.

3.6 Abundance and Population Dynamics

Historical time series of counts of upstream migrating adults are available for Benbow Dam (South Fork Eel River; 1938-1975), Sweasy Dam (Mad River; 1938-1964), and Cape Horn Dam (Van Arsdale Fish Station, Eel River; 1981-present, sporadic counts before 1980), and a handful of contemporary time series are available for various tributaries in the Eel River basin, the Mattole River, and basins to the north (Status Review Update). While none of these time series is particularly well-suited to analysis of population dynamics (Bjorkstedt and Spence, 2005), we note that the time series of adult

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[10] Predictions of self-recruitment to the Mad River [5] population are somewhat surprising given the extent of habitat predicted by the IP model. In part, the influence of the Eel River on self-recruitment to the Mad River [5] population reflects the unique structure of Humboldt Bay and its effect on how the connectivity-viability model distributes dispersers as a function of distance from the source population. The spits that separate Humboldt Bay from the Pacific Ocean present an extensive stretch of coastline with a single access point. In the connectivity-viability model, this structure results in a more extensive interval over which the Mad River [5] "collects" immigrants than would occur if each tributary to Humboldt Bay drained directly to the Pacific or if the mouth to Humboldt Bay were situated further north.

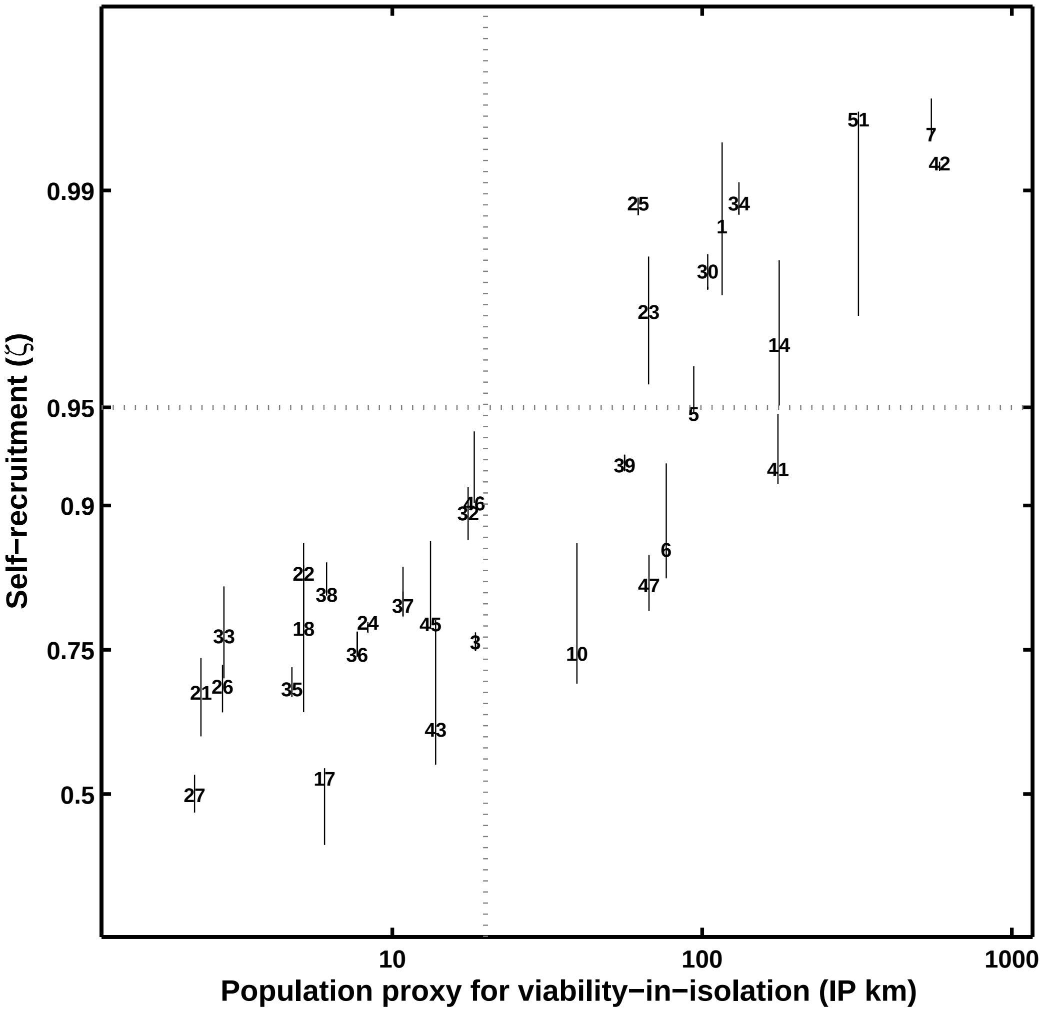

Figure 3.4. Self-recruitment and viability-in-isolation of putative populations in the CC-Chinook ESU. Only watersheds with ≥ 2.0 IP-km are included in the analysis. Fidelity rate 0.95. Vertical lines indicate self-recruitment for dispersal functions described by exponential decline with distance with parameters ranging from -0.01 to -0.1 km. Horizontal grey 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 grey dotted line indicates viability-in-isolation threshold at 20 IP-km (see text). Watershed names given in Table 1.1.

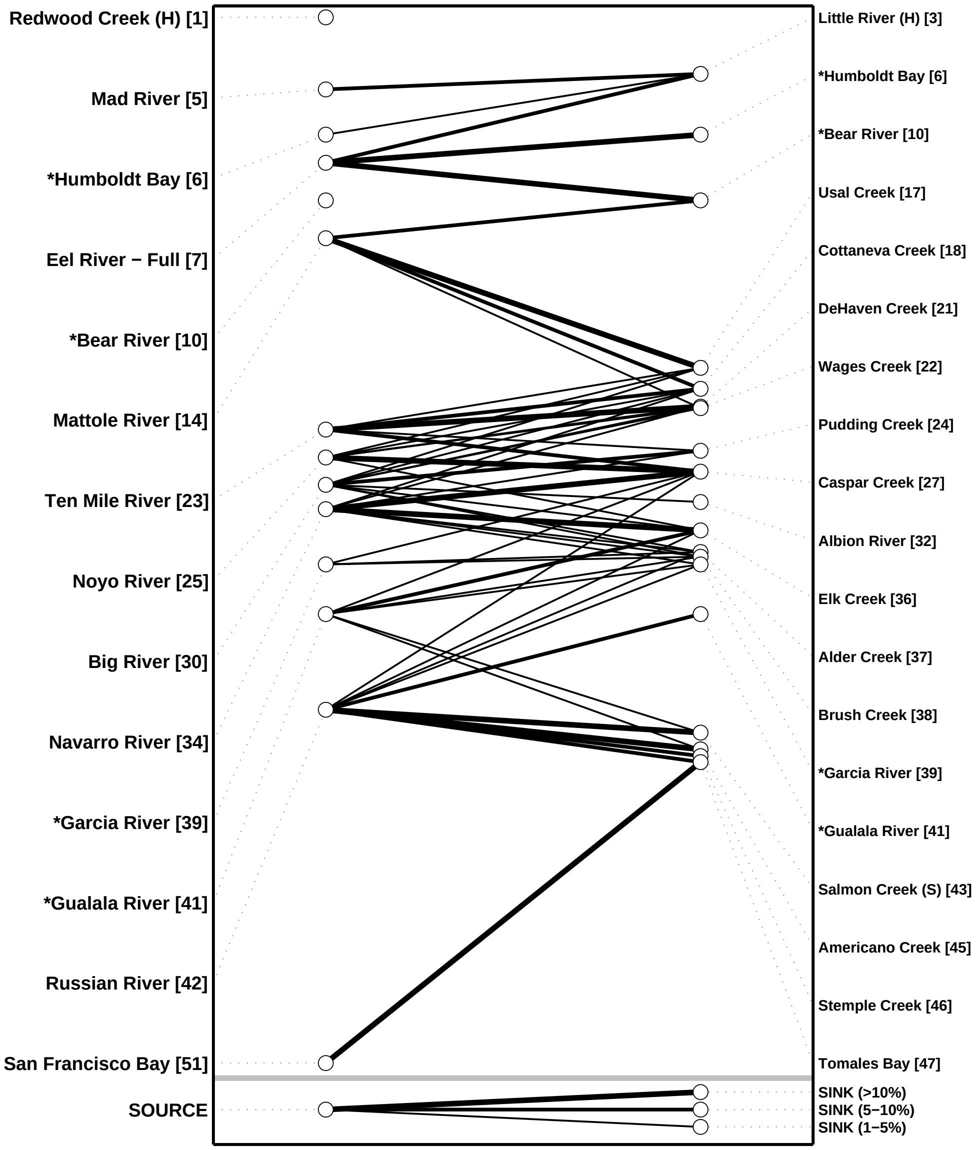

Figure 3.5. Connectivity within the CC-Chinook ESU, as measured by the contribution of source populations (on the left) to sink populations (on the right) as a function of the proportion (in excess of 1%) of the spawning run to a sink population contributed by each source population. Connectivity based on an exponential dispersal function with the decay parameter set to -0.05 km. Distribution of populations reflects distance along the coastline. Assignment of populations as source (functionally and potentially independent) or sink (potentially independent and dependent) populations is based solely on comparison of IP-km to our viability-in-isolation threshold of 20 IP-km. Potentially independent populations are indicated by an asterisk. (Self-recruitment to potentially independent populations is ignored in this plot.) Emigration from the only lower portion of the Eel River basin (tributaries downstream of the confluence of the South Fork Eel, inclusive) is included in this analysis.

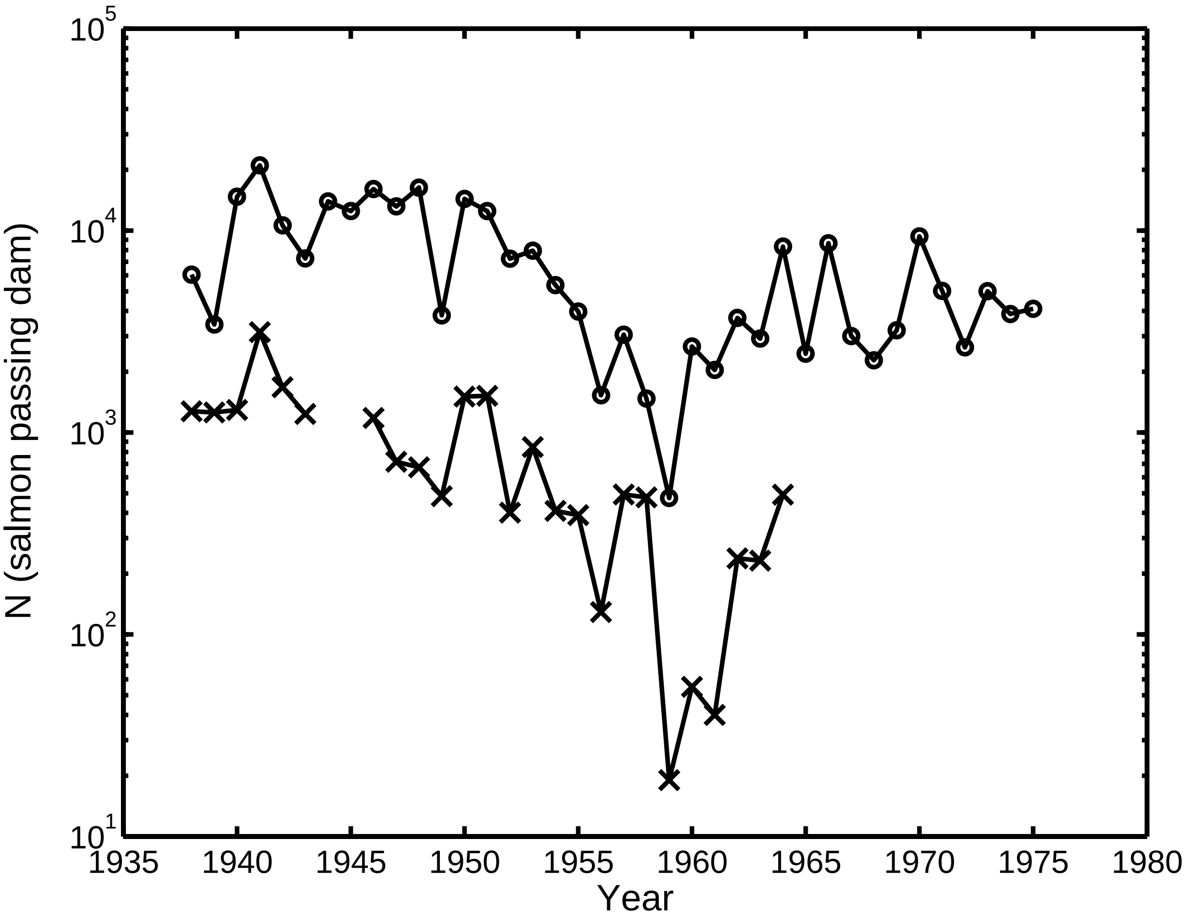

Figure 3.6. Time series of adult counts made at Benbow Dam (South Fork Eel River; ○) and Sweasy Dam (Mad River, ×).

counts in the Mad and South Fork Eel rivers exhibit strong temporal correlation (Figure 3.6); a similar pattern of correlation among observational time series is apparent in more contemporary data (Bjorkstedt and Spence, 2005). These correlations most likely reflect population responses to temporally variable environmental processes that exhibit strong coherence over large spatial scales rather than the effect of strong demographic coupling among populations in different basins.

3.7 Life History Variation

Differences in the ecology and behavior of fall- and spring-run Chinook salmon support treating populations each life-history type as distinct units, even where the two coexist in a basin. However, information on other aspects of Chinook salmon life history in the CC-Chinook salmon ESU is sparse, and in general, insufficient to quantify a consistent pattern for most populations, much less to support comparison among populations. The TRT did not find any such data informative for delineating independent populations.

3.8 Historical population structure in the CC-Chinook ESU

Biological data relevant to the issue of population structure in the CC-Chinook ESU are generally sparse (essentially non-existent for spring-run Chinook salmon) and vary considerably in space with respect to the quality and historical extent of available information. By synthesizing available biological information with model predictions and analyses based on information extracted from GIS, we are able to draw some broad conclusions regarding population structure, but find that conclusions regarding some important aspects of the historical population structure of the ESU are ambiguous at best. In the following synthesis, we outline the basis for our conclusions and highlight important uncertainties and briefly discuss their consequences for subsequent TRT analyses.

3.8.1 Historical population structure of fall-run Chinook salmon in the CC-Chinook ESU

Table 3.2 summarizes our conclusions regarding historical population structure for fall-run Chinook salmon. In the following sections, we outline the basis for our conclusions. Rather than structure our discussion in a north-to-south direction, we begin with our analysis of population structure within the Eel and Russian rivers, as many of our conclusions regarding populations in other basins are conditional on the status and structure of populations of Chinook salmon in these large basins.

Before delving into the specifics, however, one general issue warrants discussion. Given the potential for a non-linear relationship between IP-km and population carrying capacity for Chinook salmon, and the consequences of such a relationship for our connectivity-viability analysis, we believe that Chinook salmon were relatively more concentrated in functionally independent and potentially independent populations than were coho salmon and steelhead. Moreover, we believe that an extremely large proportion of Chinook salmon in the CC-Chinook ESU spawned in watersheds with measures of IP-km that fall at or above our viability-in-isolation threshold, while the number of spawners in watersheds much smaller than this threshold, say those watersheds with less than approximately 10 IP-km, is likely to have been quite small. We therefore suspect that the smaller dependent populations listed in Table 3.2 were, in fact, extremely dependent on immigration for regular occupancy. We emphasize this point as this general pattern has potentially important implications for how dependent populations are incorporated into ESU viability criteria.

Eel River

The state of available information makes it difficult to resolve the historical population structure of fall-run Chinook salmon in the Eel River, and any conclusion will therefore depend strongly on assumptions made in the course of analysis. Alternative hypotheses range from a single, structured population to a set of nine or more populations that occupy geographically or environmentally discrete subbasins and that vary with respect to viability-in-isolation and self-recruitment. Unfortunately, available genetic data do not provide a clear picture of population structure within the Eel River. Given the long history of hatchery production of Chinook salmon in the Eel River and the extent of among-basin transfers within

Table 3.2. Historical population structure of fall-run Chinook salmon in the CC-Chinook ESU.

Population	**IP km**	**Self-recruitment**	**Historical Population Status**
Redwood Creek (H) [1]	116.05	0.987	**Functionally Independent**
Little River (H) [3]	18.55	0.761	***Potentially Independent***
Mad River [5]	93.95	0.948	**Functionally Independent**
Humboldt Bay [6]	76.66	0.866	***Potentially Independent***
Lower Eel River**	67.79	0.993	**Functionally Independent**
Upper Eel River***	88.25		**Functionally Independent**
Bear River [10]	39.44	0.745	***Potentially Independent***
Mattole River [14]	177.50	0.968	**Functionally Independent**
Usal Creek [17]	6.04	0.530	dependent†
Cottaneva Creek [18]	5.17	0.779	dependent†
DeHaven Creek [21]	2.41	0.684	dependent†
Wages Creek [22]	5.17	0.843	dependent†
Ten Mile River [23]	67.18	0.975	**Functionally Independent**
Pudding Creek [24]	8.34	0.788	dependent
Noyo River [25]	62.18	0.989	**Functionally Independent**
Hare Creek [26]	2.83	0.694	dependent†
Caspar Creek [27]	2.30	0.499	dependent†
Big River [30]	104.31	0.982	**Functionally Independent**
Albion River [32]	17.57	0.895	dependent
Big Salmon Creek [33]	2.86	0.770	dependent†
Navarro River [34]	131.46	0.989	**Functionally Independent**
Greenwood Creek [35]	4.74	0.690	dependent†
Elk Creek [36]	7.70	0.744	dependent†
Alder Creek [37]	10.82	0.808	dependent†
Brush Creek [38]	6.14	0.821	dependent†
Garcia River [39]	56.22	0.924	***Potentially Independent***
Gualala River [41]	175.63	0.922	***Potentially Independent***
Russian River [42]	584.16	0.992	**Functionally Independent**
Salmon Creek (S) [43]††	13.80	0.621	dependent†
Americano Creek [45]††	13.29	0.785	dependent†
Stemple Creek [46]††	18.38	0.902	dependent†
Tomales Bay [47]††	67.35	0.831	dependent†

* The threshold for viability-in-isolation is set at 20 IP km (see text for how this value was selected). **The Lower Eel River population occupied tributaries of the Eel River downstream of the confluence of the South Fork Eel River (inclusive) and is concentrated in the South Fork Eel River. ***The Upper Eel River population occupied tributaries of the Eel River upstream of the confluence of the South Fork Eel River (exclusive) and is concentrated in the Middle Fork Eel River. †On the basis of environmental considerations and potential bias in the relation between IP km and population carrying capacity, it is unlikely that fall-run Chinook salmon consistently occupied these basins. Historical records of Chinook salmon are not available for any these basins, save Wages Creek, from which a recent sample was collected. See text for further discussion. ††These streams are south of the currently accepted range of the CC-Chinook ESU (Myers et al., 1998); we concur that persistent populations of Chinook salmon are not likely to have occupied these watersheds under historical conditions.

the basin, it is likely that whatever structure may have existed historically has been masked or altered. The degree to which genetic structure has been altered is unknown, so we remain uncertain whether current patterns represent a relatively small departure from weakly structured populations or substantial degradation of strong population genetic structure within the basin[11].

Based on available information and what we consider to be plausible assumptions regarding the historical characteristics of the Eel River basin, we conclude that fall-run Chinook salmon in the Eel River basin historically existed as two functionally independent populations: a Lower Eel River population anchored in the South Fork Eel River, and an Upper Eel River population anchored in the Middle Fork Eel River. The proposed Lower Eel River population includes fall-run Chinook salmon that spawn in the South Fork Eel River [E3] and tributaries of the mainstem Eel River downstream of the confluence of the South Fork Eel River, including the Van Duzen River [E2]. The proposed Upper Eel River population includes fall-run Chinook salmon that spawn in the mainstem and tributaries upstream of the confluence of the South Fork Eel River, including the North Fork Eel River [E5], tributaries of the middle and sections of the mainstem Eel River [E4 and E7], and is concentrated in the Middle Fork Eel River [E6] and the tributaries of the upper mainstem Eel River[12] [E8].

Three factors or assumptions form the basis for our conclusions. First, the South Fork and Middle Fork are historically identified as important basins for the production of Chinook salmon, and they are thought to have far outweighed the contribution of any other watersheds or subbasins to the production of fall-run Chinook salmon from the Eel River (CDFG, 1965). This historical pattern is borne out in part by the results of our IP model for fall-run Chinook salmon. Our IP model also highlights the potential for major tributaries to provide extensive habitat for Chinook salmon (Plate 12) (e.g., the Van Duzen River and Larabee Creek in the lower basin, and Outlet Creek, Tomki Creek, and the upper Eel River in the upper basin). However, we believe it likely that dispersal of Chinook salmon from the South Fork and Middle Fork exerted substantial influence on the dynamics of Chinook salmon spawning in neighboring tributaries and mainstem habitats. In coming to this conclusion, we assume that under historical conditions, relatively few salmon spawned in the mainstem Eel River, but that use of the mainstem for spawning was sufficient to facilitate connectivity between groups of salmon spawning in tributaries with closely co-located confluences. Such connectivity might have been greatly magnified in years of low precipitation, when access to tributary habitats was more restricted and spawning distributions were more likely to overlap in mainstem habitats.

Second, we assume that, regardless of the availability of spawning habitat in the mainstem Eel River, the gap of approximately 100 river km between the confluences of the South and North forks of the Eel River[13] restricted exchange between the upper and lower basin sufficiently for populations in the

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[11] Note that available genetic data do not rule out the alternative, albeit less likely, hypothesis that disruption of mainstem spawning habitats created fragmented populations within the Eel River, and that current patterns might reflect recent differentiation.

[12] Note that under historical conditions, the Upper Eel River population included Chinook salmon that historically spawned in reaches and tributaries that are currently inaccessible behind Cape Horn and Scott dams.

[13] Assuming that spawning is greatly limited in the mainstem Eel River, Dobbyn Creek and Chamise Creek, which enter the mainstem Eel River at points spaced at intervals approximately one-third the distance between the confluences of the South and North forks, are the only tributaries to this stretch of the Eel River that exhibit areas of appreciable, albeit relatively small,

upper and lower basin to exhibit independent dynamics and differentiation. Even if the mainstem Eel River provided some spawning habitat, the year-to-year flux of individuals over this distance is likely to have been quite small relative to the size of the populations in each part of the basin. In designating Chinook salmon spawning upstream of the confluence of the South Fork as part of the Upper Eel River population, we continue to assume that the likelihood of dispersal among spawning groups decreases with distance, but also assume that the influence of a putative population through dispersal is strongest on those spawning groups it passes during its return (upstream) migration, rather than on groups for which dispersal would require overshooting the natal stream.

Third, although the geographic range for each proposed population includes a broad range of environmental conditions, we conclude that this variability—when considered in the context of other factors that contribute to population differentiation—provides insufficient support for delineating historical populations at scales finer than the upper and lower basin. Factors that we believe reduce the potential for environmental heterogeneity to drive differentiation of fall-run Chinook salmon include (1) where fall-run Chinook salmon occur in a watershed and how long they remain in freshwater, and (2) the potential for dispersal and mixing of spawners from multiple neighboring tributaries in mainstem habitats during low-water years. For environmental heterogeneity to manifest in population structure, it must present substantially different selective environments, and the differences in selective regimes must be sufficient to overcome the homogenizing effect of dispersal (Kawecki and Holt, 2002; Lenormand, 2002). Fall-run Chinook salmon tend to spawn lower in a given watershed and spend less of the life-cycle in freshwater than do other anadromous salmonids. Each of these two characteristics reduces the potential for differences in selection based on environmental characteristics: the fish are likely to encounter to more consistent conditions, regardless of watershed, and are exposed to any variation in selective forces for a more limited part of the life cycle. Asymmetric dispersal due to the dominance of a single sub-basin in each of the two proposed populations and the potential for relatively strong, albeit perhaps sporadic, mixing in mainstem habitats within the upper and lower basins increase the ability of dispersal to counter the effects of heterogeneous selection. Therefore, despite substantial environmental variation within the Eel River basin as a whole, and within each of the two historical populations, we expect (1) that dispersal within the upper and lower basins, measured as a long-term average, is sufficiently high to prevent population differentiation, and (2) that only the relatively small amount of spawning habitat in the Lower Middle mainstem Eel limits dispersal sufficiently for clear population structure to arise. At this larger scale, we assume that dispersal is sufficiently reduced for differences in environmental characteristics between the two core basins (the South and Middle forks), although probably muted, to be the dominant environmental influences on population structure.

We think that the two-population structure proposed above for fall-run Chinook salmon in the Eel River Basin is as well or better supported by the available data than any of the continuum of plausible alternative hypotheses. We recognize, however, that alternative hypotheses exist, and that subtle shifts in our assumptions regarding the balance between dispersal on one hand and the strength and variation of selection on the other lead to other, perhaps equally plausible conclusions. For example, if dispersal were more restricted or if environmental variability resulted in stronger, more divergent selection on

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extent where IP for spawning habitat for fall-run Chinook salmon is relatively high.

fall-run Chinook salmon than we assume to have been the case, the historical population structure of fall-run Chinook salmon in the Eel River might have included functionally independent populations in the South Fork Eel River [E3] and Middle Fork Eel River [E6], functionally or potentially independent populations in at least the Van Duzen River [E2], North Fork Eel River [E5], and some or all of the upper Eel River and its tributaries [E8], and dependent populations in the larger mainstem tributaries (e.g., Larabee, Outlet, and Tomki creeks). We expect, however, that the smallest scale at which historical populations of fall-run Chinook salmon in the Eel River were differentiated was substantially larger than the corresponding scale for winter steelhead in the same basin (see §1.5.7).

In recognizing the uncertainty in our conclusion, it is also useful to consider the consequences of this uncertainty for subsequent analyses. We believe that, at least in this case, the consequences of uncertainty and the specific conclusion reached are relatively small. In part the relative inconsequence of uncertainty in delineating population structure in the Eel River arises from the need to consider spatial structure and diversity at multiple scales in evaluating population and ESU viability. In part, too, uncertainty in population structure is buffered by the likely historical distribution of Chinook salmon as a function of the structure of the Eel River basin itself. In considering the alternative hypotheses noted above, we recognized that the South and Middle forks of the Eel River consistently emerge as major components of the Eel River population or population complex. In our proposed structure, the Lower Eel River population is anchored in the South Fork, and the Upper Eel River population is anchored in the Middle Fork. If, instead, fall-run Chinook salmon existed in many populations within the Eel River basin, the South and Middle forks, by virtue of harboring functionally independent populations, would still be central to the viability of the ESU. At the other extreme, if fall Chinook salmon in the Eel River formed a single, integrated population, the South and Middle forks would still be considered the two core areas for production of fall-run Chinook salmon, and thus be considered important for both population and ESU viability, particularly with respect to diversity and the resilience afforded by spatial structure in the ESU's largest historical population.

Russian River

Information on the historical status of Chinook salmon in the Russian River is ambiguous, and clouded by the fact that the historical presence of Chinook salmon in the Russian River is itself poorly documented (Steiner Environmental Consulting, 1996, and see the Introduction). Despite the lack of clear records, the high likelihood of suitable habitat under historical conditions and recent successful reproduction by fall-run Chinook in the basin offer strong evidence that a substantial population of fall-run Chinook salmon historically existed in the Russian River (Moyle, 2002).

Based on the size of the watershed and the distribution and extent of areas with high IP for spawning habitat, fall-run Chinook salmon in the Russian River basin are likely to have comprised at least one functionally independent population under historical conditions. Three lines of evidence lead us to conclude that a single functionally independent population of Chinook salmon historically occupied the Russian River. First, the results from our IP modeling exercise and a compilation of recent records and expert opinion on the distribution of Chinook salmon indicate relatively contiguous distributions of spawning habitat, at least in the mainstem river upstream of the confluence of Dry Creek and in Dry Creek itself (Agrawal et al., 2005, Plate 12). Indeed, Chinook salmon that used any areas of spawning habitat in smaller tributaries were likely to be strongly influenced by dispersal from the larger population in the upper basin. Second, available genetic information does not offer strong support to the hypothesis that multiple populations of Chinook salmon currently occupy, and thus might have historically occupied, the Russian River basin. We note, however, that it is likely that current genetic structure in the Russian River does not accurately reflect historical structure, most likely as a consequence of the large input of hatchery fish from diverse stocks to the basin. Third, compared to the other large basin in the CC-Chinook ESU, the Eel River, environmental characteristics are not highly variable within the Russian River basin in areas where Chinook salmon were most probably concentrated, particularly during the part of the year that fall-run Chinook salmon spend in freshwater. Thus, there is little cause for partitioning Chinook salmon in the Russian River on the basis of environmental or ecological variability.

Redwood Creek to Mattole River

This historical status of populations of Chinook salmon along this stretch of coast is closely tied to the amount of dispersal from the Eel River and the source of emigrants from the Eel River. Unfortunately, genetic information in this region is likely to have been substantially altered by extensive artificial propagation and inter-basin transfers, particularly between populations in the Mad and Eel rivers. Therefore, we are forced to rely heavily on predictions from the connectivity-viability model and our analysis of environmental variation.

Results from the IP modeling exercise indicate five watersheds included sufficient habitat to support a population of fall-run Chinook salmon that is likely to have been viable-in-isolation under historical conditions: Redwood Creek (Humboldt) [1], Mad River [5], tributaries to Humboldt Bay [6], Bear River [10], and Mattole River [14]. The historical population of Chinook salmon in Little River (Humboldt) [3] lies near our threshold for viability-in-isolation.

The connectivity-viability analysis also suggests that every basin draining this stretch of coastline was likely to have received substantial numbers of immigrants from the Eel River; however, we conclude that, despite immigration from the Eel River, populations of Chinook salmon in Redwood Creek (Humboldt) [1], Mad River [5], and Mattole River [14] were sufficiently large to act as functionally independent populations under historical conditions. Although the status of the populations in the Mad and Mattole rivers is sensitive to our assumptions regarding what portions of the Eel River basin contribute immigrants, the source of effective immigration to these populations from the Eel River is likely to have been limited to the Lower Eel River population. Comparison of environmental characteristics indicates that the lower Eel River, particularly in regions likely to be occupied by fall-run Chinook salmon, is more similar to neighboring coastal basins than is the upper Eel River. Analysis of available genetic data groups samples from the Mad, Mattole, and Bear rivers with samples from the Lower Eel River population; however, structure within these groupings is not robust (Bartley and Gall, 1990; Bartley et al., 1992, §3.4.2). Unfortunately, it is difficult to resolve the degree to which such patterns reflect historical population structure or the effects of hatchery practices and interbasin transfers. The historical status of Redwood Creek (Humboldt) [1] depends on the level of dispersal from the Klamath River and other basins to the north; however, available genetic data offer some support for our assumption that dispersal from the north is negligible, which supports our conclusion that this population was functionally independent.

Populations in Humboldt Bay [5] and Bear River [10] are situated among much larger basins, including the Eel River, and are likely to have received substantial immigration from their neighbors. We therefore conclude that fall-run Chinook in Humboldt Bay [5] and Bear River [10] existed as potentially independent populations under historical conditions. As noted above, the historical population of Chinook salmon in Little River (Humboldt) [3] lies near our threshold for viability-in-isolation. This watershed is not likely to exhibit any major departure from the assumptions that underlie the hydrological component of the IP model, which reduces the concern that motivated the precautionary nature of our threshold for viability-in-isolation. We therefore conclude that Chinook salmon in Little River (Humboldt) [3] were historically a potentially independent population. We expect that consistent occurrence of Chinook salmon in any watersheds smaller than Little River (Humboldt) [3] would have depended on dispersal from one or more of the larger populations in this region.

Cape Mendocino to Point Arena

Our ability to come to satisfactory conclusions regarding the historical structure of Chinook salmon is especially hindered by a lack of information regarding the historical distribution and abundance of Chinook salmon in this part of the ESU's range. Fall-run Chinook salmon are consistently observed in the Ten Mile, Noyo, and Big rivers, and sparse accounts indicate that they occurred in the Albion, Navarro, and Garcia rivers. Predictions from the IP model are useful, but are constrained by a lack of information on how consistently Chinook salmon would have access to freshwater during the spawning season as a consequence of variation in the timing of sandbar breaching, particularly for more southern watersheds in this region. Genetic information suggests that Chinook salmon in these watersheds, at least in the northern watersheds, are not closely linked with populations in the watersheds north of Point Arena or to Chinook salmon in the Russian River. While this result is consistent with the isolation of this region from populations to the north and south by extensive stretches of coastline that lack suitable habitat for Chinook salmon, available data do not support comprehensive evaluation of this structure.

Given the substantial uncertainty surrounding information relevant to the historical population structure of Chinook salmon in this region, we considered a broad range of hypotheses for historical population structure. At one extreme, we considered the possibility that Chinook salmon consistently occupied only a few watersheds in this region and that these populations depended on immigration from the Russian River or populations to the north for long-term persistence or recolonization. At the other extreme, we considered the possibility that Chinook salmon were highly abundant in this region, and that Chinook salmon in the larger watersheds (i.e., the Ten Mile [22], Noyo [24], Big [28], Navarro [32], and Garcia [37] rivers) existed in functionally independent populations under historical conditions. Under the latter hypothesis we also considered the possibility that dispersal from the Russian River to these basins was more limited than would be predicted by the connectivity-viability model due to the extensive coastline separating the two watersheds and possible differences in the timing of spawning runs related to variation in sandbar dynamics. In considering this suite of hypotheses, we recognize that uncertainty regarding the historical status of Chinook salmon increases from a north-to-south direction, since the current lack of persistent populations of Chinook salmon in watersheds south of Big River is consistent with both the consequences of anthropogenic impacts, which were more intense at earlier times in watersheds closer to San Francisco, and the expectation of inherently less favorable environmental conditions towards the southern end of the species' range.

We conclude that the structure summarized in Table 3.2 represents the most likely historical population structure for fall-run Chinook along this stretch of coastline. Chinook salmon in the larger basins north of Point Arena (i.e., the Ten Mile [22], Noyo [24], Big [28], and Navarro [32] rivers), are likely to have existed as functionally independent populations. As support for this conclusion, we cite (1) continued occurrence of Chinook salmon in the Ten Mile, Noyo, and Big Rivers under current conditions, and (2) environmental similarities with watersheds to the north that are known to support Chinook salmon. The Navarro River [32] is larger than any of these watersheds, and although the Navarro River basin differs environmentally from other coastal basins (due largely to similarities with the Russian River basin), the magnitude of these differences during the period when Chinook salmon are in freshwater is relatively small. The population in the Garcia River [37] occupies a moderately sized watershed that lies between the set of source populations mentioned above and the Gualala and Russian rivers to the south. We therefore conclude that Chinook salmon in the Garcia River [37] comprised a potentially independent population, a conclusion based in large part on from the connectivity-viability model. Given the potential bias in our measure of population carrying capacity, and the high likelihood of infrequent or limited access to freshwater due to sandbars, we expect that historical populations of Chinook salmon in the smaller watersheds that are not mentioned here by name would all have been highly dependent on immigration from the functionally and potentially independent populations for long-term persistence or recolonization.

Coastal basins south of Point Arena

Our ability to evaluate the status of putative historical populations of Chinook salmon in coastal basins south of Point Arena is greatly constrained by lack of information. Evaluating the status of the population in the Gualala River [41] is particularly problematic. The basin exhibits sufficient habitat potential for us to expect that it was capable of supporting a population that is viable-in-isolation under historical conditions, and juvenile Chinook salmon have been observed in the Gualala River basin prior to 1945 (North Coast Watershed Assessment Program, 2003). However, we know of no records of persistent historical runs of Chinook salmon in the Gualala River.

Results for the Gualala River from the connectivity-viability analysis must be interpreted cautiously. A structural interaction between the dispersal model and the physical structure of the coastline (i.e., the absence of a suitable alternative to the Gualala River along approximately 50 km of coastline for any fish dispersing northwards from the Russian River) contributes to the prediction of substantial immigration from the Russian River, and thus may underestimate the independence of a historical population of

Chinook salmon in the Gualala River. Countering the consequences of this possibility, however, is the potential for bias in the hydrological model that underlies predictions of IP, and a higher likelihood that sandbars block access to the Gualala River with greater frequency and duration than for other basins to the north. If this is the case, the Gualala River population might have been more dependent than expected on dispersal from the Russian River for long term persistence. Therefore, we consider the historical population of Chinook salmon in the Gualala River [41] to have been potentially independent, but emphasize that substantial uncertainty surrounds this conclusion.

We concur with previous analyses, in concluding that it is unlikely that the small basins south of the Russian River harbored persistent populations of Chinook salmon, even under historical conditions. In general, these watersheds are drier and lower in elevation than watersheds to the north. As a consequence, flow is likely to have been frequently insufficient to allow Chinook salmon to enter freshwater during their return migration; indeed, in some years, sandbars may have prevented access entirely. While sandbars would not limit access by Chinook salmon to tributaries to Tomales Bay [47] (e.g., Walker and Lagunitas creeks), the late onset of winter flows might have limited access. We lack historical evidence for persistent populations of Chinook salmon in these basins[14]. Thus, it is likely that the presence of Chinook salmon in watersheds between the Russian River and the Golden Gate was dependent almost entirely on dispersal from the Russian River or, possibly, from populations in San Francisco Bay and the Central Valley.

3.8.2 Historical population structure of spring-run Chinook salmon in the CC-Chinook ESU

Information regarding the historical distribution of spring-run Chinook salmon in the CC-Chinook ESU is extremely sparse, and genetic data are entirely lacking. Anecdotal evidence suggests that spring-run Chinook salmon historically occurred in the Mad River (Myers et al., 1998), and Keter's (1995) ethnographic study documents the historical presence of persistent spring-run Chinook salmon populations in the North and possibly Middle forks of the Eel River. All three of these basins share the characteristics of higher elevation, substantial contribution of snowmelt to the annual hydrograph, and the presence of summer steelhead. The Van Duzen River, parts of the Eel River basin above the confluence of the Middle Fork, and Redwood Creek exhibit similar environmental characteristics. Summer steelhead, which have similar over-summer habitat requirements as spring-run Chinook salmon, occupy or occupied all of these basins and the Mattole River. Therefore, although we do not conclude that such populations existed, we hypothesize that spring-run Chinook salmon might have occurred historically in those basins mentioned here for which no historical evidence is available.

Table 3.3 summarizes our conclusions regarding historical population structure of spring-run Chinook salmon in the CC-Chinook ESU, in which all populations of spring-run Chinook salmon in major

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[14] Museum collections of juvenile Chinook salmon from Lagunitas Creek from 1897 and subsequent returns in 1900-01 are almost certainly the result of plantings of fry derived from Battle Creek (Central Valley). Rutter (1904) notes that the Lagunitas watershed "is not suitable for quinnat [Chinook] salmon, being entirely too small." The current population of Chinook salmon in Lagunitas Creek is a result of a recent colonization event () from an unknown source, and dam-regulated flow intended to support coho salmon in this watershed is likely to be contributing to the persistence of this population.

Table 3.3. Historical population structure of spring-run Chinook salmon in the CC-Chinook ESU.

Population	Historical Population Status
(Redwood Creek (H) [1])	**(Functionally Independent)**
Mad River [4]	**Functionally Independent**
(Van Duzen River [E2])	**(Functionally Independent)**
North Fork Eel River [E5]	**Functionally Independent**
Middle Fork Eel River [E7]	**Functionally Independent**
Upper Eel River [E8]	**(Functionally Independent)**

basins are considered to have been functionally independent. As noted previously, we assume that historical populations of spring-run Chinook salmon in the CC-Chinook ESU arose independently from fall-run Chinook salmon in the same basin, as is observed in other coastal Chinook salmon ESUs (Myers et al., 1998; Waples et al., 2004)[15]. Thus, the population structure of spring-run Chinook salmon is expected to parallel that of fall-run Chinook salmon, with the critical distinction that rates of dispersal among populations of spring-run Chinook salmon are likely to be substantially lower than those of fall-run Chinook salmon. The typical distribution of spring-run Chinook salmon holding and spawning habitats in higher elevations is likely to cause greater separation among putative populations, which supports the finer subdivision of spring-run Chinook salmon in the Eel River than is proposed for fall-run Chinook salmon.

3.9 Diversity strata

Figure 3.7 summarizes our conclusions regarding the assignment of populations to diversity strata. The most important division is based on the life history differences between fall-run and spring-run Chinook salmon. Within a life-history type, most of the structure presented in Figure 3.7 derives directly from our multivariate analysis of basin-scale environmental and ecological characteristics for the NCCCRD.

For fall-run Chinook salmon, the two Eel River populations appear in multiple places in Figure 3.7. This reflects, in part, the environmental diversity encompassed within the range of each population[16]. In this scheme, the two Eel River populations contribute with variable importance to various diversity strata. Variation in the expected historical contribution to a given diversity stratum depends on the likely historical role of the relevant portions of a population's range (or alternatively, the likely historical status of each smaller population, were we to conclude that many more than two populations of Chinook salmon occupied the Eel River basin). We expect that the diversity within each of these populations was

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[15] Looking towards the development of ESU viability criteria, it is worth noting that inclusion of spring-run Chinook salmon as part of a viable CC-Chinook ESU will require establishing environmental conditions that allow for the "re-evolution" of spring-run Chinook salmon from current fall-run Chinook salmon.

[16] As discussed in greater detail in the Introduction (§1.4), a diversity stratum, unlike a population or an ESU, is not a biological unit. Although diversity strata often correlate to biological structure at scales intermediate to populations and ESUs, diversity strata are described in terms of geography and suites of generally similar environmental and ecological characteristics, not phylogeny.

central to their likely historical role as relatively stable source populations for much of the ESU. Such diversity, and the degree to which it is represented, must be considered in any evaluation of the viability of these populations and their current role in the ESU. Specifically, a particular element of diversity must contribute robustly to a population for that population to count as contributing to the relevant diversity stratum for the ESU.

Due to having more stringent habitat requirements, historical populations of spring-run Chinook salmon did not occupy environmentally diverse basins, and thus all populations fit neatly into a single diversity stratum.

3.9.1 Diversity strata: fall-run Chinook salmon

North Mountain-Interior

This stratum includes populations or parts of populations that spawn in watersheds that penetrate considerable distances inland, and (in most cases) attain sufficient elevations for snowmelt to contribute significantly to the annual hydrograph. Two northern tributaries to the lower Eel River, the Van Duzen River and Larabee Creek, exhibit these characteristics. While we consider fall-run Chinook salmon that spawn in these tributaries to be part of the Lower Eel River population, these basins represent important environmental diversity within that population. Thus, we consider that a viable population of fall-run Chinook salmon in the Lower Eel River that included components in northern basins would contribute significantly to this diversity stratum.

North Coastal

This stratum includes populations or parts of populations of “short-run” Chinook salmon spawn in watersheds that are most strongly affected by climate conditions typical of the coast. Lower reaches and tributaries of Redwood Creek (e.g., Prairie Creek), Mad River, and lower Eel River experience these sorts of conditions; however, conditions in these watersheds–especially flow patterns–are also affected by higher, inland areas so that the contribution of Chinook populations to this aspect of ESU diversity may be limited. We include the South Fork Eel River in this diversity stratum based on its environmental similarity to coastal basins.

North-Central Coastal

This stratum includes populations that spawn in watersheds of small to moderate size along the coast between Cape Mendocino and the Albion River (inclusive). Watersheds along this coast, including the larger basins, exhibit a more comprehensive “coastal” character than those to the south, and lack extensive areas that experience warmer, drier conditions.

Central Coastal

This stratum includes populations that spawn in watersheds that tend to be warmer and drier than those to the north. The Navarro and Garcia basins are included in this stratum on the basis of environmental conditions throughout much of the interior basin, save for a narrow band along the coast. Included in this stratum would be any populations that might have occurred in watersheds south of the Russian River; we do not include these watersheds here based on the low probability that these watersheds historically supported persistent populations of Chinook salmon.

3.9.2 Diversity strata: spring-run Chinook salmon

Given the restricted environmental conditions necessary to support spring-run Chinook salmon, we consider all historical populations of spring-run Chinook salmon to have been part of the same diversity stratum. Notice that the populations for which we have strong circumstantial evidence occur in watersheds that are part of the North Mountain-Interior stratum designated for fall-run Chinook salmon. Note also that the North Mountain-Interior diversity stratum also includes all but one of the watersheds for which more tenuous evidence that conditions might have historically allowed the expression of the spring-run life history (e.g., correlates such as the contribution of snowmelt to the annual hydrograph and (historical) presence of summer steelhead). We include the potential historical population in the Mattole River in this stratum as such a population almost certainly would have occupied habitats similar to those occupied by spring-run Chinook in other basins.

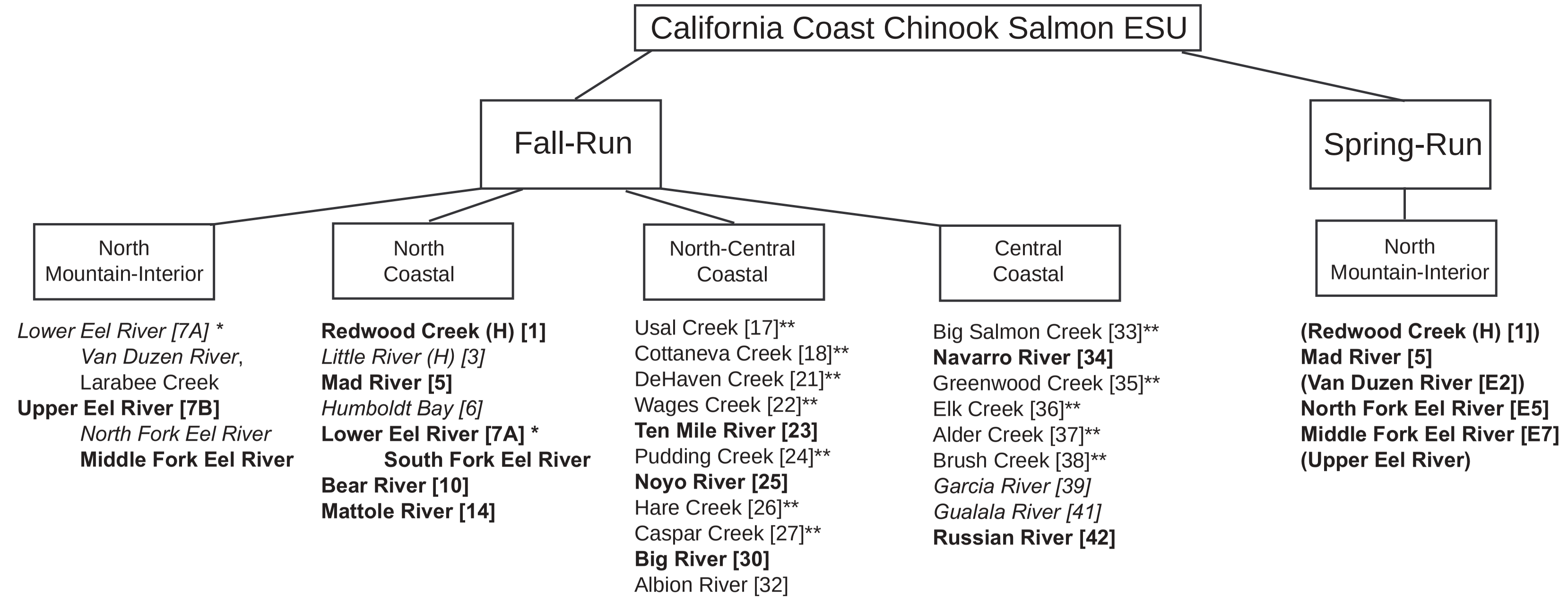

Figure 3.7. Arrangement of historical populations of the CC-Chinook ESU into diversity strata. Functionally independent populations are listed in bold font. Potentially independent populations are listed in italic font. Dependent populations are listed in regular font. Populations indicated by a single asterisk are listed under multiple diversity strata occupy environmentally diverse basins or watersheds (see text for additional explanation). Populations indicated by a double asterisk are dependent populations in small watersheds, and are expected to be critically dependent on dispersal for occupancy (see text for discussion). Spring-run Chinook salmon populations listed parenthetically are those for which potential historical existence is tentatively inferred from environmental correlates (see text for discussion).

4 Northern California Coast Steelhead ESU and Central California Coast Steelhead ESU

We consider the North-Central California Coastal Steelhead ESU and Central California Coastal Steelhead ESU jointly to take advantage of comprehensive analyses of geographical and genetic data across the range of the NCCCRD.

4.1 ESU definitions

The Northern California Steelhead (NC-Steelhead) ESU includes steelhead[1] (*Oncorhynchus mykiss*) that spawn and rear in watersheds from immediately south of the Klamath River to just south of the Gualala River[2]. The NC-Steelhead ESU includes winter-run and summer-run steelhead, as well as populations in the northern part of the ESU (Eel River) that exhibit the "half-pounder" life history. Summer-run steelhead have been reported in tributaries to the Eel River (e.g., the North Fork Eel River, the Middle Fork Eel River, the Van Duzen River), the Mad River, the Mattole River, and Redwood Creek. Winter-run steelhead occur throughout the range of the NC-Steelhead ESU.

The Central California Coastal Steelhead (CCC-Steelhead) ESU includes steelhead[3] that spawn and rear in watersheds from just north of the Russian River[4] to Soquel Creek (inclusive) and tributaries to San Francisco and San Pablo Bays, save for the Sacramento-San Joaquin River Basin. We consider Russian Gulch (Sonoma County), which lies just north of the Russian River, and Aptos Creek, which lies between Soquel Creek and the Pajaro River (the northernmost watershed of the South-Central California Coast Steelhead ESU) in our analyses of the CCC-Steelhead ESU. All steelhead in the CCC-Steelhead ESU are winter-run fish.

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[1] See §4.1.1 below for discussion of our treatment of non-anadromous *O. mykiss*, which is based on recent deliberations by the Biological Review Team (West Coast Salmon Biological Review Team, 2005).

[2] The official definition of the NC-Steelhead ESU range is from Redwood Creek (Humboldt) to the Gualala River. We also consider in our analysis steelhead in small streams on either side of this range that are otherwise excluded from any ESU.

[3] See §4.1.1 below for discussion of our treatment of non-anadromous *O. mykiss*, which is based on recent deliberations by the Biological Review Team (West Coast Salmon Biological Review Team, 2005).

[4] The official definition of the northern extent of the CCC-Steelhead ESU is the Russian River. We include steelhead in small streams just north of the Russian River in the CCC-Steelhead ESU that would otherwise be excluded from analysis.

4.1.1 Life history diversity in *O. mykiss* and the scope of our analysis

O. mykiss is unique among the species we consider in this report in the diversity of life history types exhibited within the species, and within ESUs and populations. The most important difference between *O. mykiss* and the two species of salmon is the existence of both an anadromous form, steelhead, and an non-anadromous (or "resident") form, coastal rainbow trout, which poses special challenges to efforts to evaluate the structure and status of *O. mykiss* ESUs and populations. In a recent round of Status Reviews (West Coast Salmon Biological Review Team, 2005), the Biological Review Team (BRT) considered three scenarios to guide their analysis of how resident *O. mykiss* were to be included in evaluating ESU status: (1) in cases where resident and anadromous forms were naturally sympatric, resident *O. mykiss* were to be considered part of the population or ESU in question, although the degree of demographic linkage remains unknown, (2) in cases where resident and anadromous forms were allopatric and separated by a long-standing natural barrier, resident *O. mykiss* were to not be considered as part of the population or ESU in question, and (3) in cases where resident and anadromous forms were allopatric, presumably as a consequence of a recent anthropogenic barrier, the status and contribution of resident *O. mykiss* was to be evaluated on a case-by-case basis. In the last case, it is necessary to consider whether the recently isolated population has diverged sufficiently from the downstream population to be considered part of the same population or ESU, regardless of whether such divergence was due to natural processes or due to stocking above the barrier.

The prevalence of non-anadromous *O. mykiss* in coastal basins of the NCCCRD is not well documented, particularly in waters accessible to anadromy. Most cases where resident *O. mykiss* are a substantial component of a steelhead ESU appear to be in interior basins and coastal watersheds in southern California. We therefore assume that (1) truly non-anadromous *O. mykiss* form a relatively small component of populations in small to moderately sized coastal basins in the NCCCRD, and (2) in the larger basins where substantial proportion of *O. mykiss* might exhibit non-anadromous life histories, rates of exchange between resident and anadromous *O. mykiss* in coastal basins are sufficiently low for the two forms to be considered as separate populations. On the basis of these assumptions, and lack of evidence to the contrary, we focus our analysis solely on elucidating population structure of steelhead[5]. This approach is consistent with the emphasis placed by the BRT on the anadromous form as a critical element for maintaining connectivity within an ESU (West Coast Salmon Biological Review Team, 2005).

4.2 Life history and general habitat characteristics

In terms of both geography and habitat tolerances, steelhead have the most cosmopolitan distribution, at least within California, of the species considered in this report. The two ESUs are bounded to the north,

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[5] Although we do not explicitly include any putative populations of resident *O. mykiss* in our analysis, we note that steelhead, as a consequence of their extensive migrations, typically will exhibit higher rates of dispersal and disperse over larger scales than will non-anadromous *O. mykiss*. If this assumption holds, then our conclusions regarding population structure of anadromous *O. mykiss* will correspond to the upper bound on the spatial scale of population structure in the resident form; indeed, it is likely resident *O. mykiss* exhibit population structure at smaller scales than the anadromous form.

south, and inland by other steelhead ESUs. Within this range, the NCCCRD spans broad environmental gradients in both freshwater and marine habitats, and thus the NC-Steelhead and CCC-Steelhead ESUs include populations exposed to a variety of ecological and environmental conditions; various aspects of the steelhead life history are thought to contribute to the species ability to persist over such a relatively broad range of conditions.

4.2.1 Life history

Steelhead is the term commonly used to describe the anadromous form of rainbow trout, *Oncorhynchus mykiss*. Of the Pacific salmonids, *O. mykiss* exhibit a range of diversity in life history rivaled only by coastal cutthroat trout (*Oncorhynchus clarki*) and possibly sockeye salmon (*Oncorhynchus nerka*). This complexity is apparent in numerous facets of the species's life history: degree of anadromy, timing of spawning migration, and the age-distributions of both smolts and spawning adults. *O. mykiss* occurs in both non-anadromous and anadromous forms, both of which can occur within the same population. The anadromous form displays considerable variation in periods of freshwater and marine residence (see below), and resident forms, although they remain in freshwater, can exhibit a broad range of migratory behaviors (e.g., fluvial migrations between tributary and mainstem habitats). Research using otolith microchemistry or genetic markers has demonstrated that resident forms may give rise to anadromous progeny and *vice versa* (Zimmerman and Reeves, 2002, C. Donohoe, NOAA-NMFS Santa Cruz Lab (*unpublished data*)). This diversity of life history patterns has prompted some to argue that *O. mykiss* exhibit a continuum of life histories (Behnke, 1992).

Steelhead are commonly categorized on the basis of adult run timing: winter steelhead migrate into natal streams between December and March or April, arriving in reproductive condition and spawning shortly the reafter, whereas summer steelhead migrate upstream between April and October, arriving in sexually immature condition and holding in deep, cold pools for as long as 6-8 months before moving into natal areas to spawn. Steelhead differ significantly from other species of Pacific salmon in that not all steelhead adults die after spawning; some individuals may return to the ocean and then spawn a second, third, or even fourth time. California steelhead typically spend one or two years in the ocean, though in many populations, a small fraction of fish will spend a third year at sea. Overall, the most common life-history patterns of first-time spawners in coastal basins of California are 2/1 (smolt age/ocean age), 2/2 and 1/2 (Busby et al., 1996). Roughly 10%-20% of steelhead will survive to spawn a second time, and less than 5% may spawn a third or even fourth time. In Mad and Eel rivers "half-pounders" return from the ocean after only 2-4 months of saltwater residence, are generally sexually immature, and return to sea the following spring.

Range-wide, steelhead also exhibit a broader range of freshwater residence times than other species of Pacific salmon. For anadromous *O. mykiss*, the period of freshwater residency can range from one to four years, with longer residence times more typical in northern latitudes. In most steelhead populations within the NCCCRD, the majority of fish migrate to sea for the first time after two years in fresh water (Busby et al., 1996; Moyle, 2002); however, in watersheds that include highly productive environments such as lagoons or fast flowing, but relatively warm water, juveniles can reach sufficient size to smolt after one year. Smolting juveniles migrate downstream in spring, generally between March and June or July with peaks in April and May for populations within the NCCCRD (Shapovalov and Taft, 1954, S. Harris, CDFG, *unpublished data*).

4.2.2 Evolutionary relationships between summer and winter steelhead

Adult run-timing is a strongly heritable trait in steelhead, and differences in timing and spatial distribution of spawning are thought to effectively maintain genetic and demographic separation of the two runs in a given basin (Leider et al., 1984). Analyses of genetic population structure, however, suggest that summer steelhead are more closely related to winter steelhead within the same watershed than to summer steelhead in other watershed, and support the hypothesis that summer steelhead derive from winter-run populations (see Busby et al., 1996, and references therein). This hypothesis is analogous to that proposed for the independent evolution spring-run Chinook salmon from fall-run Chinook salmon in coastal ESUs (Waples et al., 2004), and evidence for independent evolution of non-anadromous forms of rainbow trout (e.g., Docker and Heath, 2003) and sockeye salmon (*Oncorhynchus nerka*) from anadromous sources (Taylor et al., 1996).

The question of how the empirical patterns reviewed by (Busby et al., 1996) arise has important implications for how we consider dispersal among populations of summer steelhead in drawing our conclusions regarding the historical population structure of summer steelhead. Accepting, as we do, the hypothesis of polyphyletic origin of summer steelhead has important implications for how we consider dispersal among summer steelhead populations in our analysis of historical population structure. Indeed, in accepting this hypothesis, we implicitly assume that dispersal among summer steelhead populations is very low, and effectively non-existent. Very specific habitat requirements, which place an extremely high premium on high fidelity to areas known to satisfy these requirements, the relatively high degree of spatial isolation among areas where summer steelhead spawn, and the potential for iteroparity are likely to favor evolution of precise homing behaviors. Low rates of (largely but not entirely ineffectual) hybridization among summer and winter steelhead—particularly in areas affected by hatchery production (Leider et al., 1984)—might obscure the ability of neutral molecular markers to reveal effective dispersal among summer steelhead populations. Even if this is so, the observed genetic patterns imply that the level of exchange among summer steelhead populations is extremely low.

4.2.3 Typical habitat characteristics and ecological indicators

Steelhead typically spawn in small tributaries rather than large, mainstem rivers. Their spawning distribution overlaps with that of coho salmon; however, because steelhead tend to prefer higher gradients (generally 2-7%, sometimes up to 12% or more), their distribution tends to extend farther upstream. In some watersheds, steelhead will even spawn in ephemeral streams, with juveniles migrating downstream to permanent waters to rear. Summer steelhead often spawn higher in a watershed than do winter steelhead, sometimes even using ephemeral streams from which juveniles are forced to emigrate as flows drop (Behnke, 1992). Like spring-run Chinook salmon, summer steelhead most commonly occur in streams for which snowmelt contributes substantially to the annual hydrograph; spring-summer snowmelt provides access to holding pools before the onset of high summer temperatures, and charges the system with sufficient cold water to maintain cool pool habitats through the summer[6].

Following emergence in spring, fry typically adopt feeding stations in shallower portions of riffles or pools, moving into progressively faster and deeper water as they increase in size. Juvenile steelhead exhibit a streamlined body morphology that is thought to be an adaptation for life in faster water currents (Bisson et al., 1988). Where the steelhead and coho salmon coexist, steelhead tend to prefer and grow faster in pool habitats, but young-of-the year steelhead are commonly displaced to riffle habitats through competitive interactions with larger, more aggressive coho salmon when coho salmon are abundant (Bugert and Bjornn, 1991; Young, 2004). Older juvenile steelhead are not so readily displaced, and commonly occur in pool habitats. Under warmer conditions, juvenile steelhead tend to favor faster flowing environments (e.g., the head of pools, riffles, etc.) where they are better able to meet their increased foraging requirements (Smith and Li, 1983).

Lagoon habitats are a common feature of watersheds throughout the NCCCRD. Lagoons are formed when deposition of sand on beaches during the spring and summer forms a sandbar across the mouth of a river and thus blocks direct flow into the ocean. After sandbars form lagoon size is usually dramatically increased, but inflows that convert the lagoon to freshwater or very strong winds are necessary to prevent strong salinity stratification in lagoons. Such stratification, even in shallow lagoons, prevents vertical mixing of heat and oxygen and often results in warm water (especially in the bottom salt water layer), poor bottom dissolved oxygen and low production of invertebrates as food for steelhead (Smith 1990). If streamflow is sufficient to maintain freshwater in the lagoon, such environments can provide highly productive habitats for juvenile steelhead. Although the conditions under which a lagoon provides favorable habitat have been characterized in general terms, e.g., the presence of a well-mixed water column and sufficient dissolved oxygen levels Smith (1990), spatial and temporal variability in the suitability of lagoon habitats is not well understood, nor has the influence of such habitats on the dynamics of steelhead populations been adequately documented. In some small systems, though, juvenile steelhead grow extremely well in lagoon habitats, and this might have important implications for later survival in the ocean.

4.3 Historical distribution

We synthesized two complementary types of information to assess the potential distribution of steelhead throughout the NCCCRD, and thereby to frame the set of putative populations for subsequent evaluation. The first set of information consists of historical and recent records regarding the presence of steelhead in watersheds of the NCCCRD. The second set of information is drawn from the results our implementation of a GIS model to predict the intrinsic potential (IP) for habitat suitable for rearing of juvenile steelhead to occur in watersheds throughout the NCCCRD (Burnett et al., 2003; Agrawal et al., 2005).

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[6] Summer steelhead also occur in the Mattole River; however, snowmelt does not contribute significantly to the hydrograph in this basin. The Mattole River receives the highest amount of precipitation in the NCCCRD, which probably offsets the lack of snowpack, particularly under historical conditions.

4.3.1 Recent and historical distribution

Although there are no comprehensive, rigorous surveys available to provide information on the distribution of steelhead throughout the NCCCRD, it is generally believed that winter steelhead historically were pervasive throughout the region. Conventional wisdom holds that, with few exceptions, everywhere within waters accessible to anadromy that steelhead have been sought, they have been found. Most efforts to survey populations of winter steelhead rely almost entirely on measures of juvenile abundance or distribution made during the summer months; surveys that target adult winter steelhead typically face difficult conditions and have not been pursued consistently over large spatial scales. Unfortunately, in the absence of ancillary information on the parentage of the juveniles observed (e.g., otolith microchemistry that confirms the anadromous life history of the adult female), or clear evidence that non-anadromous fish represent a minor component of *O. mykiss* in a basin (or part of a basin), the focus on juvenile surveys admits some uncertainty regarding the reliability of these data as evidence for the distribution of winter steelhead. Nevertheless, we follow conventional wisdom in this respect, and assume that winter steelhead are widely distributed throughout the NCCCRD, and were so historically.

Efforts to characterize the distribution of summer steelhead are far less likely to be confounded by uncertainty regarding the identity of the fish, as these efforts focus on adult fish as they hold in deep pools during the summer. Within the NCCCRD, summer steelhead currently occur in Redwood Creek (Humboldt), Mad River, Mattole River, and the upper mainstem and Middle Fork of the Eel River. Historically, summer steelhead are thought to have occurred elsewhere in the Eel River basin, including Van Duzen River, Larabee Creek, the North Fork Eel River, and Black Butte River, a tributary to the Middle Fork Eel (Moyle, 2002); anecdotal information also suggests that summer steelhead occupied the South Fork Eel River (Jones, 1992). Summer steelhead are not reported south of the Mattole River, and given the lack of coastal basins that receive substantial snowpack in south of Cape Mendocino, we believe this to have been the case historically as well.

4.3.2 Intrinsic potential

To complement available historical information, we implemented an intrinsic potential (IP) model (following Burnett et al., 2003) to predict the distribution of areas with high potential to exhibit suitable rearing habitat for juvenile steelhead throughout the range of the NC-Steelhead and CCC-Steelhead ESUs; details regarding implementation of the model and assumptions that must be considered in interpreting the model output are provided by Agrawal et al. (2005) and reviewed in the Introduction. Available data relating density of juvenile steelhead in coastal California watersheds to the habitat characteristics used in calculating IP were sparse, and did not indicate strong support for choosing habitat suitability curves different from those developed for the Oregon Coast (Agrawal et al., 2005). We also examined the potential for temperature to exclude steelhead from parts of the NCCCRD; however, the extent of the NCCCRD where temperature might have excluded steelhead is extremely limited[7].

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[7] An analysis of environmental predictors of presence for steelhead in the South-Central California Coast ESU (D. Boughton, NOAA Fisheries, Santa Cruz Lab, *unpublished results*) suggests that a mean August air temperature of 24 °C or higher will exclude steelhead; this value is corroborated by similar analysis of the effects of water temperature on presence

The habitat suitability curves developed for coastal watersheds in Oregon, which are very similar to those used to calculate IP for this report (Agrawal et al., 2005), reflect the tendency for juvenile coho salmon to occur at greater density in pools and for juvenile steelhead to occur at greater density in riffles. The suitability curves, however, are based on data collected in watersheds of coastal Oregon in which steelhead coexist with coho salmon. Since juvenile coho salmon tend to displace young-of-the-year steelhead from preferred pool habitats (older juvenile steelhead are not so excluded) (Bugert and Bjornn, 1991; Young, 2004), these curves potentially include the consequences of interspecific competition in an implicit form, which is a source of potential concern.

The main reason for such concern with respect to the current analysis is that coho salmon appear to be excluded by high summer temperatures from certain areas of the NCCCRD[8], which requires us to consider whether and how suitability curves for steelhead in these areas should be altered to reflect the consequences of competitive release. We chose not to alter the suitability curves used to predict IP for juvenile steelhead as a function of the expected presence or absence of coho salmon for two reasons. First, and foremost, given that exclusion of coho salmon is tied to increased temperature, steelhead are not especially likely to substantially expand or shift their distribution into slower moving pool habitats. Rather, to satisfy increased in foraging requirements, juvenile steelhead are likely to remain in faster flowing habitats at the head of pools or in riffles in areas where temperatures are sufficiently high to exclude coho salmon (Smith and Li, 1983). Second, many areas in the NC-Steelhead and CCC-Steelhead ESUs where coho salmon are likely to be excluded already exhibit relatively high IP for steelhead, so any correction to or more generous interpretation of predicted IP for steelhead habitat as a function of the absence of coho salmon—under historical conditions—is likely to have limited consequences for the results of subsequent analyses based on watershed capacity. Thus, we expect temperature-related exclusion of coho salmon from a watershed or part of a watershed to have only moderate consequences for the amount of habitat suitable for juvenile steelhead. Likewise, since distributions of steelhead and coho salmon overlap at the reach scale wherever they are sympatric, we do not expect the absence of coho salmon to increase connectivity substantially among steelhead within a basin.

Watersheds within the range of the NC-Steelhead and CCC-Steelhead ESUs differ with respect to the distribution of areas with relatively high IP for juvenile steelhead (plates 14 and 15). The NC-steelhead ESU occupies watersheds with more variable topography that thus exhibit more extensive distribution of streams with moderate gradient. In contrast, many of the watersheds in the CCC-Steelhead ESU have less stark topography and exhibit characteristics more commonly associated with good coho salmon habitat. Note also that, in contrast to patterns observed for coho salmon and Chinook salmon, areas with high IP for steelhead habitat tend to have a more fragmented distribution in which areas with high IP are distributed among smaller tributaries higher in a basin and separated by areas with low IP in the lower parts of the basin (Plates 14 and 15).

We use the IP model as a source of information on habitat potential only for winter steelhead. Juvenile summer steelhead have habitat rearing requirements similar to those of juvenile winter steelhead. However, although juvenile habitat might still exert a strong control on population size, the habitat

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of *O. mykiss* (Eaton et al., 1995).

[8] See §2.3.2 in the discussion of IP in the chapter on coho salmon.

requirements of over-summering adults (e.g., deep, cold holding pools) are expected to limit the watersheds where summer steelhead can occur. These habitats are not readily predicted from available data in the current IP modeling framework.

Regional variation in hydrology and potential bias in predicted IP for steelhead. Stream hydrology is strongly influenced by a complex interaction between the amount and timing of precipitation and seasonal temperature patterns, both of which vary considerably over the range of the NCCCRD. We suspect that, despite our effort to use regional data to fit the simple hydrology model that underlies the IP model, the timing and amount of precipitation throughout the NCCCRD differ sufficiently from conditions observed in coastal Oregon for predictions of IP model to include non-negligible positive bias in at least some parts of the NCCCRD (for greater detail, refer to §1.5.1: Assumptions and the interpretation of the connectivity-viability model). It is not clear how variation in the seasonality of precipitation and temperature influence how IP translates into population carrying capacity, and we are unaware of data sets that would allow such a relation to be estimated. We therefore use a qualitative index of potential bias to guide post-hoc interpretation of analyses based on predictions from the IP model. We use the ratio of mean annual precipitation (MAP) to mean annual temperature (MAT) (each averaged at the watershed scale) as the underlying basis for this index[9], but also consider other information (e.g., finer scale information on MAP/MAT relative to the distribution of areas with high IP and ecological indicators) in evaluating how the IP model might be biased for each watershed (see Plate 6).

Lagoon habitat

Our IP model does not include one potentially important element of juvenile steelhead habitat: estuaries and coastal lagoons that form behind sandbars as a consequence of dropping stream flow and wave patterns that favor sand deposition on the beach during the spring and summer. Lagoons are a common feature of streams in the NCCCRD, and can present highly favorable environments for growth of juvenile steelhead when conditions are favorable for maintaining a well-mixed water column and sufficient dissolved oxygen levels (Smith, 1990).

Inclusion of lagoon habitats in our analysis is constrained by two factors. First, the spatial extent and dynamics of estuarine and lagoon habitats has not been well documented and available information includes substantial uncertainty. Second, the contribution of such habitats to population dynamics and the consistency with which they present favorable conditions is not well understood. Nevertheless, we consider the potential contribution of lagoon habitats in setting our viability-in-isolation threshold, and as a qualitative factor in evaluating populations against this threshold.

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[9] For watersheds in southern coastal Oregon (e.g., Pistol River, Chetco River, and Elk River), MAP/MAT is approximately 24 mm/°C. In the NCCCRD, this ratio ranges from below 4 mm/°C in the southeastern San Francisco Bay to over 16 mm/°C in northern, coastal watersheds. We use this ratio as the initial basis for assigning a bias index of "severe" ($\text{MAP/MAT} < 6\text{mm}/^\circ\text{C}$), "high" ($6\text{mm}/^\circ\text{C} \leq \text{MAP/MAT} < 9\text{mm}/^\circ\text{C}$), "moderate" ($9\text{mm}/^\circ\text{C} \leq \text{MAP/MAT} < 12\text{mm}/^\circ\text{C}$), or "low" ($12\text{mm}/^\circ\text{C} \leq \text{MAP/MAT} < 16\text{mm}/^\circ\text{C}$) to each watershed.

4.3.3 Synthesis of historical information and GIS model predictions

We combined information from historical records and predictions from the IP model (modified by the temperature mask) to develop a working list of putative winter steelhead populations for further consideration and analysis. Primarily this consisted of using predictions of IP to offset the lack of explicit information on the historical distribution of winter steelhead in many small coastal watersheds in which ecological conditions appear to be favorable for steelhead. We did not include in this set all of the smaller watersheds where winter steelhead might be or once have been. Rather, we limited this set to those with $\geq$ 1.6 IP-km, or one-tenth the amount of habitat thought necessary to support a population that would be viable-in-isolation (see below). Although this set almost certainly does not include every stream where steelhead might occur, it represents well over 99% of the expected available habitat, and includes almost every watershed that consistently provides habitat for winter steelhead.

4.4 Population genetic structure of steelhead ESUs in the NCCCRD

4.4.1 Historical artificial propagation

Records from the early (pre-1950) history of artificial propagation of steelhead in California are of limited use for our purposes, particularly because records commonly fail to note the source of eggs used in a hatchery and generally report releases in terms of the number of fish released by county. Additional confusion arises in cases where both resident and anadromous forms of *O. mykiss* were propagated, sometimes with no apparent effort to separate the two forms (Busby et al., 1996). Despite its limitations, however, the historical record indicates that transfer of fish among basins and across ESU boundaries was common in throughout the state, including the coastal regions after about 1910.

More extensive distribution records are available after 1970, and these indicate that inter-basin and inter-ESU transfers continued to occur throughout the 1970s, 1980s and, in some cases (e.g., the Russian River and coastal streams south of San Francisco), into the early 1990s. Table 4.1 summarizes available information on the timing, duration, and size of among-basin transfers within the NC-Steelhead ESU, and of transfers of fish from sources outside the NC-Steelhead ESU into populations of the NC-Steelhead ESU. Table 4.2 summarizes similar information for the CCC-Steelhead ESU. These tables focus on the period from 1970 to the present, and this is the information we draw on most heavily for context as we interpret population genetic data. Some earlier records are also mentioned; however, we caution that these scattered pieces of information can be as deceptive as they are informative with respect to interpreting modern genetic studies, because they will reflect only a small fraction of the historical transfers of fish.

A few general patterns regarding historical transfers of steelhead are worth highlighting here. First, hatchery fish derived from populations of (winter) steelhead in the Mad, Eel, and San Lorenzo rivers comprise the majority of documented out-of-basin releases. Second, fish derived from a given source are often widely distributed among different watersheds spread throughout the range of both ESUs. Third, although not documented in Table 4.2, which focuses on releases into populations of steelhead in the NCCCRD, substantial transfers of steelhead from CCC-Steelhead ESU populations to northern populations in the South-Central California Coast (SCCC) Steelhead ESU have taken place as recently as the 1990s (NRC, 1996).

Tables 4.1 and 4.2 summarize direct transfers between basins and ESUs. In a number of cases, "local" broodstocks have been combined with fish from other basins, or were founded entirely with fish from other basins, in which case it is worth considering the level of subsequent within-basin artificial propagation. In particular, the Mad River Hatchery stock of winter steelhead was founded with fish trapped from the South Fork Eel River in 1971, and augmented with fish from the Eel River until 1974 (Cramer et al. 1995, cited in Busby et al., 1996). Although Mad River winter steelhead contributed a small proportion of the original hatchery stock, ongoing production was based almost entirely on hatchery returns. Thus, in effect, the Mad River has received ongoing plants of juvenile steelhead (over 9 million fish, most of which were yearlings) derived from Eel River stocks.

Some aspects of steelhead life history (i.e., spending a substantial portion of the life cycle in habitats that have a fragmented distribution) potentially favor substantial population structure within a basin. Therefore, since artificial propagation can reduce the effectiveness of the homing response and thus increase dispersal (Pascual and Quinn, 1995), we also considered more thoroughly the potential implications of artificial propagation on population structure of steelhead within the two large basins within the NCCCRD. In the case of the Russian River, over 11.5 million steelhead (dominated by yearlings and fingerlings) from a single (possibly composite) stock have been released at various locations in the Russian River basin (NRC, 1996). Given the intensity of this stocking effort and the practice of distributing fish throughout the basin it is difficult to imagine that artificial propagation has not altered the historical population genetic structure of steelhead the Russian River. In the case of the Eel River, the number of fish released is substantially smaller, but of these, a little over one-half million fish (mostly yearlings derived from Eel River fish) were reared at the Mad River Hatchery (NRC, 1996). By reducing the time during which fish were exposed to Eel River water, this practice might have reduced the effectiveness of the homing tendency of these fish. These fish are released at Van Arsdale Fish Station (VAFS) near the current upstream terminus of anadromy on the mainstem Eel River, but it is unknown how consistently these fish return to VAFS or how widely distributed they might be within the Eel River basin.

4.4.2 Genetic data sets and analyses

Allozyme data: Busby et al. (1996) Status Review

Busby et al. (1996) present results from a suite of analyses based on 40-51 polymorphic allozyme loci in steelhead from Washington, Oregon and California, including samples from watersheds in the NC-Steelhead and CCC-Steelhead ESUs (Figure 4.1). A number of results from these data appear useful for identifying historical population structure. First, we note that steelhead from the Van Duzen River consistently group with steelhead in basins to the north (Redwood Creek and Mad River), yet this group does not include steelhead from the Middle Fork Eel River. Second, steelhead from a San Francisco Bay Tributary (Alameda Creek) do not group with any coastal populations, but appear to be quite distant from steelhead populations to the north and south. Third, steelhead from Scott Creek and the San Lorenzo River consistently group together. Fourth, some groups include samples from multiple ESUs, e.g., Ten

Table 4.1. Known out-of-basin and out-of-ESU releases of steelhead fry and fingerlings into rivers and streams of the NCCC-Steelhead ESU.

Basin[*]	**Period (Years)**[**]	**Egg Source (Hatchery)**[***]	**Numbers**[**]	**Reference**
Redwood Creek				
(Prairie Creek)	1972, 1988 (2)	unknown	46,940	NRC (1996)
Stone Lagoon	1973 (1)	unknown (via PRCH)	45,633	NRC (1996)
	1982 (1)	***Klamath R (via IGH)***	***279,000***	NRC (1996)
	1987 (1)	Prairie Cr (via HC)	30,905	NRC (1996)
Big Lagoon	1974-1981 (3)	Mad R (via MRH)	860,573	NRC (1996)
Mad River	1972-1981 (4)	***Washougal R, WA***[†] (via MRH/TRH)	248,480[††]	NRC (1996)
	1972-1974 (3)	SF Eel R (via MRH)	335,562[†††]	NRC (1996)
	1973 (1)	***San Lorenzo R (unknown)***	***100,800***	Busby et al. (1996)
	1985 (1)	***Russian R (via MRH)***	***19,958***	NRC (1996)
	1989-1990 (2)	***Russian R (unknown)***	***86,500***[‡]	Busby et al. (1996)
Humboldt Bay				
(Freshwater Creek)	1974-1981 (2)	Mad R (via MRH)	423,687	NRC (1996)
	1980-1981 (2)	Klamath R IGH (via TRH)	425,710	NRC (1996)
	1981 (1)	Trinity R (via TRH)	31,500	NRC (1996)
Eel River				
(unknown location)	1972, 1987 (2)	unknown	30,695	NRC (1996)
	1974-1991 (10)	Mad R (via MRH)	655,294	NRC (1996)
	1985 (1)	***Russian R, Dry Cr (via MRH)***	***76,452***	NRC (1996)
	1973 (1)	SF Eel (via MRH)	68,220	NRC (1996)
(lower mainstem)	1988 (1)	Gualala R (via GRSP)	29,000	NRC (1996)
	1985-1987 (2)	Prairie Cr (via PRCH)	2,640	NRC (1996)
	1987 (1)	unknown (via PLC)	11,970	NRC (1996)
(upper mainstem)	1990 (1)	Mad R (via MRH)	1,200	NRC (1996)
	1974-1983 (6)	Mad R (via MRH)	144,095	NRC (1996)
	1985 (1)	Russian R., Warm Springs (via SOS)	***20,128***	NRC (1996)
(South Fork Eel River)	1985 (1)	***Sacramento R, Mill Cr (via GRC)***	***9,300***	NRC (1996)
	1972 (1)	***Trinity R (via TRH)***	***500***	NRC (1996)
	1975-1983 (7)	Mad R (via MRH)	559,164	NRC (1996)
	1985 (1)	Humboldt Cr, coastal (via GRC)	7,000	NRC (1996)
	1985 (1)	***Russian R, Dry Cr (via WSH)***	***999***	NRC (1996)
(Van Duzen River)	1990 (1)	Shelter Cove (via GRC)	10,000	NRC (1996)
	1975-1982 (4)	Mad R (via MRH)	226,725	NRC (1996)
	1978 (1)	***Klamath R (via IGH)***	***64,376***	NRC (1996)
	1993 (1)	Freshwater Cr (via PLC)	4,600	NRC (1996)
Mattole River	1972 (1)	SF Eel R (via MRH)	30,065	NRC (1996)
	1973 (1)	***San Lorenzo R (via MRH)***	***19,067***	NRC (1996)
	19751981 (2)	Mad R (via MRH)	76,872	NRC (1996)
Ten Mile River		No recent records		
Noyo River	1973 (1)	***San Lorenzo R (via MRH)***	***40,100***	NRC (1996); Busby et al. (1996)
Big River		No recent records		
Navarro River	1972 (1)	Eel R (via MRH)	40,950	NRC (1996); Busby et al. (1996)
	1973 (1)	***San Lorenzo R (via MRH)***	***40,057***	NRC (1996); Busby et al. (1996)
	1975-1981 (3)	Mad R (via MRH)	99,013	NRC (1996); Busby et al. (1996)

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Basin*	**Period (Years)****	**Egg Source (Hatchery)*****	**Numbers****	**Reference**
	1985 (1)	***Russian R, Warm Springs (via SOS)***	***3,439***	NRC (1996); Busby et al. (1996)
Albion River		No recent records		
Garcia River	1975-1976 (2)	Mad R (via MRH)	20,333	NRC (1996); Busby et al. (1996)
Gualala River	1972 (1)	Eel R (via MRH)	1,950	NRC (1996); Busby et al. (1996)
	1972-1974 (2)	SF Eel R (via MRH)	46,800	NRC (1996); Busby et al. (1996)
	1973 (1)	***San Lorenzo R (via MRH)***	***20,345***	NRC (1996); Busby et al. (1996)
	1975-1976 (2)	Mad R (via MRH)	20,106‡‡	NRC (1996)

*Blocks indicate distinct individual coastal basins or regional groups of small watersheds; streams named parenthetically are tributaries known to have received specified transfers. **Records from 1950 to the present. Plantings of fewer than 500 fish not listed. ***Hatchery abbreviations are as follows: GRC=Garberville Rotary Club Inc.; GRSP=Gualala River Steelhead Project; HC=Humboldt County; IGH=Iron Gate; MRH=Mad River; PLC=Pacific Lumber Company, Scotia; PRCH=Prairie Creek; SKF=Silverking Farms; SOS=Save Our Salmon; TRH=Trinity River; WSH=Warm Springs. †Summer-run steelhead, Skamania stock Busby et al. (1996). ††Busby et al. (1996) list the total as 349,880. †††Busby et al. (1996) list the total as 292,210. ‡Combined fry and fingerlings. ‡‡Busby et al. (1996), list the total 30,830 for period 1975-1982.

Mile and Lagunitas; Scott Creek, San Lorenzo River and Carmel River; Redwood Creek and basins to the north.

Microsatellite data: Santa Cruz Laboratory

Recent work at the NOAA Santa Cruz Laboratory provides additional genetic data for evaluation of population structure of steelhead throughout coastal California (Garza et al., 2004, and *in prep.*). This data set (SCL2001) is based on samples collected during the summer of 2001 at 60 sites in 40 coastal basins, of which 32 samples were collected from 19 basins within the range of the NC-Steelhead ESU and 16 samples were collected in 11 basins within the range of the CCC-Steelhead ESU. The sample set was structured to allow direct evaluation of the hypothesis that rates of dispersal within a basin is substantially greater than rates of dispersal among basins. Samples consisted of tissue samples (fin clips) taken from 50-75 young-of-the-year (YOY) juvenile steelhead for each sample site. Juvenile steelhead were collected from a continuous series of habitat units according to a protocol designed to reduce both the likelihood of sampling siblings as well as the likelihood of sampling multiple populations. Despite these efforts, many samples include at least a few closely related individuals. Data were collected for 18 microsatellite loci, one of which was omitted for tree-building analyses due to a probable null allele not observed in all populations.

These samples exhibit a high variability, and a high degree of population structure, in that every pairwise comparisons using an exact test of population differentiation (Raymond and Rousset, 1995) yielded a highly significant result (Garza et al., 2004). While the inclusion of kin-biased samples in this analysis contributes somewhat to the large magnitude of genetic distances observed among samples, it does not obscure the general patterns apparent in the data set or undermine any of the inferences regarding population structure drawn from these data. However, the presence of siblings in samples might contribute to the high resolving power of individual assignment tests. These data contain no evidence of including recently derived hybrids between steelhead and coastal cutthroat trout (*Oncorhynchus clarki*).

Table 4.2. Known out-of-basin and out-of-ESU releases of steelhead fry and fingerlings into rivers and streams of the CCC-Steelhead ESU.

Basin[*]	**Period (Years)**[**]	**Egg Source (Hatchery)**[***]	**Numbers**[**]	**Reference**
Russian River	1957-1959 (2)	***Sacramento R, Battle Cr (via CNFH)***	***9,128***	NRC (1996)
	1972 (1)	***Eel R (via MRH)***	***85,140***	NRC (1996); CDFG 1994[†]
	1973 (1)	San Lorenzo R (via MRH)	83,350	NRC (1996);CDFG 1994[†]
	1973 (1)	unknown (via CLH)	22,100	NRC (1996)
	1975-1991 (8)	***Mad R (via MRH)***	***587,111***[††]	NRC (1996)
	1980-1981 (2)	***Washougal R, WA***[†††] (via MRH)	***270,410***	NRC (1996);CDFG 1994[†]
Tomales Bay				
(Lagunitas Creek)	1972 (1)	***SF Eel R (via MRH)***	***10,080***	NRC (1996);CDFG 1994[†]
	1973 (1)	San Lorenzo R (via MRH)	4,500	NRC (1996);CDFG 1994[†]
	1976-1981 (4)	***Mad R (via MRH)***	***55,610***	NRC (1996);CDFG 1994[†]
(Walker Creek)	1984 (1)	Russian R, Dry Cr (via WSH)	10,000	NRC (1996)
San Francisco Bay				
(Napa River)	1972 (1)	***SF Eel R (via MRH)***	***20,200***	NRC (1996);CDFG 1994[†]
	1973 (1)	San Lorenzo R (via MRH)	14,400	NRC (1996);CDFG 1994[†]
	1979-1981 (3)	***Mad R (via MRH)***	***40,171***[‡]	NRC (1996);CDFG 1994[†]
	1985-1987 (3)	Russian R (via NRSA)	8,500	NRC (1996)
(Other tributaries)	1979 (1)	***Mad R (via MRH)***	***3,153***	NRC (1996);CDFG 1994[†]
	1981-1989 (6)	***Sacramento R (via NH/FRH)***[†††]	***1,531,892***	NRC (1996)
San Gregorio Creek	1985 (1)	Russian R (via WSH)	8,140	NRC (1996)
Pescadero Creek	1972 (1)	***SF Eel R (via MRH)***	***7,650***	NRC (1996);CDFG 1994[†]
	1973 (1)	San Lorenzo R (via MRH)	9,000	NRC (1996);CDFG 1994[†]
	1975-1981 (5)	***Mad R (via MRH)***	***55,759***[‡]	NRC (1996);CDFG 1994[†]
	1985 (1)	Russian R (via WSH)	8,140	NRC (1996)
Davenport Landing	1981-1982 (2)	unknown (SKF)	1,785	NRC (1996)
San Vicente Creek	1993-1994 (2)	Scott Cr (via MBSTP) check	4,860	NRC (1996)
San Lorenzo River	1972 (1)	***Eel R (via MRH)***	***20,250***	NRC (1996);CDFG 1994[†]
	1972 (1)	***SF Eel R (via MRH)***	***20,000***	NRC (1996)
	1975-1981 (5)	***Mad R (via MRH)***	***173,450***[‡‡]	NRC (1996);CDFG 1994[†]
	1985 (1)	***Salinas R (via MBSTP)***	***237,140***	NRC (1996)
	1984-1994 (10)	Scott Cr/Big Cr (via MBSTP)	48,330[‡‡‡]	NRC (1996)
Soquel Creek	1985 (1)	***Salinas R (via MBSTP)***	***9,604***	NRC (1996)
	1984-1994 (8)	Scott Cr/Big Cr (via MBSTP)	90,842[§]	NRC (1996)
	1990-1991 (2)	San Lorenzo R (via MBSTP)	32,790	NRC (1996)

[*] Blocks indicate distinct individual coastal basins or regional groups of small watersheds; streams named parenthetically are tributaries known to have received specified transfers. [**] Records from 1950 to the present. Plantings of fewer than 500 fish not listed. [***] Hatchery abbreviations are as follows: CLH=Crystal Lake; CNFH=Coleman National Fish Hatchery; FRH=Feather River; MBSTP=Monterey Bay Salmon and Trout Project; MCH=Mill Creek (Sacramento Basin); MRH=Mad River; NH=Nimbus (American River); NRSA=Napa River Steelheaders Assoc.; SKF=Silverking Farms; WSH=Warm Springs. [†] As cited in Busby et al. (1996).[††] Busby et al. (1996) list the total 483,954 for period 1975-1981. [†††] Summer-run steelhead, Skamania stock Busby et al. (1996). [‡] Busby et al. (1996) list the total 20,165 for period 1979-1980. [†††] Most from Nimbus hatchery; source unknown for 199,402 fish, but likely from Sacramento River system. [‡] Busby et al. (1996) list the total 44,659 for period 1975-1981. [‡‡] Busby et al. (1996) list the total 149,090 for period 1975-1981. [‡‡‡] NRC (1996) lists 26,625 fish planted in San Lorenzo River in 1984 as Big Creek, Oregon, stock; however this entry appear to be in error. We believe these fish originated from Big Creek in Santa Cruz County. [§] NRC (1996) lists 7,500 fish planted in San Lorenzo River in 1984 as Big Creek, Oregon, stock; however this entry appear to be in error. We believe these fish originated from Big Creek in Santa Cruz County.

Phylogeographic trees. In our analysis of phylogeographic trees, we concentrate on bootstrap consensus trees as a way to focus our attention on the internal branch structure. In doing so, we gloss over the long terminal branches that reflect the relatively large genetic distances observed among samples in the data set (Garza et al., 2004). Much of the internal branch structure of the consensus tree has fairly weak bootstrap support[10]—particularly at the scale of populations, and in some regions. Nevertheless, the consensus tree provides useful insight to the population genetic structure of steelhead throughout much of coastal California.

Phylogeographic trees indicate strong concordance between geography and population genetic structure at the ESU scale, including the clear separation between the NC-Steelhead and CCC-Steelhead ESUs, but differentiation among samples is weaker at smaller scales, which prevents unambiguous comparison of geographical and genetic structure (Figures 4.2 and 4.3). Exceptions to these patterns can be understood in the context of historical stock transfers among populations (Tables 4.1 and 4.2).

Within the NC-Steelhead ESU, samples taken north of the Lost Coast tend to group together, with the exception of a single sample from Prairie Creek[11] (a.k.a. “Redwood Creek (Humboldt)^c” in Figures 4.2 and 4.3), samples south of the Lost Coast group together, and the single sample from the Lost Coast, Big Creek (Humboldt) lies intermediate to the northern and southern clusters. This pattern confirms that the Lost Coast presents a relatively effective barrier to dispersal of steelhead along the coast, and provides a robust example of population genetic structure mirroring geographic structure at relatively large spatial scales. However, population genetic structure in the area between the Eel and Klamath Rivers exhibits a more complex pattern. On one hand, there is evidence of strong population structure in the form of robust grouping of samples from Redwood Creek (Humboldt), except the Prairie Creek sample mentioned previously, and Humboldt Bay (Freshwater Creek) to the exclusions of both the cluster of samples from the Klamath Mountains Province ESU and the cluster of samples centered on the Eel River. In contrast, samples from the Eel, Mad, Mattole, and Bear rivers cluster together, and samples from the Mad and Eel rivers intermingle (Figures 4.2 and 4.3). In light of the substantial exchange of hatchery fish between the Eel and Mad rivers, such intermingling is not surprising (Table 4.1). Concordance between spatial and population genetic structure is less clearly resolved in the southern range of the NC-Steelhead ESU, south of the Lost Coast. In this region, basins tend to be smaller and thus the potential for dispersal among populations or among-basin stock transfers to have substantial influence on population genetic structure is increased. In almost all cases in this area, samples taken within the same basin tend fall in the same region of the tree, even when the arrangement of such groups does not appear to agree with the geographical arrangement of the basins from which they are drawn (Figures 4.2 and 4.3).

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[10] Weak bootstrap support should not be interpreted as a poor fit in this case, as most alternative configurations were not strikingly different from one another, with only a few samples in slightly different positions.

[11] Closer examination of the data indicates that the Prairie Creek sample is indeed similar to other samples taken from Redwood Creek (Humboldt), but also shows similarities to populations further to the south. This similarity might be the result of among-basin transfers, possibly associated with the operation of a hatchery on Prairie Creek. Behnke (2002) points out that many early hatchery stocks of steelhead and rainbow trout were derived from steelhead San Francisco Bay tributaries. That more such results do not occur is surprising given the size of the data set and the frequency of interbasin transfers of *O. mykiss* in California.

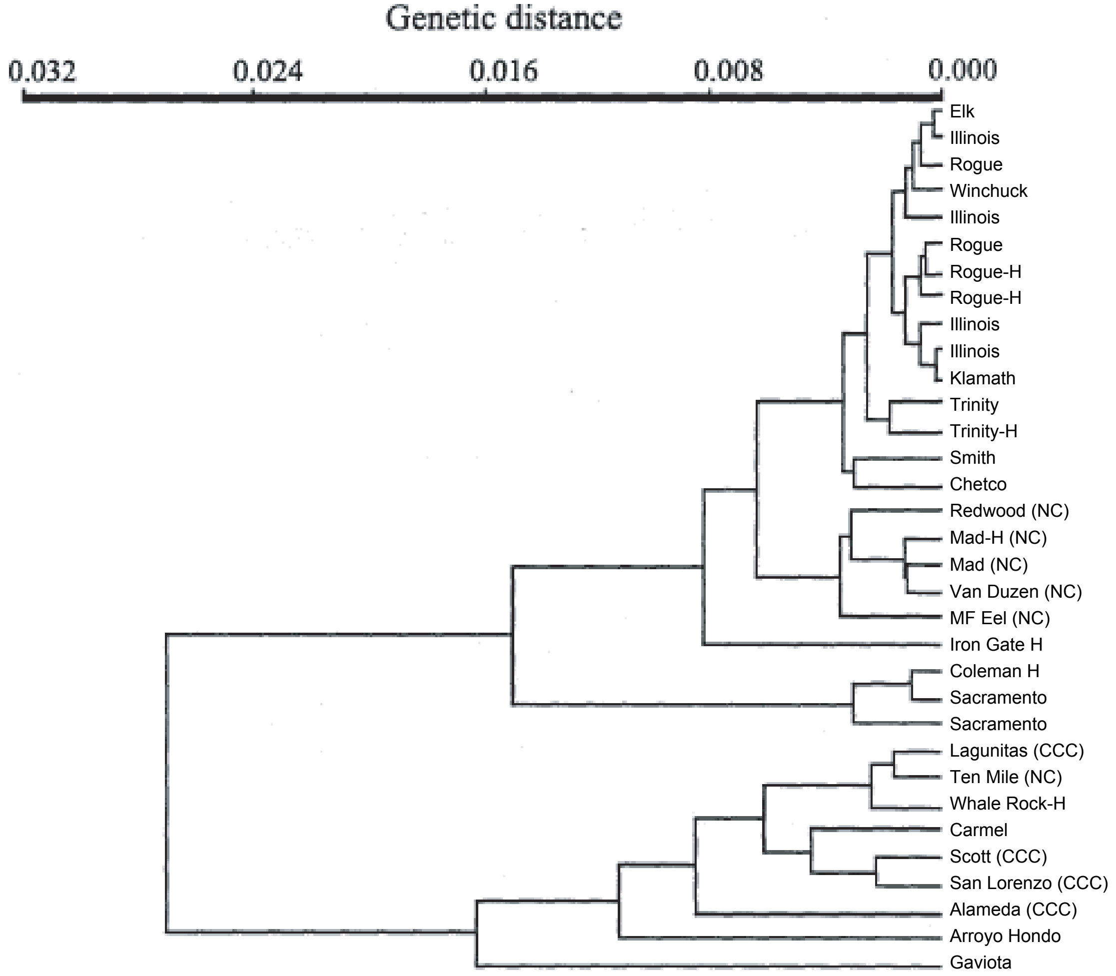

Figure 4.1. Dendrogram based on UPGMA applied to Nei's D calculated from 51 polymorphic allozyme loci for 33 West Coast populations of steelhead, including hatchery (H) populations. Redrawn from Busby et al. (1996) (their Figure 3). See Busby et al. (1996) for details regarding samples and analysis. Samples from populations within the NCCCRD are indicated by ESU designations. "H" indicates a hatchery population.

Within the CCC-Steelhead ESU, population genetic structure is less clearly concordant with geography. North of San Francisco Bay (inclusive), there appears to be reasonable concordance; however, samples from the southern part of the CCC-Steelhead ESU are intermingled with samples collected from populations in the South-Central California Coast (SCCC) Steelhead ESU (Figures 4.2 and 4.3). Again, information on among-basin and among-ESU transfers suggests the genesis of this structure. Although not presented in Table 4.2, which focuses on transfers to populations in the CCC-Steelhead ESU, substantial transfers *from* the CCC-Steelhead ESU *to* populations in the SCCC-Steelhead ESU have occurred over the past two decades.[12]

Population differentiation and inferred relative migration rates. Comparison of estimates of pairwise F_{ST} for pairs of samples within the same basin to those for pairs of samples from different basins indicates that, on average, gene flow within basins is greater than among basins for both ESUs (NC-Steelhead ESU: $\overline{F_{ST}}_{,within} = 0.0412$, $\overline{F_{ST}}_{,among} = 0.0614$; CCC-Steelhead ESU: $\overline{F_{ST}}_{,within} = 0.0463$; $\overline{F_{ST}}_{,among} = 0.0601$)[13]; this pattern is consistent with that observed for the entire SCL2001 data set (Figure 4.4). Estimates of pairwise F_{ST} also indicate gene flow between Redwood Creek (Humboldt) and basins to the north, particularly watersheds in the Klamath River and Wilson Creek (detailed data not shown). Likewise, gene flow is indicated across the southern boundary of the CCC-Steelhead ESU, which is consistent with the greater mingling of populations from these ESUs in the tree-building analyses and the expected consequences of substantial among-basin transfers in this area.

The concordance between geography and genetic population structure suggested by the phylogeographic trees is clearly apparent as a robust isolation-by-distance signal over the entire range of the SCL2001 data set and within more restricted data sets for each of the two ESUs considered here (Figure 4.5). Approximately 20% of the genetic variance[14] among populations (samples) can be explained as a function of the geographic distance between sample locations, measured “as the fish swims” along the stream network and coastline (omitting the inner edge of major estuaries such as San Francisco Bay and Humboldt Bay).

Assignment tests proved to be highly successful in assigning individuals to their actual population of origin with 93.2% of individuals correctly assigned to population of origin in the entire data set. This proportion rose only slightly to 93.8% of individuals correctly assigned when a misassignment to another population from the same basin was not considered an error. The presence of siblings within each sample is likely to have contributed to the high degree of correct assignments in this analysis, although how strongly is not clear (Garza et al., 2004). Within the NC-Steelhead ESU 93.6% of individuals were

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[12] For example, NRC (1996) reports transfers to two watersheds directly south of the CCC-Steelhead ESU: (1) between 1984 and 1994, the Monterey Bay Salmon-Trout Project (MBSTP) transferred a total of 172,152 steelhead of Scott Creek or San Lorenzo River origin to the Pajaro River and its tributaries; and (2) between 1986 and 1994, MBSTP transferred a total of 49,653 steelhead of San Lorenzo River origin to the Salinas River and one tributary (Arroyo Seco).

[13] If the sample from Walker Creek is included in the same basin as samples from Lagunitas Creek (i.e., Tomales Bay), the contrast between within and among basin gene flow is slightly sharper ($\overline{F_{ST}}_{,within} = 0.0435$; $\overline{F_{ST}}_{,among} = 0.0608$).

[14] F_{ST} is negatively correlated with effective population size in the SCL2001 data set, which is likely to contribute substantially to the variation apparent in Figure 4.5. The effect of this correlation manifests as the contrast between the diffuse upper edge and the distinct lower edge of the cloud of data points.

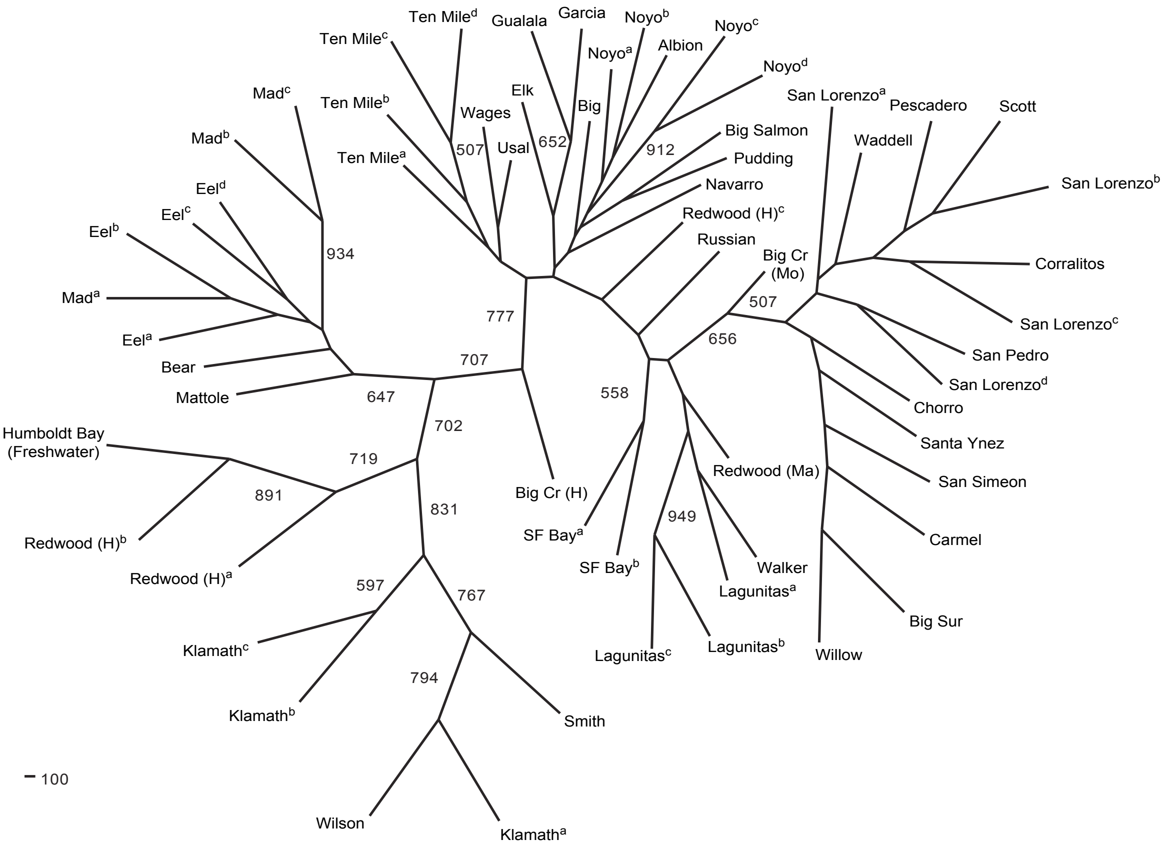

Figure 4.2. Bootstrap consensus tree based on pairwise CSE Chord distance for steelhead from coastal California. Bootstrap support for internal branches indicated by branch length; see scale on figure for length corresponding to 100 instances. Internal branches observed in $>$500 of 1000 boostrap iterations are indicated by numbers on branches. Terminal branch lengths are scaled for clarity and are not informative. Within basin samples indicated by superscripts. Klamath River: ^{a}Hunter Cr, ^{b}Horse Linto Cr, ^{c}Blue Cr; Redwood Creek (Humboldt): ^{a}Panther Cr, ^{b}Lost Man Cr, ^{c}Prairie Cr; Eel River: ^{a}Hollow Tree Cr (South Fork Eel), ^{b}Indian Cr (South Fork Eel), ^{c}Willits, ^{d}Lawrence Cr; Mad River: ^{a}Blue Cr, ^{b}Canon Cr, ^{c}Sullivan Cr; Ten Mile River: ^{a}Little North Fork, ^{b}South Fork, ^{c}Smith Cr, ^{d}Redwood Cr; Noyo River: ^{a}mainstem, ^{b}South Fork, ^{c}Kass Cr, ^{d}Little North Fork; San Lorenzo River: ^{a}Bear Cr, ^{b}Boulder Cr, ^{c}Zayante Cr, ^{d}Carbonera Cr; Lagunitas Cr: ^{a}mainstem, ^{b}Olema Cr, ^{c}Blue Line Cr; San Francisco Bay: ^{a}Los Trancos Cr, ^{b}Miller Cr.

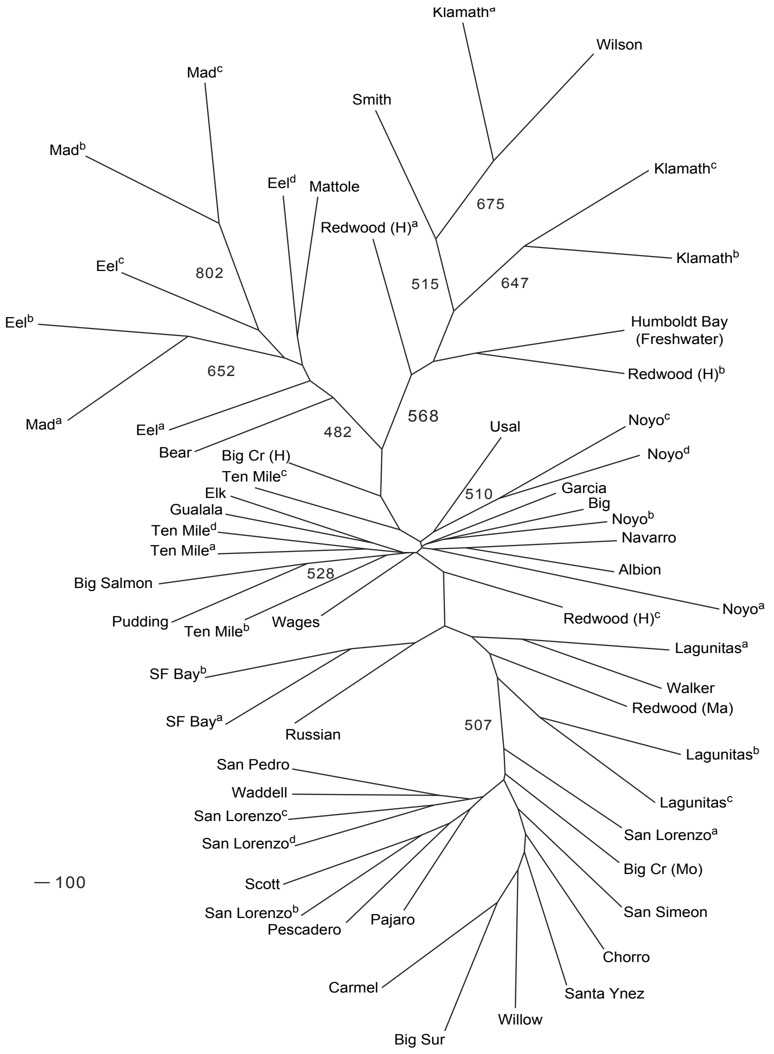

Figure 4.3. Bootstrap consensus tree based on pairwise Nei's D for steelhead from coastal California. Bootstrap support for internal branches indicated by branch length; see scale on figure for length corresponding to 100 instances. Internal branches observed in $>$500 of 1000 boostrap iterations are indicated by numbers on branches. Terminal branch lengths are scaled for clarity and are not informative. Within basin samples indicated by superscripts. Klamath River: ^{a}Hunter Cr, ^{b}Horse Linto Cr, ^{c}Blue Cr; Redwood Creek (Humboldt): ^{a}Panther Cr, ^{b}Lost Man Cr, ^{c}Prairie Cr; Eel River: ^{a}Hollow Tree Cr (South Fork Eel), ^{b}Indian Cr (South Fork Eel), ^{c}Willits, ^{d}Lawrence Cr; Mad River: ^{a}Blue Cr, ^{b}Canon Cr, ^{c}Sullivan Cr; Ten Mile River: ^{a}Little North Fork, ^{b}South Fork, ^{c}Smith Cr, ^{d}Redwood Cr; Noyo River: ^{a}mainstem, ^{b}South Fork, ^{c}Kass Cr, ^{d}Little North Fork; San Lorenzo River: ^{a}Bear Cr, ^{b}Boulder Cr, ^{c}Zayante Cr, ^{d}Carbonera Cr; Lagunitas Cr: ^{a}mainstem, ^{b}Olema Cr, ^{c}Blue Line Cr; San Francisco Bay: ^{a}Los Trancos Cr, ^{b}Miller Cr.

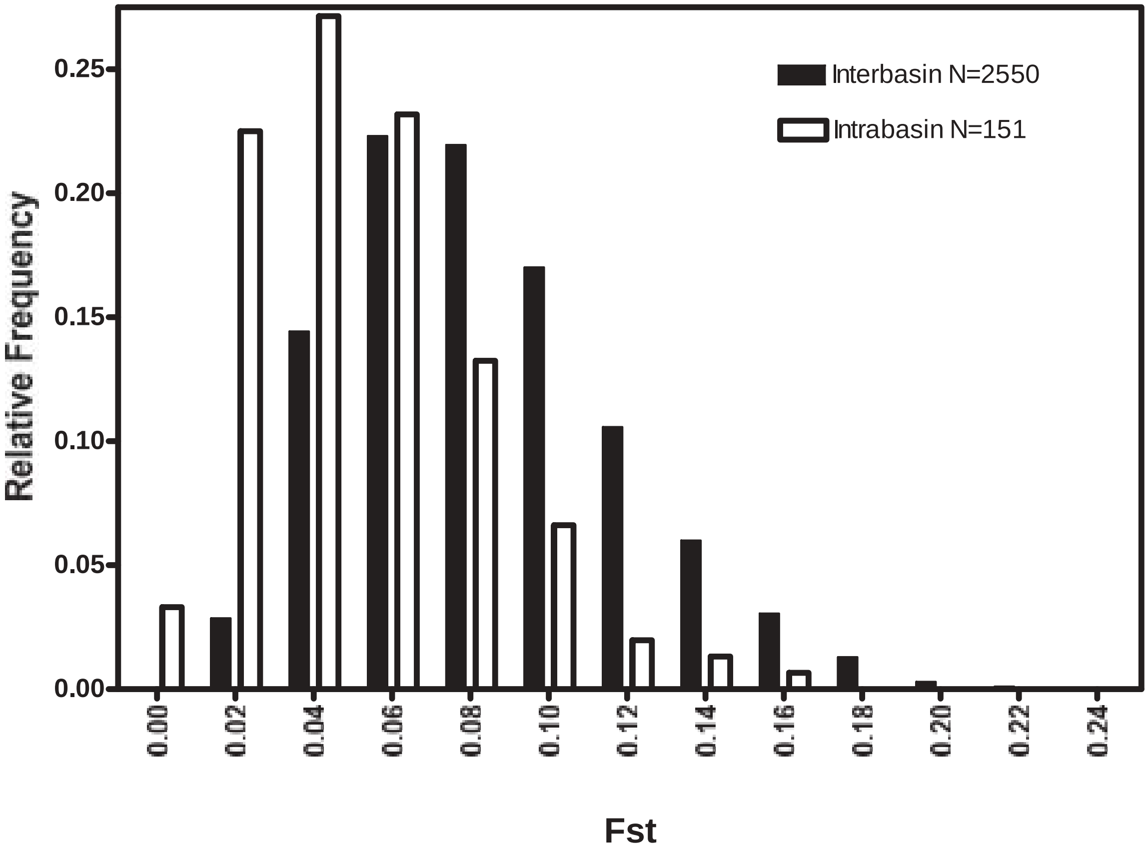

Figure 4.4. Frequency distribution of estimated pairwise F_{ST} among sites within the same basin (white bars) and among sites in different basins (black bars) for steelhead throughout coastal California.

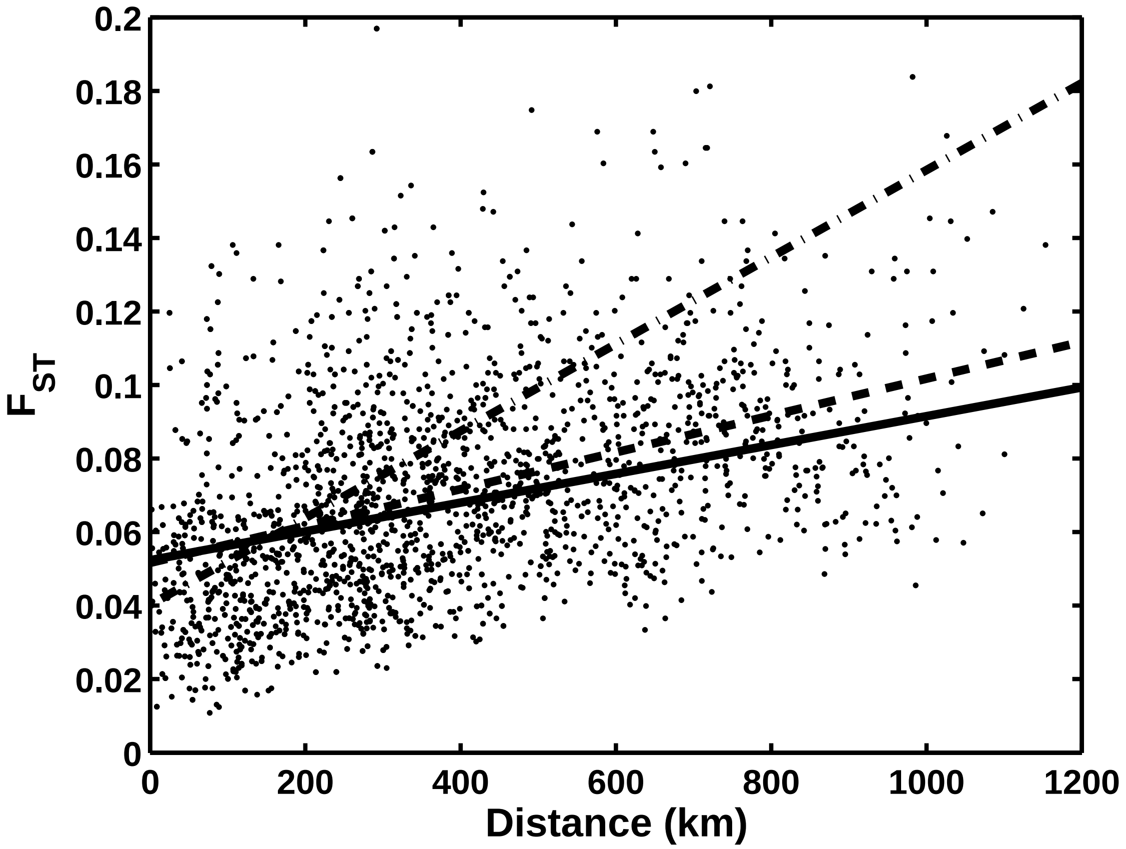

Figure 4.5. Isolation-by-distance in steelhead based on pairwise F_{ST} and geographic distance for samples from the NC-Steelhead ESU (dashed line), CCC-Steelhead ESU (dot-dash line) and throughout coastal California, including populations north and south of the NCCCRD (solid line). For samples from different basins, geographic distance is calculated as the sum of the length of the coastal contour (omitting major bays such as the San Francisco Bay) between stream mouths and the upstream distance of each sample location. For samples from within the same basin, geographic distance is calculated as the distance "as-the-fish-swims" within the stream network.

Table 4.3. Summary of assignment test accuracy and the proportion of misassigned individuals that are assigned to another sample the correct basin for the NCCC-Steelhead and CCC-Steelhead ESUs. "Single Sites" indicate correct assignments to basins for which only a single sample was collected. Results from analysis of the SCL2001 steelhead data set (Garza et al., 2004).

	Correct Sample	Correct Basin	% Out-of-sample retained within basin
NCCC-Steelhead			
Redwood Creek (H)	0.9091	0.9091	0.0000
Mad River	0.9671	0.9737	0.2006
Eel River	0.8490	0.9528	0.6874
Tenmile River	0.9510	0.9592	0.1673
Noyo River	0.9344	0.9672	0.5000
Single Sites	0.9446		
CCC-Steelhead			
Lagunitas Creek	0.9390	0.9672	0.4623
San Lorenzo River	0.8559	0.8784	0.1561
Single Sites	0.9492		

assigned to the location where they were sampled; in the CCC-Steelhead ESU, 91.6% of individuals were correctly assigned. The proportion of incorrectly assigned individuals that were assigned to another location in the same basin ranged from 0% for samples from Redwood Creek to 68.7% for samples from the Eel River (Table 4.3).

After collapsing the data so that all assignments to the basin-of-origin are considered correct, the distribution of misassignments as a function of an ordinal distance (the number of basins away from the basin-of-origin) shows a clear decline in recent migration with distance (Figure 4.6). Misassignments were more common among basins between San Francisco and Monterey Bay, with 10, 5, and 3 misassignments occurring at intervals of 1, 2, and 3 basins, respectively. The overall signal remains strong even if this regional pattern is removed (Figure 4.6). For all but two populations, there was not a strong signal of misassignment to a particular population. The two exceptions are Prairie Creek (a tributary to Redwood Creek (Humboldt)) populations, where 58% of incorrect assignments (7 of 12) were to San Francisco Bay[15] and Freshwater Creek, where 44% of incorrect assignments (8 of 18) were to Redwood Creek (Humboldt), and specifically to Prairie Creek. The latter result is perhaps not surprising, with only one intervening basin between the two samples. However, the former result is dramatic, as the two samples are separated by hundreds of kilometers. What these results imply is uncertain, but the results themselves are consistent with the position of the Prairie Creek sample in Figures 4.2 and 4.3.

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[15] Behnke (2002) points out that San Francisco Bay populations were the original source of numerous *O. mykiss* hatchery stocks. Given the long history of the Prairie Creek hatchery, it is possible that such a distantly historical transfer underlies the observed genetic similarity between steelhead in Prairie Creek and San Francisco Bay.

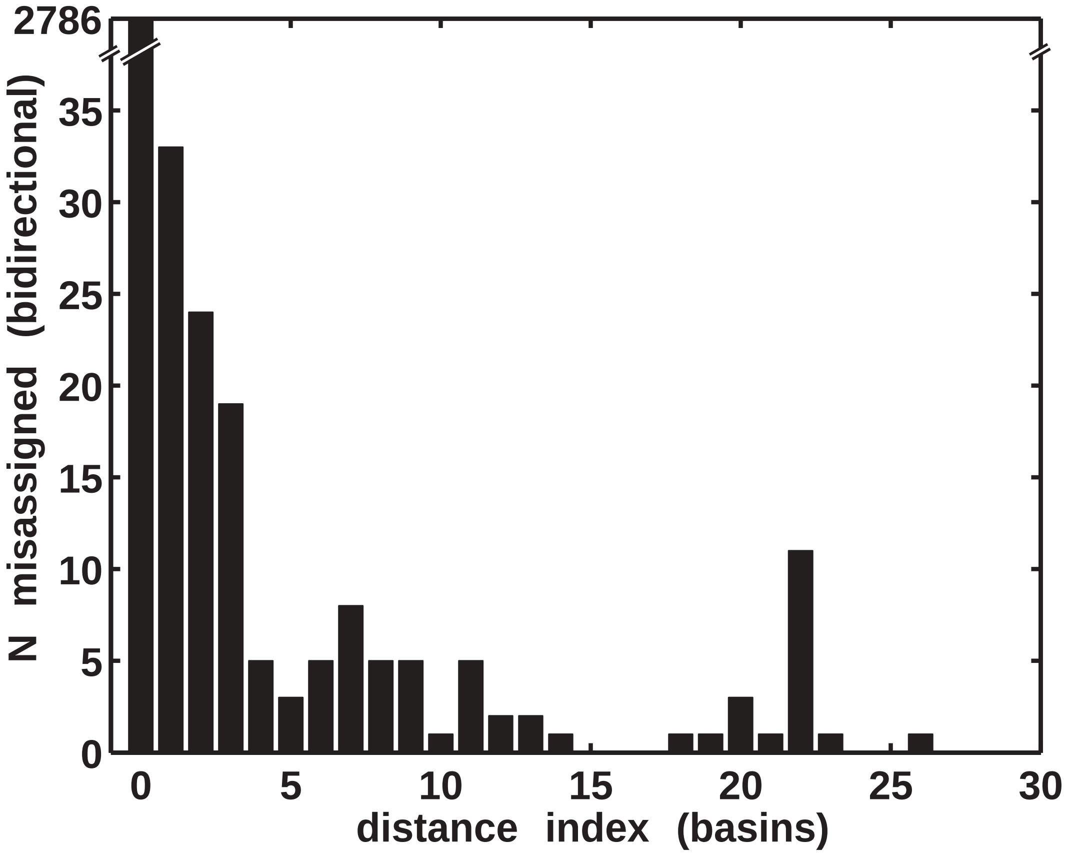

Figure 4.6. Number of individuals assigned to a basin as a function of the number of basins between the basin-of-origin and the assigned basin. Data for samples from the NC-Steelhead and CCC-Steelhead ESUs combined. “0” indicates correct assignment to basin. The spike at 23 basins consists largely of individuals from Prairie Creek (tributary to Redwood Creek (Humboldt)) that were assigned to San Francisco Bay populations. Note that 2,786 of 3,014 individuals were correctly assigned to their basin of origin.

Geographical "breaks" in gene flow. The SCL2001 data were also subject to an analysis designed to detect significant breaks in population structure. The analysis consists of (1) identifying the most likely separation between populations[16] under the assumption that the entire data set represents k populations, (2) calculating the fractional likelihood that each individual's genome belongs each of the 1 to k populations identified in the previous step according to the individual's genotype and the allele frequencies calculated for each of the populations, (3) averaging the mean ancestry across all individuals within each *sample*, and (4) identifying as a "break" the *location* for which the (sample) mean ancestry switches between the populations identified in the first step, and interpreting this in terms of the spatial arrangement of samples along the coast[17]. Note that the analysis ignores geography until the final step. To identify and rank locations at which apparent barriers to gene flow exist, this analysis was repeated for $k = 2, 3, \ldots, 10$ hypothetical populations. The results for the set of analyses are then summarized by tallying the number of tests in which each break appears. Note that a break identified for a given hypothetical number of populations (k) is almost always observed in tests for higher k, especially for those breaks that are identified in tests with k. Thus, the number of tests in which a break appears, or alternatively, the lowest k for which a break is identified, is a rank measure of how strongly gene flow is reduced across a particular geographic location.

Figure 4.7 summarizes the results from this analysis across the entire SCL2001 data set, and shows robust breaks between the Russian River and Gualala River, across the Lost Coast, just south of the Golden Gate, and near Humboldt Bay. Breaks of moderate strength also occur along the Mendocino Coast. Breaks between populations of steelhead in the Monterey Bay area appear only when the hypothetical number of populations represented in the sample is relatively high. Note that the major breaks coincide with major structures apparent in the phylogeographic trees (Figures 4.2 and 4.3) and geographic structure. Note also, that while this analysis provides strong support for the boundary between the NC-Steelhead and CCC-Steelhead ESUs, it offers little support for the current southern boundary of the CCC-Steelhead ESU, and suggests that substantial barriers to gene flow exist within the NC-Steelhead and CCC-Steelhead ESUs as currently defined.

Microsatellite data (Eel River): A. Clemento and J. C. Garza, *unpublished data*

Figure 4.8 illustrates relationships for a broader set of samples collected within the Eel River. The data set on which this analysis is based includes both winter- and summer-run steelhead and also includes samples from above barriers to anadromy (A. Clemento and J. C. Garza, unpublished data).

All samples from the Middle Fork Eel River save Plaskett Creek[18] group together to the exclusion

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[16] Here, the term "population" is used to identify a group of individuals *absent geographic context*. Such populations were delineated with the program STRUCTURE (Pritchard et al., 2000).

[17] To simplify interpretation of the results, a break was identified only if (1) all samples from within a basin were assigned to the same putative "population" (the Prairie Creek sample was excluded from this analysis), (2) all populations on either side of the break fell in the same group (i.e., the breaks were geographically consistent), and (3) a new assignment persisted across subsequent tests with greater k.

[18] Plaskett Creek lies above a small dam and has been planted with fish from the American River hatchery, which likely explains why it departs from other samples.

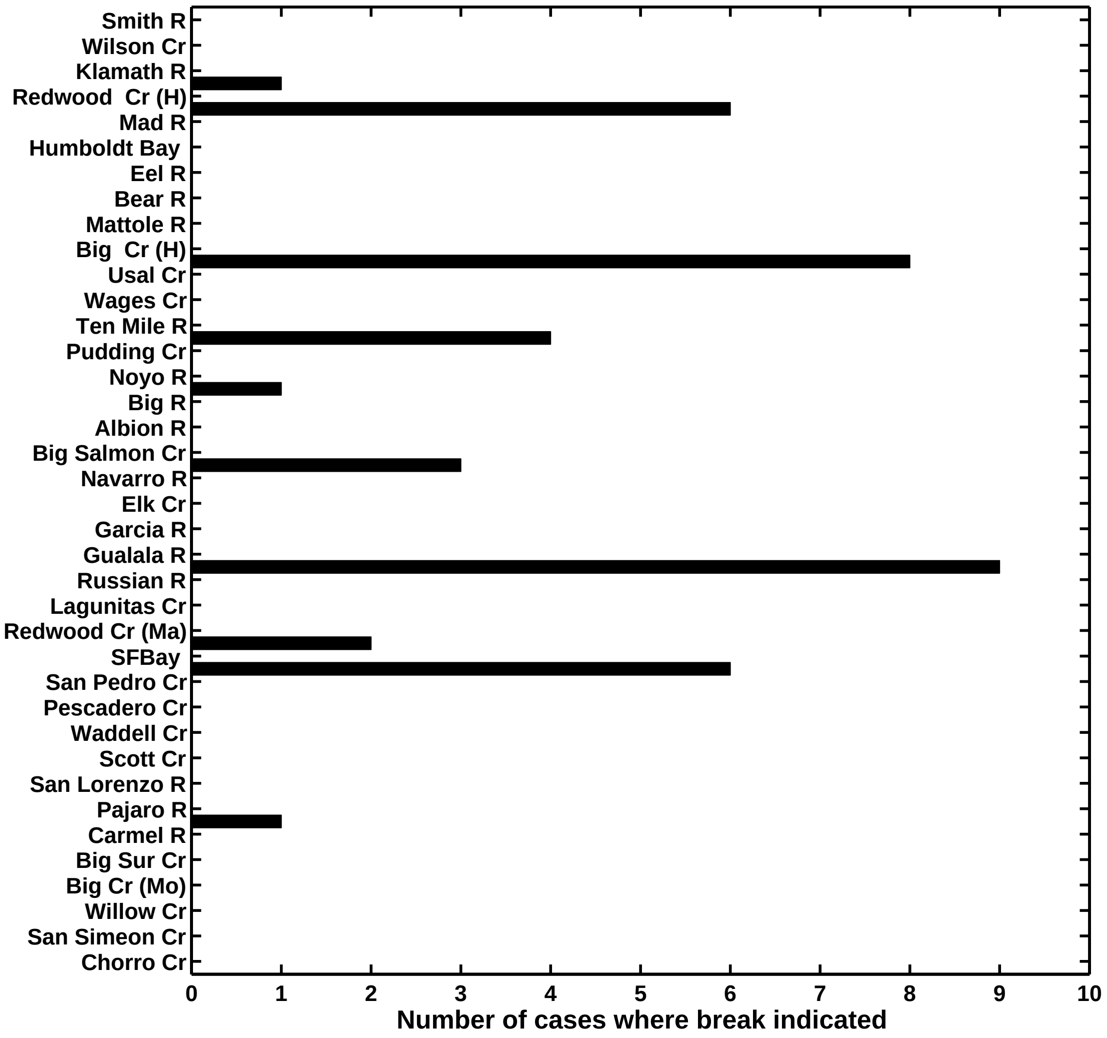

Figure 4.7. Location of geographical "breaks" in the population genetic structure of steelhead throughout coastal California. Robustness of breaks is based on the number of cases, each defined by a unique number of hypothetical "populations" represented in the entire data set, in which a particular break is observed. See text for description of underlying analysis.

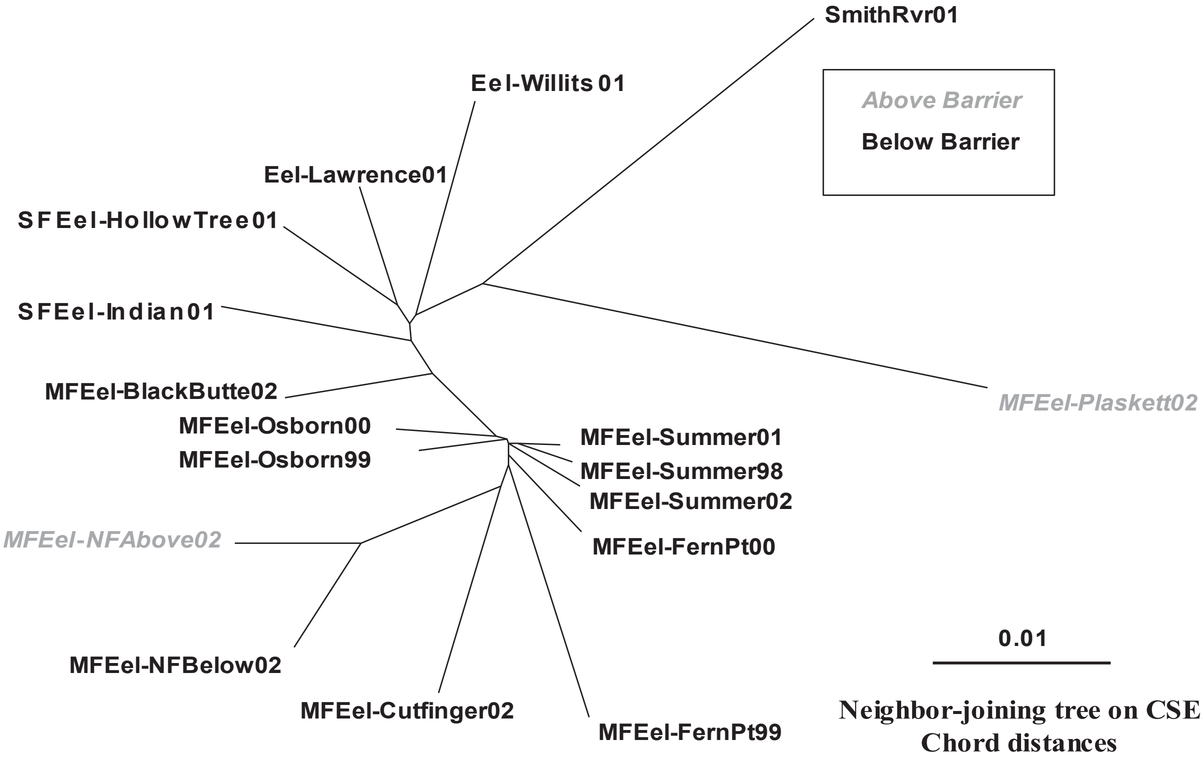

Figure 4.8. Neighbor joining tree based on pairwise CSE Chord distance for steelhead from the Eel River. Data collected for 17-18 microsatellite loci. Summer steelhead data are from adult fish, and are likely to include more than one cohort. All other below-barrier samples are based on collections of presumptive young-of-the-year juveniles; however, the life-history of the parents is unknown. Above-barrier collections may include more than one cohort.

of samples from the South Fork Eel River, Van Duzen River and upper mainstem Eel River (Figure 4.8). Note that temporally separated samples for summer steelhead cluster together, but do not fall outside the cluster of winter steelhead samples from the Middle Fork Eel River.

Microsatellite data (Russian River): Deiner (2004)

Deiner (2004) examined the population genetic structure of *Oncorhynchus mykiss* in the Russian River basin based on data obtained for twelve microsatellite loci. Estimates of pairwise F_{ST} for samples of *O. mykiss* in waters accessible to anadromy are consistent with the range observed in the SCL2001 study among samples within a basin (F_{ST} in the Russian River ranged from 0.02-0.08; Figure 4.4). Little or no concordance between geography and genetic structure was observed in the data set for the Russian River (Deiner, 2004).

4.4.3 Synthesis of information on population genetic structure

Available genetic data for coastal steelhead ESUs from a variety of sources, most notably a data set based on allozyme markers (Busby et al., 1996) and a data set based on microsatellite markers (Garza et al., 2004), yield a consistent picture of population genetic structure for steelhead throughout coastal California. Overall, the SCL2001 data, by virtue of the greater number, concentration, and spatial arrangement of samples and the potential for microsatellite DNA markers to have greater resolving power at the temporal scales of interest, are more informative with respect to structure across the boundary of the southern NC-Steelhead ESU and northern CCC-Steelhead ESU and within each ESU. Within the NC-Steelhead ESU, both data sets yield trees in which samples from the Mad and Eel rivers are intermingled and samples from Redwood Creek (Humboldt) exhibit affinities with basins to the north. Within the CCC-Steelhead ESU, analyses of both data yield weaker concordance between geography and population genetic structure, and find that samples from the CCC-Steelhead ESU and ESUs to the south are often co-mingled.

Most apparent discrepancies between geography and population genetic structure are readily resolved in the context of historical transfers among basins and among ESUs. For example, transfers among basins probably attenuated any structure that might have existed historically among steelhead populations in the region spanning the southern end of the NCCCRD. Likewise, substantial transfers between the Mad River, Eel River and nearby basins are likely to have reduced the concordance between geographic and genetic structure among steelhead in the northern part of the NCCCRD. Similarly, movement of hatchery fish might underlie the lack of structure observed in some basins.

Despite evidence that among-basin transfers and intense local hatchery production have had detectable effects at local to regional scales in specific areas, such transfers do not appear to have disrupted an overall, geographically concordant pattern in the population genetic structure of steelhead throughout the NCCCRD. We therefore conclude that a hierarchical, geographical model for population structure is warranted for steelhead in the NCCCRD. The general concordance between geography and population genetic structure observed in phylogeographic trees supports this conclusion, but we find the hierarchical structure of pairwise F_{ST} and the robust isolation-by-distance signal to be even more compelling evidence for a geographical model. Furthermore, we conclude, albeit more cautiously, that the large genetic distances observed between samples, including those collected within the same basin, supports examination of population structure at a somewhat finer scale than is considered for coho salmon and Chinook salmon. This conclusion is further motivated and corroborated by the general tendency for areas of high IP for suitable habitat to exhibit a more fragmented distribution in the upper portions of watersheds (Plates 14 and 15).

In addition to offering general support for the use of a geographical model to evaluate population structure of steelhead, the SCL2001 data resolve areas where important structure is observed (Figure 4.7). One interpretation of these data is that the current ESU definitions might not reflect the actual population genetic structure of steelhead in coastal California, and that substantial gene flow occurs among steelhead populations across the northern and southern boundaries of the NCCCRD as well as within the NCCCRD. The question of ESU delineation is one that must be addressed by the appropriate Biological Review Team, and We therefore proceed with our analysis according to the existing delineation of ESUs. However, since the genetic data raise this possibility, we are compelled to consider a somewhat broader approach to analysis of population structure of steelhead in the NCCCRD. We therefore conduct our analysis to ensure that our conclusions are relevant under the current ESU structure, yet are readily translated to any revised ESU structure. Specifically, we take into account the potential for dispersal into the NCCCRD in our analysis of geographic structure, and, in contrast to analyses for other species, we consider genetic structure more explicitly in delineating diversity strata within the NC-Steelhead and CCC-Steelhead ESUs. By doing so, we seek to avoid introducing model uncertainty into our conclusions so that they will provide a sound basis for recovery planning regardless of any future deliberations regarding ESU delineation. Note that adopting a broader approach also limits the sensitivity of our conclusions to differences of opinion regarding the effects of stock transfers on population genetic structure of steelhead in the NCCCRD.

With respect to the evolutionary relationship between summer and winter steelhead, analysis of the one new genetic data set that includes explicit comparison of summer and winter steelhead supports the hypothesis that summer and winter steelhead in the same basin are more closely related than steelhead of the same life history in different basins (A. Clemento, et al., *unpublished data*). While this data set lacks samples from other summer steelhead populations, the conclusions drawn from the analysis are consistent with the current understanding of evolutionary relationships between winter and summer steelhead elsewhere in the Pacific Northwest (Busby et al., 1996).

4.5 Geographic structure of the NC-Steelhead and CCC-Steelhead ESUs

Insights gained from genetic data generally support the assumptions of the geographic model for historical population structure of steelhead in the NCCCRD. Therefore, we use the connectivity-viability model, which is outlined in general terms in the Introduction, to synthesize information on the relative size of historical populations of winter steelhead and their distribution along the coast. In this section, we develop the parameters for the connectivity-viability model for populations in the NC-Steelhead and CCC-Steelhead ESUs, and review results of the analysis in the context of the assumptions that underlie the model.

Translating IP-km into a proxy measure of population size

We use predictions from the IP model as the basis for our habitat-based population proxy, and (following the reasoning outlined in the Introduction) assume that carrying capacity of winter steelhead populations is linearly proportional to the integrated length of accessible habitat within a watershed weighted by the intrinsic potential for habitat suitable for juvenile rearing (IP-km).

Viability-in-isolation threshold for winter steelhead

In our analysis of coho salmon, we were able to draw on the results of viability modeling based on a substantial data set and explicit comparisons between IP measures and historical abundance to develop a threshold for viability-in-isolation. Similar analyses are not yet available for steelhead. Although the premise of the coho salmon analysis is relevant to steelhead, direct use of results from coho salmon for winter steelhead is not warranted due to a number of important differences between the two species. However, we also lack sufficient information to develop a threshold for viability-in-isolation from first principles. Therefore, we selected 16 IP-km, which is one-half the threshold used for coho salmon, as the threshold for viability-in-isolation of winter steelhead populations.

This threshold is based on the following assumptions regarding how differences between the two species affect habitat capacity and population viability. First, we expect that a given reach of equal species-specific IP will be capable of supporting more juvenile steelhead than coho salmon since steelhead readily use a wider variety of habitats and tolerate a broader range of environmental conditions. We note, however, that older age-classes of juvenile steelhead, which may contribute disproportionately to adult returns, are more likely to use pool habitats similar to those preferred by coho salmon. Second, the life history diversity of winter steelhead tends to buffer population responses to environmental variation. For example, unlike Pacific salmon, steelhead are iteroparous, and in contrast to coho salmon in particular, steelhead have broader distributions of age-at-ocean-entry and age-at-maturation, and exhibit greater flexibility in the timing of life history transitions in response to environmental conditions such as drought. These traits allow for effective temporal dispersal within a population, which reduces the susceptibility of a cohort to extinction and increases population viability in the face of environmental variability (Hill et al., 2003). Third, steelhead tend to spawn and rear in smaller headwaters tributaries that are located higher in a watershed, which spreads risk of disturbance over space, and spawn over a longer season, which reduces the potential for catastrophic destruction of redds in a given year. Note that the habitat suitability curves for steelhead IP explicitly reflect this pattern, so that for a given amount of integrated habitat potential (IP-km), areas with higher IP will tend to be distributed among tributaries for steelhead but be more concentrated in lower reaches of spawning tributaries for coho salmon. Finally, the IP model does not identify lagoon habitats that may be extremely productive under the right conditions. The degree and consistency with which lagoon habitats contribute currently (much less historically) to the productivity of steelhead populations is not well known. Given this uncertainty, we do not quantitatively incorporate lagoon habitats in our analysis of viability-in-isolation.

We think a value of 16 IP-km to be a plausible threshold for viability-in-isolation for a population of winter steelhead. Our selection of this threshold also reflects a precautionary approach, in which we choose to err on the high side of the plausible range of watershed sizes likely to span the actual average threshold for habitat required to support a viable population. By doing so, we concentrate on populations most central to ESU structure and persistence, and greatly reduce the likelihood that subsequent analysis and conclusions regarding ESU viability criteria will rest on populations that are not truly viable-in-isolation. Future analysis of viability criteria may require that this threshold be revised, probably downwards; however, such revision will not alter the relative rankings of populations in the connectivity-viability analysis that follows. If a reduced threshold for viability-in-isolation is warranted, more options for viable ESU configurations may arise, but this will not necessarily change the overall form of the final result due to other constraints that shape ESU viability criteria.

Note that populations occupying watersheds with less than 16 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 100s of years.

Consequences of potential hydrological and ecological biases in steelhead IP

Violations of assumptions that underlie the IP model are expected to yield a latitudinal gradient of bias in the predictions of the IP model, largely as a consequence of regional differences in hydrology[19] and, perhaps, the ecological interaction between steelhead and coho salmon that is implicit in the structure of the habitat suitability functions used to calculate IP for juvenile steelhead[20]. Areas where ecological bias is most likely are concentrated in parts of the interior Eel River and Russian River basins, and the northern and southeastern regions of the San Francisco Bay basin where coho salmon are likely to be excluded by temperature. However, increased foraging requirements of steelhead at higher temperatures are likely to prevent steelhead from exploiting slow flowing pool habitats in areas where coho are not present. Therefore, we expect exclusion of coho salmon due to temperature to have limited consequences for the capacity of a basin for steelhead over what is predicted from the IP model.

Connectivity-viability analysis

We conducted a more extensive set of connectivity-viability analyses for steelhead than for the two species of salmon. These analyses included the conventional analysis of populations arranged along the coast. We also examined the potential for population structure at a finer scale within the three large basins of the NCCCRD: Eel River, Russian River, and San Francisco-San Pablo Bay. Our motivation for doing so is described in greater detail below. On the basis of apparent population genetic structure, we also conducted somewhat more formal sensitivity analyses to account for the potential implications of immigration from steelhead populations outside the NCCCRD. In the course of these analyses, we generally focus on overall patterns, recognizing that the results of these analyses (especially if compared to absolute thresholds) are sensitive to the form of the dispersal function and fidelity rate selected for the analysis.

ESU boundaries. In the course of our analysis, we generally observed definitions of ESU ranges consistent with the original definitions in Busby et al. (1996) and subsequent assessments. Steelhead ESUs in the NCCCRD are surrounded by other steelhead ESUs on their north[21], south[22], and inland[23] boundaries, which requires that we consider whether and how to include populations from outside the NCCCRD in our analyses. Moreover, available genetic data highlight the need for more explicit analysis of the sensitivity of our conclusions regarding the status of populations near the edge of the NCCCRD to

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[19] For greater detail, refer to §1.5.1: 'Assumptions and the interpretation of the connectivity-viability model' in the Introduction

[20] For greater detail, refer to §4.3.2, above.

[21] Klamath Mountains Province Steelhead ESU

[22] South-Central California Coast Steelhead ESU

[23] Central Valley Steelhead ESU

assumptions regarding dispersal from coastal populations to the north and south (cf. §4.4.2, and Figure 4.7).

Rather than extend the range of our study area well beyond the NCCCRD, we examine sensitivity to immigration from the north and south with heuristic representations of steelhead populations outside the NCCCRD. Specifically, we conduct the connectivity-viability analysis for populations of steelhead in the NCCCRD in isolation, and compare the results to those for an analysis that includes a substantial population to the north and one to the south. We set the relative size of these external populations to mimic a plausible, aggregated source of immigrants from the entire ESU, taking into account the attenuation of dispersal over distance. In the north, we considered immigration only from the lower tributaries of the Klamath-Trinity basin, and other coastal basins (e.g., the Smith River). In the south, we considered immigration primarily from the Pajaro and Salinas rivers. We also included immigration from the Central Valley, but limited the intensity of this immigration due to the tremendous distances that separate spawning habitats in the Central Valley from those in tributaries of San Francisco and San Pablo bays.

Coastwide analysis. We used the model outlined in the introductory chapter (§1.5.1) to generate predictions of self-recruitment under a set of simple assumptions and using IP as a proxy for population size. All direct tributaries to the Pacific Ocean with ≥ 1.6 IP-km were included in the analysis[24], and major basins or estuaries with multiple tributaries were considered as single units. Although genetic data indicate a clear break in population structure at the boundary of the ESUs (between the Gualala and Russian rivers), we conducted the connectivity-viability analysis for the NC-Steelhead ESU and CCC-Steelhead ESU as a pooled unit. The distance matrix generated in the course of the connectivity-viability analysis included a substantial break in the region between the mouths of the Russian and Gualala rivers, which corresponds exactly with the break observed in the genetic data, so we are confident that the connectivity-viability analysis does not suffer undue bias as a consequence of the integrated analysis.

We considered the Eel River as a single population for purposes of modeling connections among populations separated by saltwater. The Eel River basin spans a wide range of environmental conditions, and thus has the potential to harbor multiple populations. It is possible, indeed it is likely, that separate populations within the Eel River basin exhibit different rates of dispersal to populations in neighboring coastal watersheds. We therefore also examined results from a connectivity-viability analysis in which steelhead from only the South Fork Eel River, Van Duzen River, and tributaries of the lower Eel River interact strongly with neighboring watersheds. Results were not strongly sensitive to this distinction, and we present results from analyses that incorporate a “restricted” Eel River below.

Figures 4.9 and 4.11 summarize the ranking of putative populations in the NC-Steelhead ESU and CCC-Steelhead ESU, respectively, in terms of self-recruitment and a proxy measure for viability-in-isolation. Figures 4.10 and 4.12 summarize the contribution of source populations to sink populations within each ESU. Note that cross-ESU contributions to sink populations is predominantly in a northward

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[24] Given the prevalence of steelhead in small watersheds, this threshold is much less worrisome than the analogous threshold for Chinook salmon.

direction, with emigration from the CCC-Steelhead ESU (primarily from the Russian River) having a substantial influence as far north as Greenwood Creek [35] (Figure 4.10). The lack of a very large population in the southern portion of the NC-Steelhead ESU limits the amount of dispersal in the reverse direction.

In the NC-Steelhead ESU, ten populations fall robustly into the functionally independent quadrant: Redwood Creek (Humboldt) [1], Eel River [7], Mattole River [14], Ten Mile River [23], Noyo River [25], Big River [30], Albion River [32], Navarro River [34], Garcia River [39], and Gualala River [41] (Figure 4.9). Another fifteen populations are predicted to be at least potentially independent, the largest of which are Mad River [5], Humboldt Bay [6], Bear River [10], Maple Creek (Big Lagoon) [2], Little River [3], Alder Creek [37], and Pudding Creek [24]; the remaining potentially independent populations include somewhat smaller basins along the Mendocino and Sonoma county coasts (Figure 4.9). Note that the application of a lower threshold for viability-in-isolation will increase the number of potentially independent populations, but does not yield any additional functionally independent populations. Self-recruitment to populations in the northern part of the NC-Steelhead ESU is somewhat sensitive to immigration from the north[25], but immigration from this northern proxy population was not sufficient to change the prediction of a functionally independent population in Redwood Creek (Humboldt) [1], and generally did not have substantial effects on predictions for other populations (results not shown).

Connectivity patterns within the NC-Steelhead ESU indicates that the Eel River population strongly influences the independence of populations in watersheds of moderate to large size in the northern part of the NCCCRD (e.g., Mad River [5] and Humboldt Bay [6]; Figures 4.9 and 4.10); however, this in part reflects the interaction between the dispersal model and the effect of the spits that separate Humboldt Bay from the Pacific Ocean on the physical structure of the coastline in this region. Southward dispersal from the Eel River and other large, northern basins is predicted to have a strong influence on smaller populations, but its influence on larger populations is greatly attenuated by the extent of the Lost Coast (Figure 4.10). In contrast, the connectivity-viability analysis predicts that dependent and potentially independent populations along the coast between the Lost Coast and Point Arena can receive substantial immigration from a relatively broad range of source populations. The influence of immigration from the populations in the CCC-Steelhead ESU, primarily from the Russian River, might be substantial, but is concentrated primarily in the Gualala River and smaller watersheds that lie between the Gualala and Russian rivers. Of course, the influence of any source population scales with its size, and the degree of connectivity apparent in Figure 4.10 is sensitive to the width of the dispersal function used in the underlying analysis.

In contrast to the NC-Steelhead ESU, the CCC-Steelhead ESU is largely dominated by two large populations: one in the Russian River [42] and the other in the (combined) tributaries of San Francisco Bay [51] (Figures 4.11 and 4.12). Due to the physical barrier to dispersal presented by Point Reyes, these two populations most strongly influence distinct parts of the coast (Figure 4.12). Four populations

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[25] To mimic immigration from the lower Klamath River basin and other populations in the Klamath Mountains Province Steelhead ESU, we ran the connectivity-viability model for a data set that included a proxy basin of 1000 IP-km located at the mouth of the Klamath River.

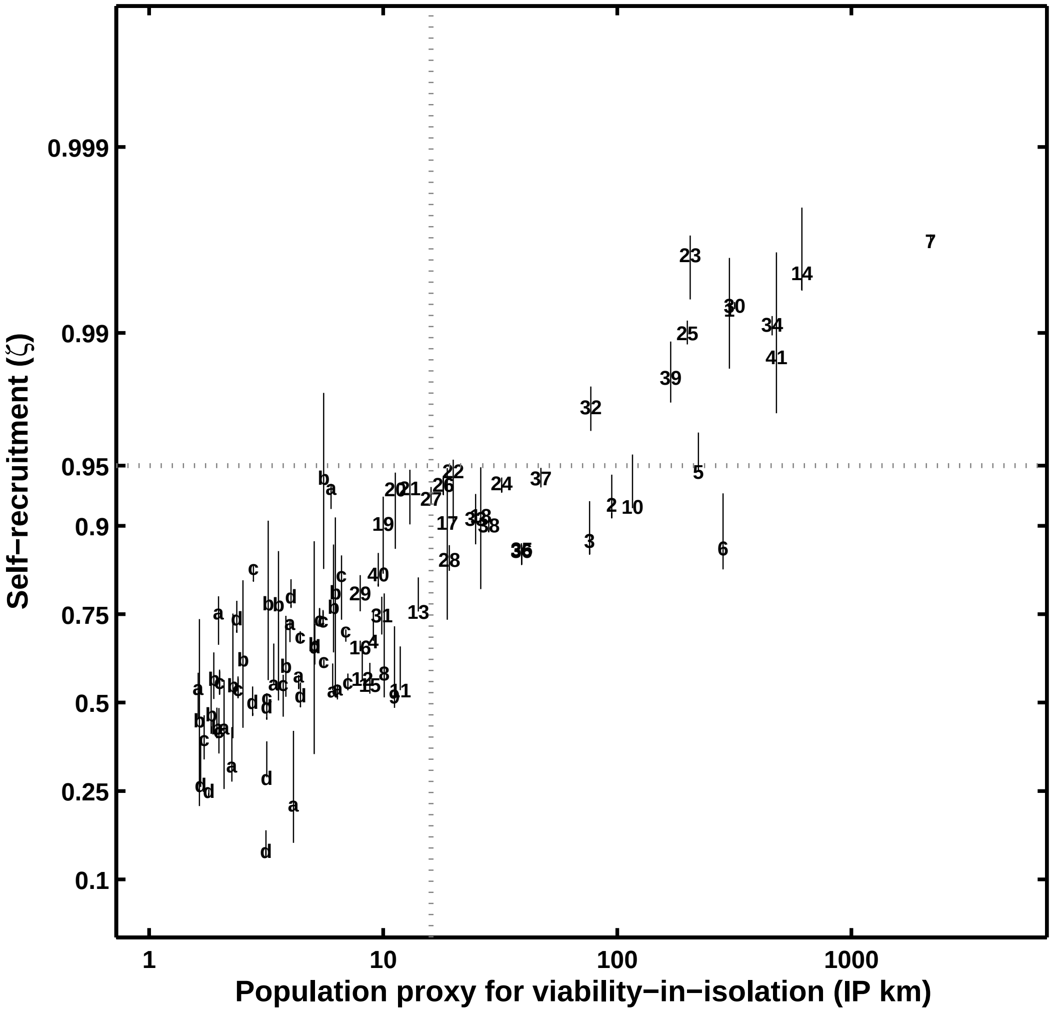

Figure 4.9. Self-recruitment and viability-in-isolation for putative populations in selected watersheds within the geographical range of the NC-Steelhead ESU. Populations are identified by watershed (see Table 1.1). Only populations in watersheds with $\geq$ 1.6 IP-km are included in the analysis. Analysis conducted for all such populations in both ESUs, and results are partitioned here solely for clarity. 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 to -0.10 km. Horizontal grey dotted line demarcates source populations (populations above the line for which self-recruitment exceeds fidelity, set at 0.95) from sink or pseudo-sink populations (populations below the line for which fidelity exceeds self-recruitment). Vertical grey dotted line at 16 IP-km indicates threshold for viability-in-isolation.

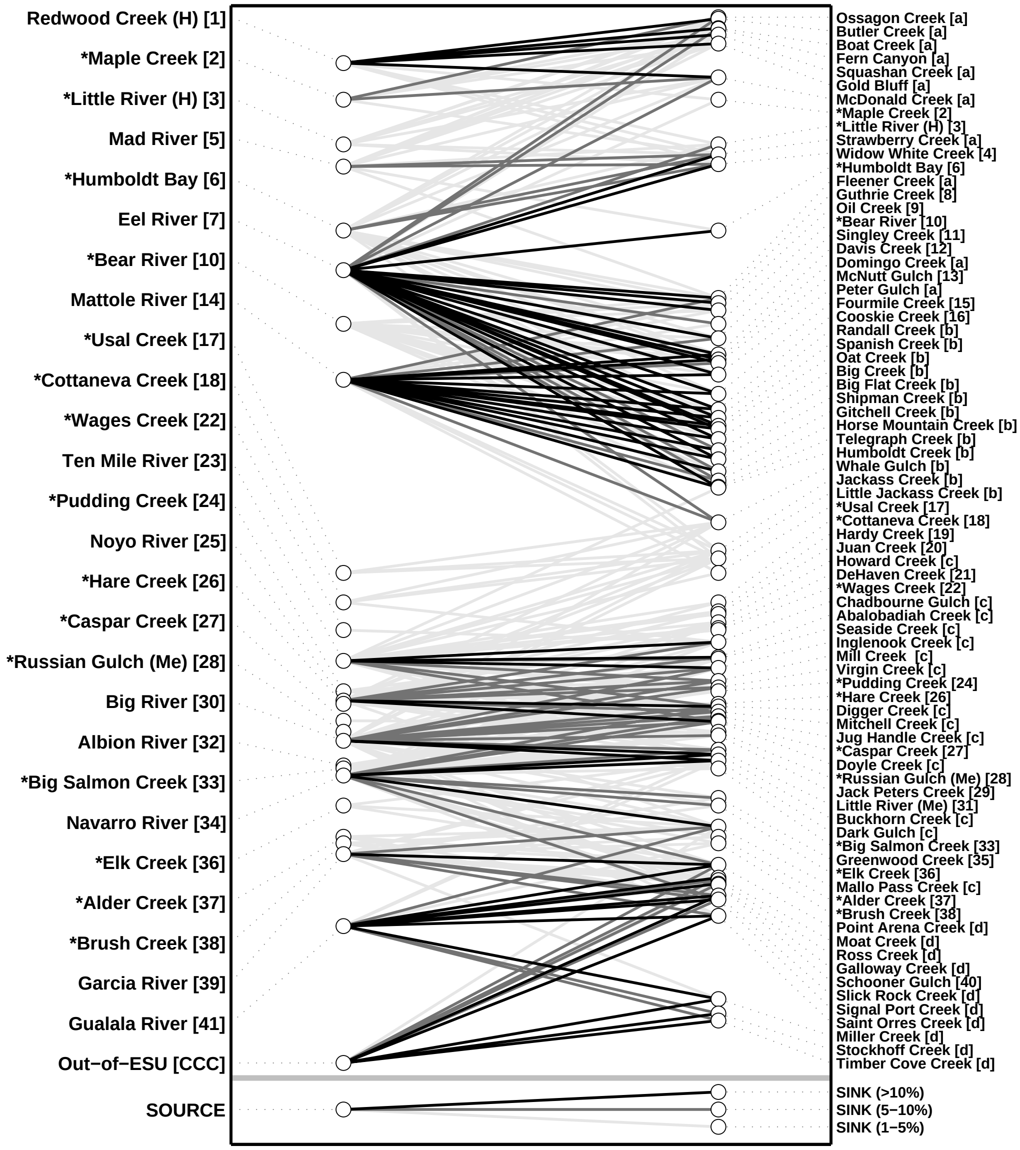

Figure 4.10. Connectivity within the NC-Steelhead ESU, as measured by the contribution of source populations (on the left) to sink populations (on the right) as a function of the proportion (in excess of 1%) of the spawning run to a sink population contributed by each source population. Connectivity based on an exponential dispersal function with the decay parameter set to -0.05 km. Distribution of populations reflects distance along the coastline. Assignment of populations as source (functionally and potentially independent) or sink (potentially independent and dependent) populations is based solely on comparison of IP-km to our viability-in-isolation threshold of 16 IP-km. Immigration from all populations in the CCC-Steelhead ESU is pooled and treated as a single source population. Potentially independent populations are indicated by an asterisk and included as source populations and sink populations. (Self-recruitment to potentially independent populations is ignored in this plot.)

south of the Golden Gate also fall out as functionally independent populations (San Lorenzo River [63], San Gregorio Creek [54], Pescadero Creek [56], and Soquel Creek [64]); however, only the San Lorenzo River [63] is robustly functionally independent (Figure 4.11). The status of Soquel Creek [64] is sensitive to the inclusion or exclusion of dispersal from the South-Central California Coast Steelhead ESU[26]; however, such immigration does not qualitatively influence the status of the San Lorenzo River [63] (results not shown). The status of steelhead in tributaries of Tomales Bay [47] (e.g., Walker Creek and Lagunitas Creek) depends strongly on dispersal from the Russian River [42] and San Francisco Bay [51], whereas the status of Scott Creek [59] depends mostly on the extent of dispersal from San Francisco Bay [51] and San Lorenzo River [63] (Figure 4.12). Potentially independent populations are predicted to occur in watersheds of moderate size between the Russian River and the Golden Gate (Salmon Creek (Sonoma) [43], Americano Creek [45], and Stemple Creek [46]), and south of the Golden Gate (Tunitas Creek [52], Gazos Creek [57], Waddell Creek [58], Scott Creek [59], and Aptos Creek [65]).

Within-basin analyses: motivation, methods and results. In contrast to our analyses for coho salmon and Chinook salmon, we also applied the connectivity-viability analysis within three major basins: Eel River, Russian River, and San Francisco-San Pablo Bay[27]. Our major motivation for doing so within the two large river basins is based on the fragmented distribution of areas with high potential for steelhead rearing habitat. In contrast to patterns observed in coho salmon and Chinook salmon, mainstem areas in large basins are likely to present more substantial barriers to dispersal among populations in steelhead for which spawning habitats are typically concentrated higher in watersheds. Also, the distribution of areas with high IP suggests that steelhead populations are more directly exposed to the environmental characteristics of a basin and may therefore be more likely to respond to differences in selective environments. A secondary motivation for this exercise is based on the observation that within the two large river basins and San Francisco Bay, a substantial number of major tributaries that appear to be discrete also exceed our viability-in-isolation threshold. The combination of sufficient size and potential isolation seems to warrant more formal consideration of how the physical structure of these major basins might influence the population structure of steelhead within these basins.

How one interprets the results of this analysis depends strongly on available information (or assumptions) regarding rates of dispersal among spawning groups in separate tributaries and the potential for divergent selection. Of the species considered in this report, steelhead exhibit life history traits that are most likely to satisfy the requirements for substantial structure within a basin (See §1.5.7). Moreover, genetic data for steelhead indicate that although average rates of gene flow are greater within basins

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[26] To mimic dispersal of steelhead in the Pajaro and Salinas rivers, we included a relatively large population (twice the size of the San Lorenzo River) located at the mouth of the Pajaro River in our sensitivity analysis.

[27] We do not develop such analyses for other basins within the NCCCRD or for the major subbasins in the large systems, even though some, such as the Gualala River, also exhibit fragmented areas of high IP in discrete tributaries. Our main reason for not doing so is that, unlike the mainstem in each of the two large rivers, mainstem habitats in these basins are more likely to have provided suitable habitat conditions for spawning and rearing, and gaps between confluences tend to be much shorter. Thus, the mainstem in watersheds of moderate size or smaller are less likely to have presented substantial breaks in distribution. Moreover, since we do not consider results of such analyses to offer sufficient support for delineating distinct populations in a basin, there is little motivation to consider such analyses for populations in basins of moderate size or smaller.

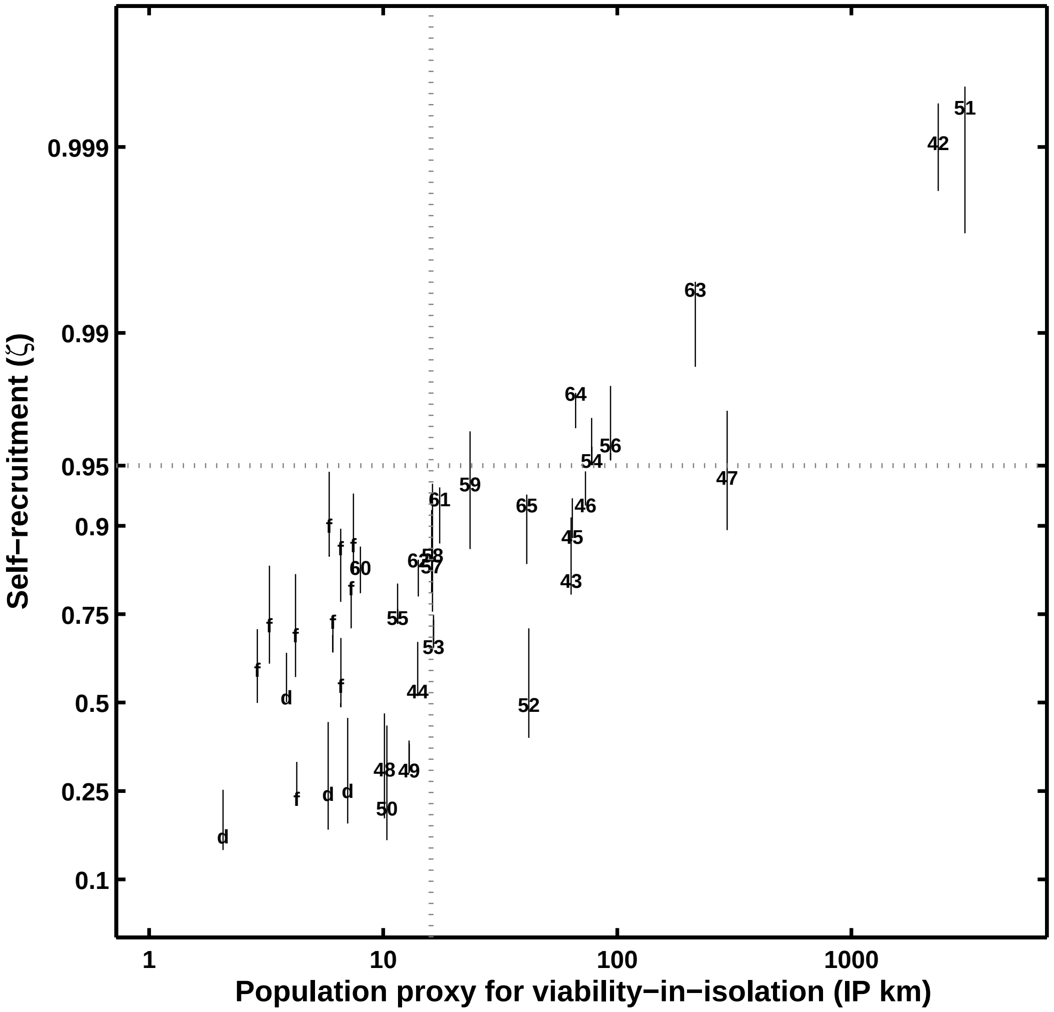

Figure 4.11. Self-recruitment and viability-in-isolation for putative populations in selected watersheds within the geographical range of the CCC-Steelhead ESU. Populations are identified by watershed (see Table 1.1). Only populations in watersheds with $\geq$ 1.6 IP-km are included in the analysis. Analysis conducted for all such populations in both ESUs, and results are partitioned here solely for clarity. 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 to 0.10 km. Horizontal grey dotted line demarcates source populations (populations above the line for which self-recruitment exceeds fidelity, set at 0.95) from sink or pseudo-sink populations (populations below the line for which fidelity exceeds self-recruitment). Vertical grey dotted line at 16 IP-km indicates threshold for viability-in-isolation.

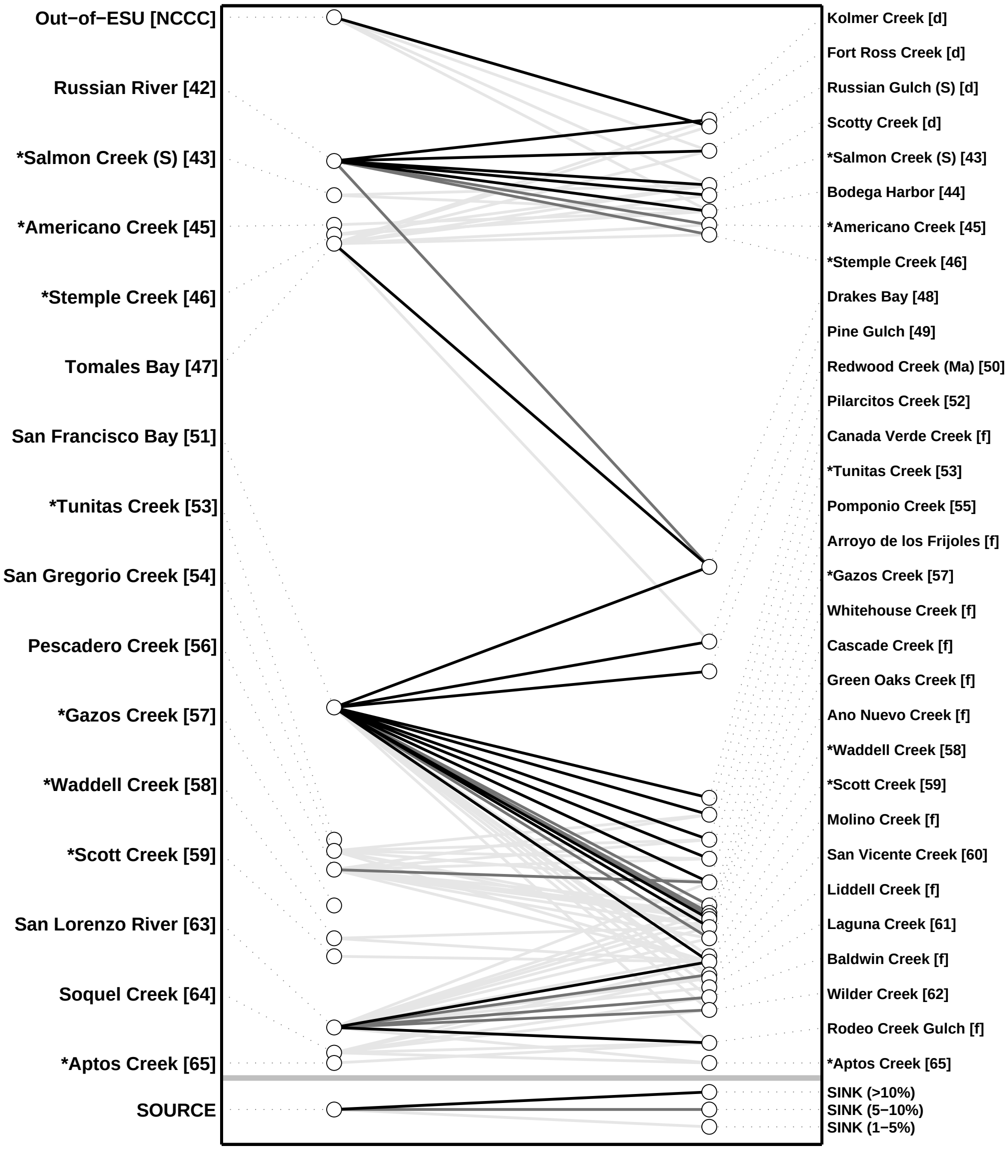

Figure 4.12. Connectivity within the CCC-Steelhead ESU, as measured by the contribution of source populations (on the left) to sink populations (on the right) as a function of the proportion (in excess of 1%) of the spawning run to a sink population contributed by each source population. Connectivity based on an exponential dispersal function with the decay parameter set to -0.05 km. Distribution of populations reflects distance along the coastline. Assignment of populations as source (functionally and potentially independent) or sink (potentially independent and dependent) populations is based solely on comparison of IP-km to our viability-in-isolation threshold of 16 IP-km. Immigration from all populations in the NC-Steelhead ESU is pooled and treated as a single source population. Potentially independent populations are indicated by an asterisk and included as source populations and sink populations. (Self-recruitment to potentially independent populations is ignored in this plot.)

than among basins (Figure 4.4), but the distribution of estimates of among- and within-basin rates of gene flow overlap substantially[28]. For these reasons, we are more inclined to consider the potential for substantial population structure among steelhead within large basins and to interpret the results of connectivity-viability analyses accordingly[29].

Evidence from genetic data for greater dispersal within a basin than among basins (e.g., Figure 4.4) means that evaluation of population independence with relative self-recruitment must use a more stringent standard than the source-sink threshold used to differentiate among populations in direct ocean tributaries. To compare the consequences of increased dispersal within a basin to those of dispersal among basins on a consistent basis, we held the standard for independence constant at that used to determine independence among basins that are direct tributaries to the ocean: self-recruitment equal to 95%. We assume that the rate of dispersal within a basin is twice that among basins, and conducted within-basin connectivity-viability analyses with a fidelity rate of 90%. While this analysis still lacks the ability to resolve the actual effects of dispersal on population extinction risk, it does provide an appropriate comparison against an arbitrary "absolute" threshold.

We used a broader set of dispersal functions to explore the potential consequences of longer average dispersal distances within a basin (10-1000 km) than was used for the coastwide analyses[30]. For simplicity, we neglected the influence of immigration from external populations; the coastwide analysis identified each of these populations as as a functionally independent population with a very high rate self-recruitment, so the effects of immigration can safely be ignored[31].

To conduct these analyses for the Eel and Russian rivers, we assumed that the mainstem river could be treated as a coastline and calculated dispersal accordingly. We calculated IP-km for each tributary of the mainstem river and for an uppermost basin defined as the watershed above the point at which relatively high IP (IP $\gtrsim$ 0.7) is more or less continuously distributed. Tributaries that entered the mainstem within 0.2 km of one another were combined into a single unit located at the mouth of the larger tributary. Tributaries were selected for inclusion if they exhibited substantial areas of high IP for steelhead; tributaries with only areas of low IP, were excluded regardless of extent. For the San Francisco Bay, we assumed that dispersal movements were restricted to a narrow band along the shoreline so that populations could be treated as being arranged in a ring around San Francisco Bay, and calculated dispersal rates accordingly.

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[28] The distinction between among- and within-basin gene flow is much more apparent in available genetic data for Chinook salmon and coho salmon.

[29] Note that regardless of the conclusions drawn from the synthesis of available information, the results of this exercise provide a basis for identifying important spatial structure within a basin. Such spatial structure might be considered at the ESU level, in terms of populations within a basin that are separate populations within the ESU, or at the population level, in terms of tributaries that might be core production areas or serve to connect a (spatially) more extensive population within a basin.

[30] "Average dispersal distance" is a characteristic of the exponential curve, and does not necessarily describe the actual distribution of individuals given the limited space available for dispersal. The upper end of dispersal distances examined here yields increasingly flat dispersal curves.

[31] Immigration to the Eel River for the intermediate dispersal function is the equivalent of a population in a stream with 6.96 IP-km dispersing at a rate of 100% (i.e., with 0% fidelity) directly into the basin. The effect is even smaller for the Russian River (2.23 IP-km) and San Francisco Bay (0.65 IP-km).

Eel River. To conduct the connectivity-viability analysis in the Eel River basin, we assumed that the mainstem river does not provide suitable habitat for spawning and rearing below the confluence of Bucknell Creek, which enters the mainstem approximately 280 km from the mouth of the Eel River. The mainstem and its tributaries above this point were treated as a single population.

Figure 4.14 illustrates results from the internal connectivity-viability analysis of the Eel River. Many of the tributaries to the mainstem Eel River exceed our threshold for viability-in-isolation, and thus are of similar in size to coastal basins that we consider capable of harboring potentially or functionally independent populations of steelhead. The five major subbasins of the Eel River (the Van Duzen River [E2], the South Fork Eel River [E3], North Fork Eel River [E5], Middle Fork Eel River [E7], and the Upper Eel River [E8][32]) all fall in the functionally independent quadrant as do three of the largest minor tributaries (Larabee [C], Outlet [N], and Tomki [P] creeks), although somewhat less robustly (Figure 4.14). Most other tributaries fall below the source-sink threshold. The one obvious exception, Price Creek [A], enters the mainstem Eel River close to where it enters the Pacific Ocean, and thus exhibits an “edge effect” in the form of less immigration pressure than experienced by analogous streams that enter the Eel further upstream. Price Creek [A] would be likely to receive most of the immigration coming into the Eel River, which would reduce its level of self-recruitment. With the possible exception of Tomki Creek [P], it appears that none of the minor mainstem tributaries robustly satisfies our threshold for independence within the Eel River basin.

Russian River. To conduct the connectivity-viability analysis in the Russian River basin, we assumed that the mainstem river does not provide suitable habitat for spawning and rearing below the confluence of confluence of Big Sulphur Creek (approximately 119 km upstream from the mouth of the Russian River), but that spawning can take place in the mainstem above this point [33].

Figure 4.16 illustrates results from the connectivity-viability analysis of the Russian River. With the exception of the population in the upper basin (Upper Russian [H]), the Russian River includes few large watersheds comparable to the major forks of the Eel River. As a consequence, almost all of the moderately large tributaries to the Russian River fall into the functionally independent quadrant (Austin Creek [A], Green Valley Creek [C], Mark West Creek [D], Dry Creek [E], and Maacama Creek [F]). These watersheds are not sufficiently large to act as dominant source populations in the lower basin, which increases the apparent independence of putative populations in smaller tributaries (Figure 4.16). We are cautious in drawing conclusions that some of these populations are truly “ephemeral”, but expect that spawning might not occur consistently in some tributaries.

San Francisco Bay. Under historical condition, northern tributaries of San Pablo Bay and southern San Francisco Bay drained through extensive wetlands before finally entering the Bay itself, and a layer of freshwater frequently and consistently covered much of the Bay. Although this structure might be expected to blur the freshwater-saltwater distinction between watersheds, we used the current, con-

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[32] Here defined as the mainstem and tributaries upstream of the confluence with Bucknell Creek.

[33] See map at http://www.krisweb.com/krisrussian/krisdb/webbuilder/bw_m16.htm. Note that this is well upstream of where the current influx of water from Sonoma Lake via Dry Creek substantially alters the nature of the mainstem Russian River.

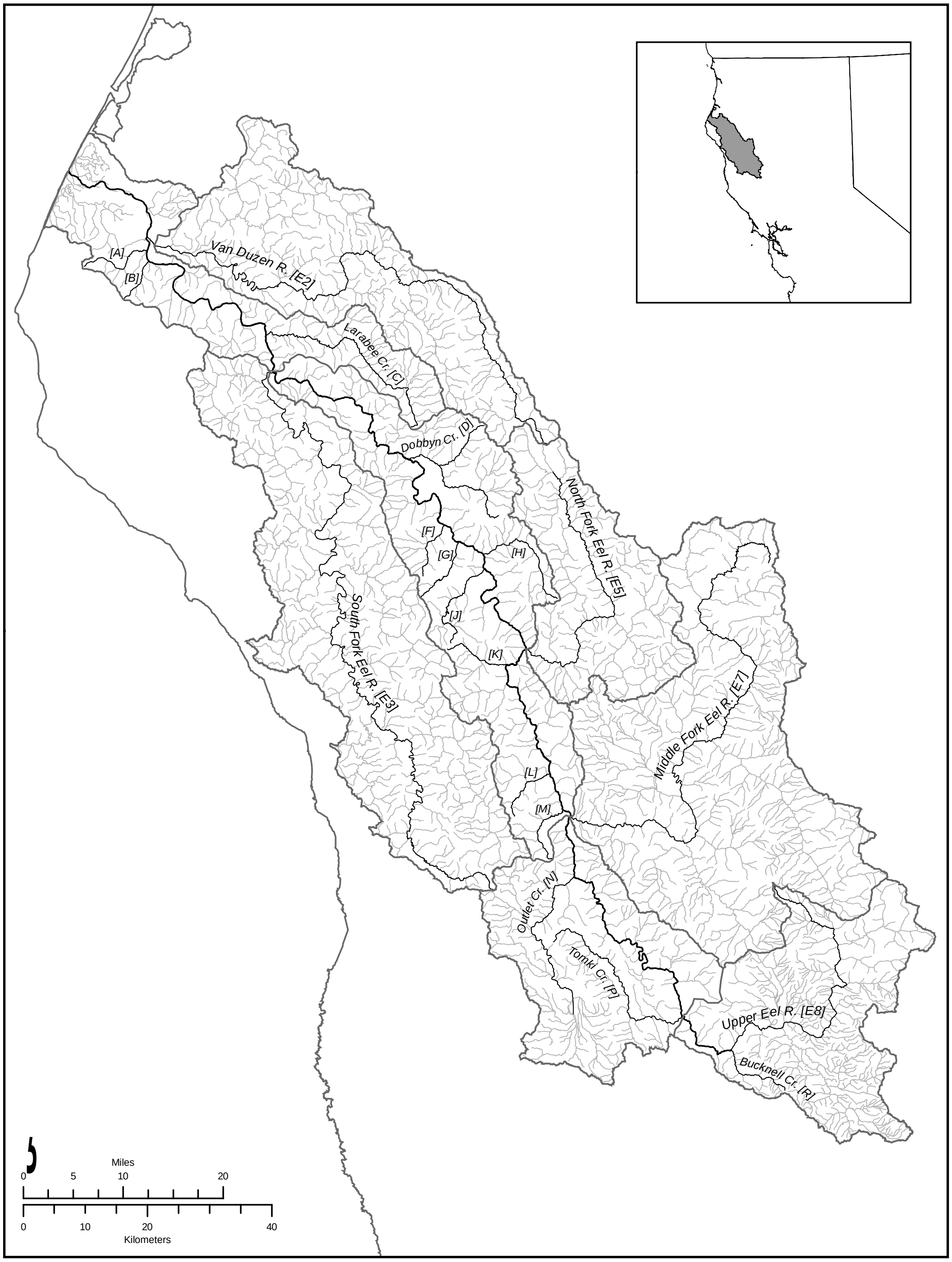

Figure 4.13. Eel River basin, showing major subbasins and larger minor tributaries to the mainstem Eel River specifically identified in the connectivity-viability analysis. Thicker portion of the mainstem Eel River indicates area assumed to lack suitable habitat; the basin above the confluence of Bucknell Creek (exclusive) is treated as a single unit.

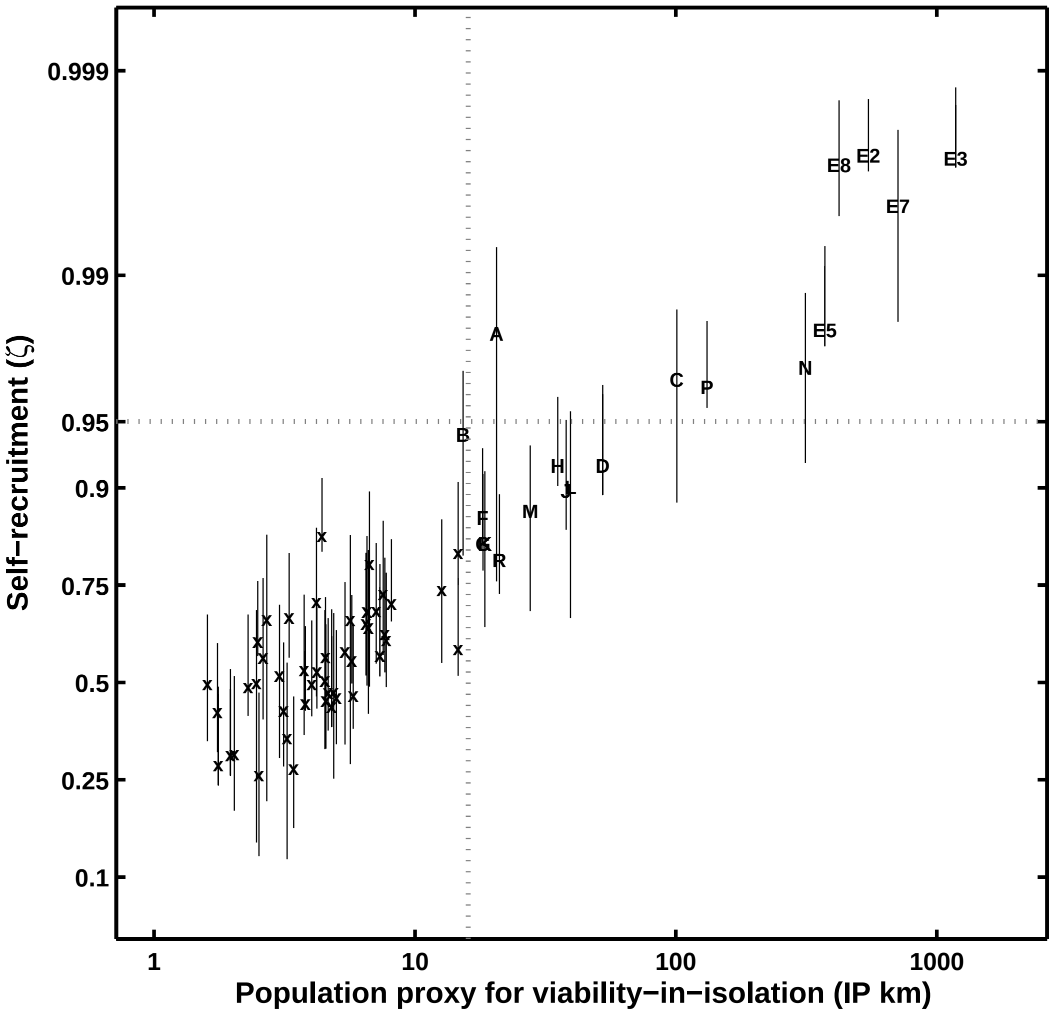

Figure 4.14. Self-recruitment and viability-in-isolation of populations of steelhead in tributaries of the Eel River. Solid vertical lines indicate the range of self-recruitment observed for dispersal functions defined by exponential decay over distance with decay parameters ranging from -0.001 km to -0.10 km. Analysis is run for a fidelity rate of 0.90 to reflect the assumption that dispersal within a basin is greater than dispersal among basins; however, the horizontal grey dotted lines indicates an independence threshold based on a fidelity rate of 0.95, as was used for the coastwide comparisons, and thus is a consistent benchmark for evaluating independence (see text). Vertical grey dotted line at 16 IP-km indicates threshold for viability-in-isolation (see text). Selected tributaries identified as follows: E2: Van Duzen River; E3: South Fork Eel River; E5: North Fork Eel River; E7: Middle Fork Eel River; E8: Upper Eel (above the confluence of Bucknell Creek); A: Price Creek; B: Howe Creek; C: Larabee Creek; D: Dobbyn Creek; F: Jewett Creek; G: Pipe Creek; H: Kekawaka Creek; J: Chamise Creek; K: Bell Springs Creek; L: Woodman Creek; M: Burger Creek; N: Outlet Creek; P: Tomki Creek; R: Bucknell Creek. All other tributaries are indicated by “x”.

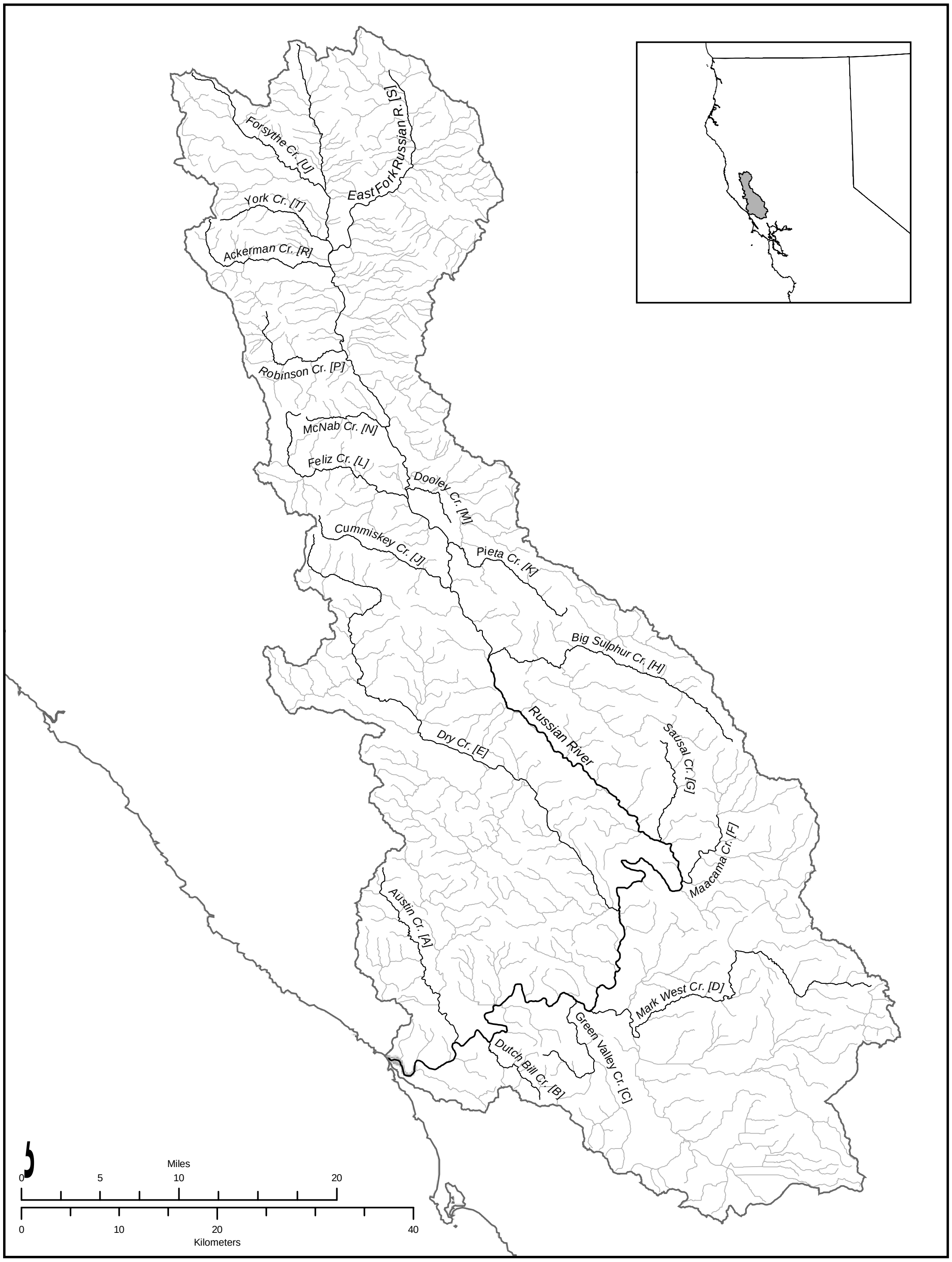

Figure 4.15. Russian River basin, showing major subbasins and larger minor tributaries to the mainstem Russian River specifically identified in the connectivity-viability analysis. Thicker portion of the mainstem Russian River indicates area assumed to lack suitable habitat. The basin upstream of the confluence of Big Sulphur Creek (inclusive) is treated as a single unit: Upper Russian River [H] in the analysis.

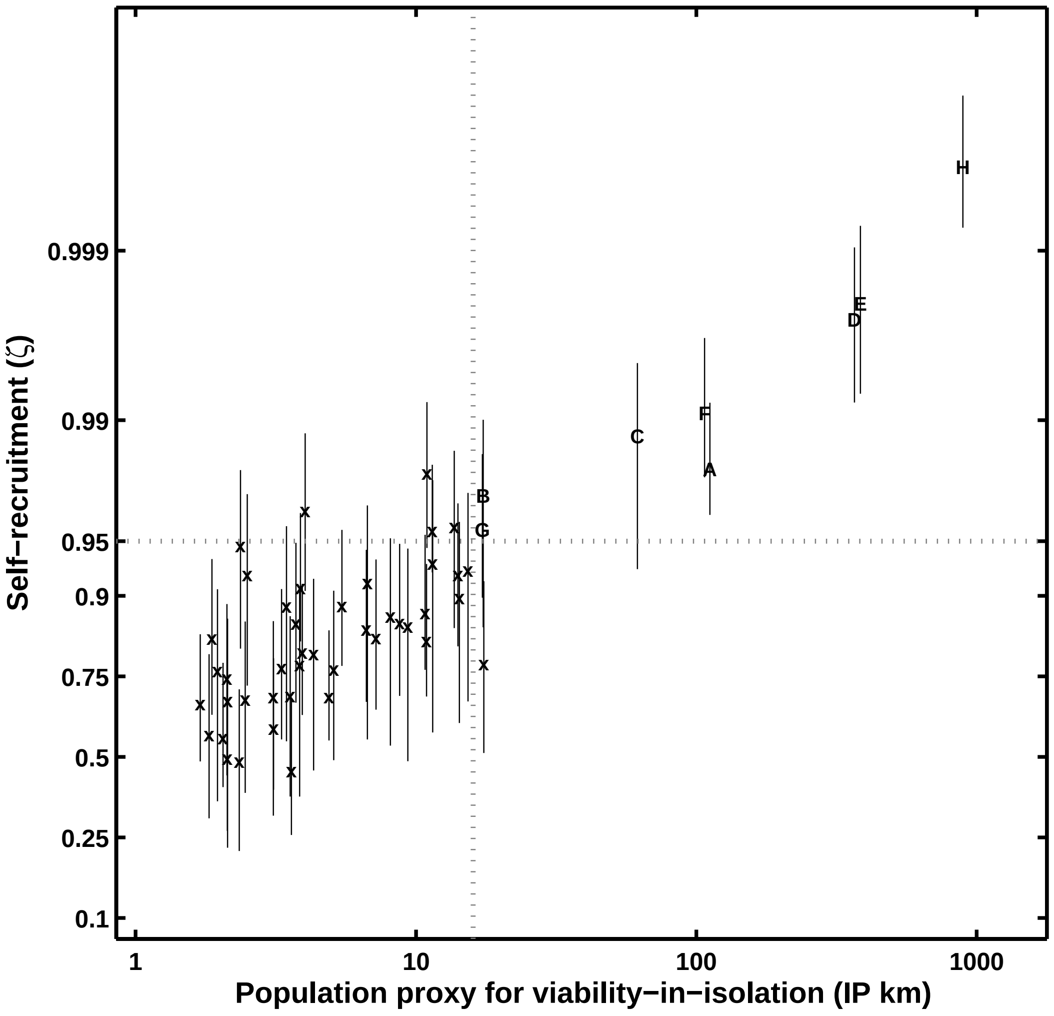

Figure 4.16. Self-recruitment and viability-in-isolation of populations of steelhead in tributaries of the Russian River. Solid vertical lines indicate the range of self-recruitment observed for dispersal functions defined by exponential decay over distance with decay parameters ranging from -0.001 km to -0.10 km. Analysis is run for a fidelity rate of 0.90 to reflect the assumption that dispersal within a basin is greater than dispersal among basins; however, the horizontal grey dotted lines indicates an independence threshold based on a fidelity rate of 0.95, as was used for the coastwide comparisons, and thus is a consistent benchmark for evaluating independence (see text). Vertical grey dotted line at 16 IP-km indicates threshold for viability-in-isolation (see text). Selected tributaries identified as follows: A: Austin Creek; B: Dutch Bill Creek; C: Green Valley Creek; D: Mark West Creek; E: Dry Creek; F: Maacama Creek; G: Sausal Creek; H: mainstem Russian River and tributaries upstream of confluence with Big Sulphur Creek (inclusive). All other tributaries are indicated by “x”.

ventional mouth of each stream where it enters the Bay as its location. GIS models that generate stream networks do not perform well along the margin of San Francisco Bay, which made comprehensive, accurate inclusion of minor tributaries effectively infeasible. To compensate, we inserted small (4 IP-km) tributaries at interpolated intervals among major watersheds; the number of tributaries included between major watersheds is based on counts of such basins from a 1:100K topo map. We inserted tributaries in areas where the presence of such tributaries is most likely to have a substantial influence on the results of this analysis, including the southwestern shore of the Bay and the eastern shore directly across from the Golden Gate; elsewhere, small "tributaries" would likely have been little more that wetland sloughs, and as such, would not have provided suitable spawning habitat for steelhead. Given the unusual structure of the San Francisco Bay and the difficulty of characterizing the structure of watersheds near the shore of the Bay, results from this analysis must be considered cautiously and in the context of the likely physical structure of the Bay under historical conditions.

Figure 4.17 summarizes the results from the connectivity-viability analysis for populations of steelhead in tributaries of San Francisco Bay, absent immigration from the Central Valley Steelhead ESU. Save for Arroyo Corte Madera del Presidio [S1] all basins exceed both our threshold for viability-in-isolation for coastal basins. This analysis predicts that populations of steelhead in Alameda Creek [S11], Napa River [S7], Sonoma Creek [S6], Guadalupe River [S13], and San Lorenzo Creek [S10] were functionally independent. Steelhead in all other basins are predicted to exist as potentially independent populations. Note that the status of the population in Sonoma Creek [S6] is sensitive to the width of the dispersal function used in the analysis. Immigration from Napa River [S7] and Sonoma Creek [S6] limit the Petaluma River population to potential independence. Likewise, Coyote Creek [S12] receives substantial immigration from both Alameda Creek [S11] and Guadalupe River [S13]. Including immigration from the Central Valley Steelhead ESU[34] greatly reduces the set of conditions under which steelhead in Napa River [S7] and Sonoma Creek [S6] appear as functionally independent populations (results not shown). The status of populations elsewhere, particularly in the southern San Francisco Bay is largely insensitive to the inclusion of immigration from Central Valley populations in the analysis.

4.6 Abundance and Population Dynamics

Population data for the NC-Steelhead ESU and CCC-Steelhead ESU have been summarized as part of the comprehensive Status Review and Status Review Updates (Busby et al., 1996; Boughton and Bjorkstedt, 2005b,a). None of these data support rigorous examination of correlation in population dynamics. Comparison of population trajectories of winter steelhead and summer steelhead in the Klamath Mountains Province Steelhead ESU provides qualitative evidence that the dynamics of the two life history types are not demographically coupled even in basins where both runs occur.

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[34] To mimic immigration from basins in the Central Valley, we included a relatively large population (1000 IP-km) where the Carquinez Strait opens into San Pablo Bay; including larger proxy populations did not substantially alter our conclusions regarding the sensitivity of populations' status to inclusion of immigration from the Central Valley.

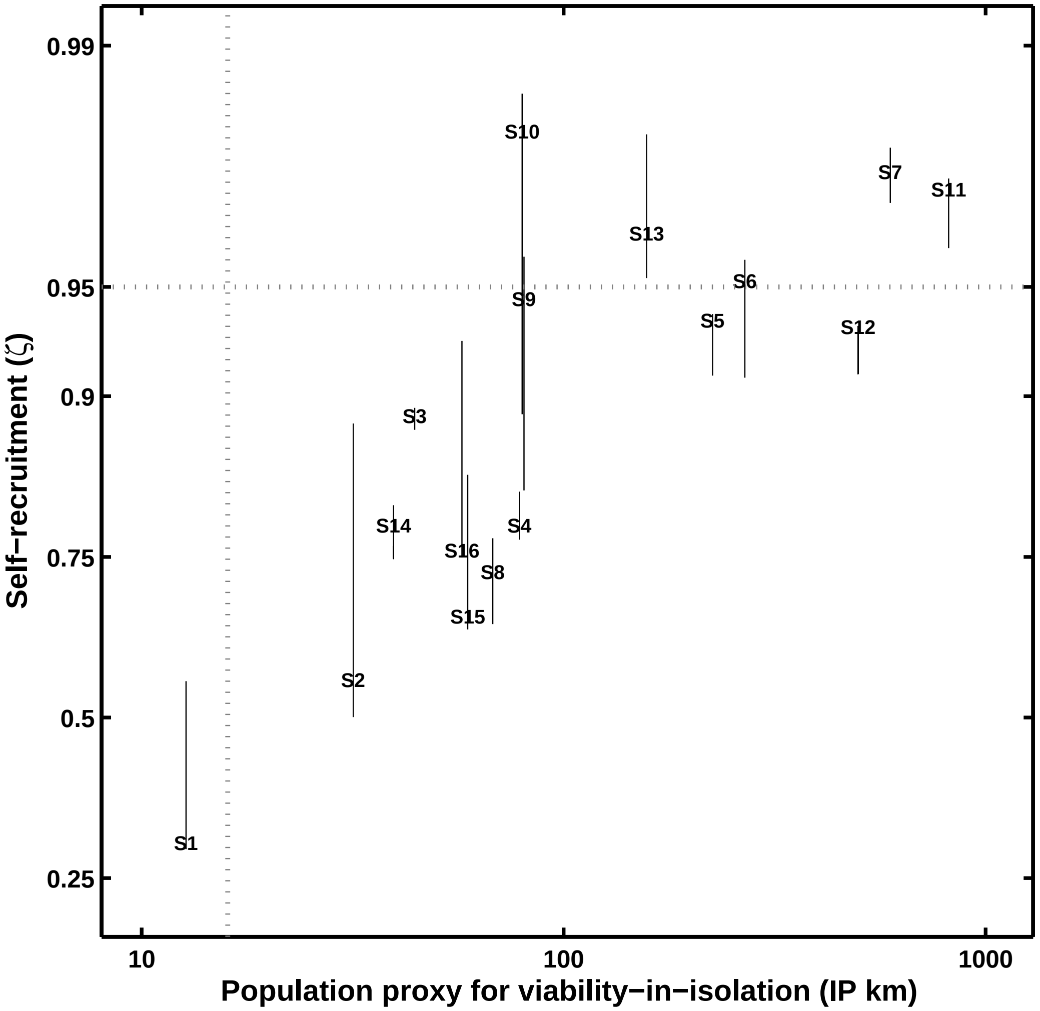

Figure 4.17. Self-recruitment and viability-in-isolation of populations of steelhead in selected major tributaries of San Francisco Bay. Solid vertical lines indicate the range of self-recruitment observed for dispersal functions defined by exponential decay over distance with decay parameters ranging from -0.001 km to -0.10 km. Analysis is run for a fidelity rate of 0.90 to reflect the assumption that dispersal within a basin is greater than dispersal among basins; however, the horizontal grey dotted lines indicates an independence threshold based on a fidelity rate of 0.95, as was used for the coastwide comparisons, and thus is a consistent benchmark for evaluating independence (see text). Vertical grey dotted line at 16 IP-km indicates threshold for viability-in-isolation (see text). Selected tributaries identified as follows: S1: Arroyo Corte Madera Del Presidio; S2: Miller Creek; S3: Corte Madera Creek; S4: Novato Creek; S5: Petaluma River; S6: Sonoma Creek; S7: Napa River; S8: San Pablo Creek; S9: San Leandro Creek; S10: San Lorenzo Creek; S11: Alameda Creek; S12: Coyote Creek; S13: Guadalupe River; S14: Stevens Creek; S15: San Francisquito Creek; S16: San Mateo Creek.

4.7 Life history variation

The most striking aspect of life history variation among steelhead in the NCCCRD is the distinction between summer and winter steelhead in the larger watersheds in the northern part of the range of the NC-Steelhead ESU[35]. This distinction is heritable, and, as noted above, winter and summer steelhead in the same watershed appear to exhibit independent dynamics, which supports treating different runs of steelhead in the same basin as separate populations.

For winter steelhead, we found only one example of life history variation that warrants consideration with respect to historical population structure. Historical daily dam counts at Sweasy Dam (Mad River) consistently peak approximately a month earlier than those made at Benbow Dam (South Fork Eel River). Whether this reflects real biological differences, a simple consequence of differences in the onset of higher stream flows in response to winter storms, or differences in the distance between freshwater entry and the counting station is not clear. Therefore, we do not consider this information to be highly informative.

For summer steelhead, we likewise found only one example of life history variation that warrants consideration with respect to historical population structure. Puckett (1975) (cited in Busby et al., 1996) reports differences in the life history schedule of summer-run steelhead from the Van Duzen and Middle Fork Eel rivers. In the Van Duzen, all sampled individuals had spent one year in freshwater, and most returned to spawn for the first time after two (62%) or three (29%) years at sea. In contrast, most (71%) individuals from the Middle Fork Eel River spent two years in freshwater with 17% spending three, yet most returned to spawn for the first time after only one (56%) or two (42%) years at sea. It is unclear whether this variation indicates underlying genetic differences or is a phenotypic response to different ecological conditions in the two watersheds.

4.8 Historical population structure of steelhead ESUs in the NCCCRD

We present our conclusions regarding historical population structure separately for winter steelhead in the NC-Steelhead ESU, summer steelhead in the NC-Steelhead ESU, and winter steelhead in the CCC-Steelhead ESU (summer steelhead do not occur in the CCC-Steelhead ESU). Winter and summer steelhead in the NC-Steelhead ESU are considered as separate on the basis of substantial, heritable differences in life history, apparent divergence in recent demographic trajectories, and clear differences in habitat requirements. These differences provide more than sufficient evidence that winter and summer steelhead exist as distinct populations, even in basins where both are present. We do not consider the population structure of non-anadromous *O. mykiss* in this report[36].

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[35] Recall that in this report we focus solely on the population structure of steelhead, and assume that rates of exchange between non-anadromous ("resident") and anadromous *O. mykiss* in coastal basins are sufficiently low for the two forms to be considered as separate populations. See §4.2.1 for further discussion regarding the role of resident *O. mykiss* in the NC-Steelhead and CCC-Steelhead ESUs.

[36] See §4.2.1 for further discussion of our assumptions regarding resident *O. mykiss* in the NC-Steelhead and CCC-Steelhead ESUs.

For the most part, the conclusions outlined below are drawn from the results of the connectivity-viability analysis. Genetic data suggests that the population genetic structure of steelhead in coastal California is strongly coupled to geography (Figures 4.2, 4.3, and 4.5), and thus support the use of simple approaches for translating geographical structure into biological structure, such as the connectivity-viability model, to evaluate historical population structure within these ESUs. That predictions of population connectivity from the connectivity-viability model agree qualitatively with inferences drawn from the genetic data is not entirely surprising; the underlying structure of the connectivity-viability model is very similar to that of genetic stepping-stone models that yield patterns of isolation-by-distance (Figure 4.5).

4.8.1 Historical population structure of winter steelhead in the NC-Steelhead ESU

Table 4.4 summarizes our conclusions regarding historical population structure for winter steelhead in the NC-Steelhead ESU for the set of direct tributaries to the Pacific considered in our analysis. We summarize the evidence in support of our conclusions below in a generally north-to-south direction, with an initial focus on the Eel River, as it exerts a dominant influence on much of the northern part of the NC-Steelhead ESU.

Eel River

The structure of the Eel River basin is such that it is almost certain that multiple populations of winter steelhead occupied the basin. Environmental conditions vary substantially across the Eel River basin, and in many cases differ between geographically adjacent tributaries that drain opposite sides of the the mainstem Eel River. The distribution of spawning and rearing habitats is likely to be discontinuous, with the clearest, most extensive breaks occurring along the mainstem. In combination, these conditions would favor population differentiation. Therefore, if our assumption that the historical distribution of winter steelhead spawning grounds reflects the distribution of areas with high IP for juvenile rearing habitat holds, then winter steelhead are likely to have exhibited a fragmented distribution, and existed in multiple populations, within the Eel River. Unfortunately, we have little information with which to evaluate explicitly dispersal and connectivity between steelhead spawning in subbasins or between steelhead in subbasins and nearby minor tributaries. Genetic data for steelhead in the Eel River indicates differentiation among the major basins from which samples are available, but these data do not provide clear evidence of robust concordance between basin structure and population genetic structure (e.g., Middle Fork and South Fork Eel River; Figures 4.2, 4.3, and 4.8).

We conclude that functionally independent populations of winter steelhead historically occupied each of the major subbasins of the Eel River: the Van Duzen River [E2], South Fork Eel River [E3], North Fork Eel River [E5], Middle Fork Eel River [E7], and the mainstem Eel River and its tributaries above the confluence of Bucknell Creek (Table 4.5). Each of these watersheds greatly exceeds our threshold for viability-in-isolation. Moreover, likely spawning/rearing areas in each subbasin are sufficiently separated from the mainstem Eel River to suggest (1) that populations were exposed to the environmental conditions unique to each watershed, and (2) that spawning groups in separate basins

Table 4.4. Historical population structure of winter steelhead in the NCCC-Steelhead ESU.

Population	**IP km**	**IP Bias Index**	**Self-recruitment**	**Historical Population Status**
Butler Creek [a]	1.98	low	0.755	dependent
Boat Creek [a]	1.62	low	0.547	dependent
Fern Canyon [a]	5.99	low	0.936	dependent
Squashan Creek [a]	4.00	low	0.730	dependent
Gold Bluff [a]	4.35	low	0.585	dependent
Redwood Creek (H) [1]	301.07	low	0.993	**Functionally Independent**
McDonald Creek [a]	6.38	low	0.545	dependent
Maple Creek/Big Lagoon [2]	94.67	low	0.922	***Potentially Independent***
Little River (H) [3]	76.16	low	0.882	***Potentially Independent***
Strawberry Creek [a]	6.08	low	0.539	dependent
Widow White Creek [4]	9.07	low	0.683	dependent
Mad River [5]	221.73	low	0.947	**Functionally Independent**
Humboldt Bay [6]	283.02	low	0.873	***Potentially Independent***
Eel River - Full [7]	4029.44		0.997	**See Table 4.5**
Fleener Creek [a]	4.14	low	0.221	dependent
Guthrie Creek [8]	10.10	low	0.592	dependent
Oil Creek [9]	11.17	low	0.520	dependent
Bear River [10]	116.03	low	0.920	***Potentially Independent***
Singley Creek [11]	11.83	low	0.539	dependent
Davis Creek [12]	8.14	low	0.574	dependent
Domingo Creek [a]	3.41	low	0.561	dependent
McNutt Gulch [13]	14.14	low	0.756	dependent
Peter Gulch [a]	2.26	low	0.315	dependent
Mattole River [14]	613.88	low	0.995	**Functionally Independent**
Fourmile Creek [15]	8.77	low	0.557	dependent
Cooskie Creek [16]	7.98	low	0.666	dependent
Randall Creek [b]	1.95	low	0.424	dependent
Spanish Creek [b]	1.89	low	0.574	dependent
Oat Creek [b]	1.84	low	0.465	dependent
Big Creek [b]	3.84	low	0.614	dependent
Big Flat Creek [b]	6.14	low	0.768	dependent
Shipman Creek [b]	2.28	low	0.554	dependent
Gitchell Creek [b]	2.52	low	0.632	dependent
Horse Mountain Creek [b]	3.23	low	0.775	dependent
Telegraph Creek [b]	5.57	low	0.943	dependent
Humboldt Creek [b]	1.64	low	0.446	dependent
Whale Gulch [b]	5.07	low	0.675	dependent
Jackass Creek [b]	3.57	low	0.798	dependent
Little Jackass Creek [b]	6.25	low	0.774	dependent
Usal Creek [17]	18.79	low	0.904	***Potentially Independent***
Cottaneva Creek [18]	26.09	low	0.911	***Potentially Independent***
Hardy Creek [19]	10.01	low	0.903	dependent
Juan Creek [20]	11.26	low	0.934	dependent
Howard Creek [c]	6.64	moderate	0.831	dependent

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Population	IP km	IP Bias Index	Self-recruitment	Historical Population Status
DeHaven Creek [21]	13.01	moderate	0.935	dependent
Wages Creek [22]	19.93	low	0.947	***Potentially Independent***
Chadbourne Gulch [c]	3.74	moderate	0.560	dependent
Abalobadiah Creek [c]	6.92	moderate	0.712	dependent
Seaside Creek [c]	2.79	moderate	0.843	dependent
Ten Mile River [23]	204.70	moderate	0.996	**Functionally Independent**
Inglenook Creek [c]	3.19	moderate	0.518	dependent
Mill Creek [c]	5.58	moderate	0.628	dependent
Virgin Creek [c]	4.42	moderate	0.695	dependent
Pudding Creek [24]	32.04	moderate	0.939	***Potentially Independent***
Noyo River [25]	199.06	moderate	0.990	**Functionally Independent**
Hare Creek [26]	18.06	moderate	0.938	***Potentially Independent***
Digger Creek [c]	2.00	moderate	0.565	dependent
Mitchell Creek [c]	5.54	moderate	0.737	dependent
Jug Handle Creek [c]	5.35	moderate	0.739	dependent
Caspar Creek [27]	16.00	moderate	0.927	***Potentially Independent***
Russian Gulch (Me) [28]	19.18	moderate	0.855	***Potentially Independent***
Jack Peters Creek [29]	7.98	moderate	0.796	dependent
Big River [30]	316.62	high	0.993	**Functionally Independent**
Little River (M) [31]	9.87	moderate	0.748	dependent
Buckhorn Creek [c]	1.72	moderate	0.391	dependent
Dark Gulch [c]	1.99	moderate	0.414	dependent
Albion River [32]	77.06	high	0.975	**Functionally Independent**
Big Salmon Creek [33]	24.83	high	0.908	***Potentially Independent***
Navarro River [34]	458.16	high	0.991	**Functionally Independent**
Greenwood Creek [35]	8.64	high	0.871	dependent
Elk Creek [36]	24.09	high	0.869	***Potentially Independent***
Mallo Pass Creek [c]	7.07	moderate	0.565	dependent
Alder Creek [37]	47.12	high	0.942	***Potentially Independent***
Brush Creek [38]	28.25	high	0.901	***Potentially Independent***
Garcia River [39]	169.01	high	0.983	**Functionally Independent**
Point Arena Creek [d]	4.43	moderate	0.523	dependent
Moat Creek [d]	5.11	moderate	0.669	dependent
Ross Creek [d]	4.04	moderate	0.790	dependent
Galloway Creek [d]	2.37	moderate	0.742	dependent
Schooner Gulch [40]	9.52	moderate	0.832	dependent
Slick Rock Creek [d]	2.77	moderate	0.503	dependent
Signal Port Creek [d]	3.18	moderate	0.490	dependent
Saint Orres Creek [d]	1.80	moderate	0.251	dependent
Gualala River [41]	478.03	high	0.987	**Functionally Independent**
Miller Creek [d]	3.16	moderate	0.137	dependent
Stockhoff Creek [d]	3.18	moderate	0.283	dependent
Timber Cove Creek [d]	1.66	moderate	0.266	dependent

were less likely to be linked by dispersal. We assume that dispersal within each of these subbasins was sufficient to integrate spawning groups of steelhead throughout the basin into a single population, but recognize, but recognize that our analysis of population structure of steelhead spawning in mainstem tributaries might be applicable to tributaries to the lower mainstem of the larger forks of the Eel River.

We conclude that, in addition to the functionally independent populations identified above, as many as thirteen potentially independent populations of winter steelhead historically spawned in the larger minor tributaries to the mainstem Eel River, e.g., Larabee Creek [C] and Outlet Creek [N] (Table 4.5). A number of the populations identified as potentially independent occupy tributaries that are near our threshold for viability-in-isolation, and for which predictions of the IP model are likely to include some non-negligible positive bias. We do not downgrade these populations to "dependent" because, unlike streams that drain directly to the ocean, populations in these tributaries have access to a freshwater mainstem that can potentially serve as a more-or-less habitable buffer. Likewise, although it is possible that immigration from larger populations might reduce the productivity (fitness) of these smaller populations, particularly if the source and sink populations occupy environmentally different basins (Kawecki and Holt, 2002; Lenormand, 2002), we expect that this will have little effect on the "viability-*in-situ*" (i.e., the apparent viability of the population in the context of the full set of populations around it) of potentially independent populations in the larger tributaries. Populations for which it appears that immigration has the greatest potential to constrain local adaptation and perhaps reduce population independence include Woodman [L] and Burger [M] creeks (opposite Middle Fork Eel River [E7]), and Chamise [J] and Bell Springs [K] creeks (opposite North Fork Eel River [E5]). Both pairs of creeks are near large source populations, but drain basins that are environmentally different from these sources.

Coastal basins: north of Punta Gorda

We conclude that winter steelhead north of Punta Gorda historically existed as functionally independent populations in Redwood Creek (Humboldt) [1], Mad River [5], Humboldt Bay [6] and Mattole River [14], and that potentially independent populations occurred in Maple Creek (Big Lagoon) [2], Little River [3] and Bear River [10]. Any populations of winter steelhead in other, smaller direct tributaries to the Pacific were likely to have been dependent on immigration from larger populations for continued persistence or recolonization.

For two populations, Mad River [5] and Humboldt Bay [6], these conclusions represent a departure from the results of the connectivity-viability model. We believe that dispersal rates among populations of steelhead are sufficiently low to justify this departure. Genetic samples from the Eel, Mad, Mattole and Bear rivers form an intermingled cluster in our genetic analyses (Figures 4.2 and 4.3). This structure is consistent with the position of the Eel River as a dominant source population in the connectivity-viability analysis (Figure 4.10); however, application of the dispersal model across the long spits that separate Humboldt Bay from the Pacific Ocean yields an unusually high prediction for the influence of immigration from the Eel River on the Mad River population. Stock transfers between the Eel River, Mad River, and Mattole River probably contribute to this genetic structure (Table 4.1)[37]. Moreover, the

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[37] In contrast, we know of no documented transfers of steelhead to the Bear River, so genetic similarities between samples

Table 4.5. Historical population structure of winter steelhead in the Eel River basin.

Watershed	**IP km***	**IP Bias Index**	**Self-recruitment**	**Historical Population Status**
Lower Mainstem Eel River**		moderate		dependent populations
Price Creek [A]	20.56	low	0.981	***Potentially Independent***
Howe Creek [B]	15.29	low	0.943	dependent
Larabee Creek [C]	100.95	low	0.968	***Potentially Independent***
Van Duzen River [E2]	547.07	low	0.997	**Functionally Independent**
South Fork Eel River [E3]	1182.14	low	0.997	**Functionally Independent**
Lower Middle Mainstem Eel River**		low		dependent populations
Dobbyn Creek [D]	52.47	low	0.920	***Potentially Independent***
Jewett Creek [F]	18.17	low	0.866	***Potentially Independent***
Pipe Creek [G]	18.22	low	0.828	***Potentially Independent***
Kekwaka Creek [H]	35.27	low	0.921	***Potentially Independent***
Chamise Creek [J]	37.95	low	0.897	***Potentially Independent***
North Fork Eel River [E5]	372.83	low	0.982	**Functionally Independent**
Upper Middle Mainstem Eel River**		moderate		dependent populations
Bell Springs Creek [K]	18.54	moderate	0.828	***Potentially Independent***
Woodman Creek [L]	39.42	moderate	0.901	***Potentially Independent***
Burger Creek [M]	27.64	moderate	0.874	***Potentially Independent***
Outlet Creek [N]	313.80	moderate	0.972	***Potentially Independent***
Tomki Creek [P]	131.73	moderate	0.966	***Potentially Independent***
Middle Fork Eel River [E7]	584.26	low	0.995	**Functionally Independent**
Bucknell Creek [R]	21.07	moderate	0.800	***Potentially Independent***
Upper Mainstem Eel River***	422.13	moderate	0.997	**Functionally Independent**

* The threshold for viability-in-isolation 16 IP km. See text for how this value was selected. ** Indicate the set of small watersheds tributary to each section of the mainstem Eel River that are not listed by name in this table. *** The Upper Mainstem Eel River population occupies the mainstem and tributaries above the confluence of Bucknell Creek (exclusive), and thus differs slightly from the basin designated "Upper Eel Mainstem River" in the multivariate environmental analysis.

single genetic sample from a Humboldt Bay tributary (Freshwater Creek) is more similar to samples from Redwood Creek (Humboldt), which suggests that dispersal from the Eel and Mad rivers (which have been somewhat mixed by transfers) to Humboldt Bay is limited[38]. We therefore think that natural dispersal among populations in the Eel, Mad and Mattole river is substantially lower than what might be inferred from current genetic data, and furthermore, we expect that historical rates of dispersal among the large basins north of Punta Gorda were relatively low. If this conclusion (assumption) holds, then designating steelhead in Mad River [5] and Humboldt Bay [6] as functionally independent populations is warranted.

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from the Bear, Mattole, and Eel rivers might be evidence of natural dispersal to Bear River from the larger populations.

[38] Alternatively, undocumented transfers between Humboldt Bay and Redwood Creek underpin the observed structure, but we can not evaluate this hypothesis.

Coastal basins: Lost Coast to Point Arena

We believe that, under historical conditions, winter steelhead existed as a suite of functionally independent populations in the larger watersheds that drain this coast, i.e., Ten Mile River [23], Noyo River [25], Big River [30], Albion River [32], Navarro River [34], and Garcia River [39] (Table 4.4). Potentially independent populations historically existed in many of the somewhat smaller basins (e.g., Usal Creek [17], Pudding Creek [24], Alder Creek [37], etc.; Table 4.4). We find support for these conclusions from both genetic analyses (Figures 4.2 and 4.3) and geographical synthesis of relative population size and location (Figure 4.9). The combination of (1) a relatively consistent spacing and size distribution of watersheds along this coast, and (2) isolation of this stretch of coast from large populations to the north and south, leads to a fairly straightforward relation between watershed size and self-recruitment. Note that a number of the larger watersheds in this area exhibit fragmented distributions of areas with high IP for steelhead habitat, analogous to that observed in larger basins such as the Eel River. We assume, however, on the basis of the ecological bias in the IP model, that intervening stream reaches provide sufficient habitat to maintain connectivity within a basin (Plate 14). Regardless, in the absence of evidence for strong environmental differences among these smaller watersheds, we do not believe that this structure is sufficient to warrant consideration of separate populations within these basins. We again emphasize the important contributions of such spatial structure to population viability.

Coastal basins: Point Arena to Gualala River (inclusive)

We conclude that steelhead in the Gualala River comprise a functionally independent population (Table 4.4). It is the only sizeable basin along this stretch of coast, and is isolated from large populations to the north and south by extensive stretches of coastline in which all watersheds are too small to support persistent populations of steelhead. Analysis of genetic data suggests that the extensive coastline that lies between the mouths of the Gualala and Russian rivers effectively reduces gene flow across the ESU boundary (Figures 4.2, 4.3), and 4.7). Predictions from the connectivity-viability model are consistent with the genetic data (Figures 4.9 and 4.10).

4.8.2 Historical population structure of summer steelhead in the NC-Steelhead ESU

We conclude that summer steelhead existed as a distinct, functionally independent population in each basin or, in the case of the Eel River, each major tributary[39] where they were historically present (Table 4.6). Empirical data to evaluate this hypothesis directly are largely unavailable. Rather, we base this conclusion on two general lines of thinking. First, available genetic data indicate that summer-run steelhead are more closely related to winter-run steelhead in the same basin than they are to summer-run steelhead in other basins, which implies that gene flow among summer steelhead populations is lower than gene flow among winter and summer steelhead within a basin. Despite this gene flow,

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[39] Jones (1992) summarizes evidence, most of which is anecdotal, regarding the historical occurrence of summer steelhead in many parts of the Eel River basin. Much of this information is based on accounts from the 1930s and suggests that even then, summer steelhead were rare and potentially subject to considerable harvest pressure in most basins.

Table 4.6. Historical population structure of summer steelhead in the NCCC-Steelhead ESU.

Population	**Historical Population Status***
Redwood Creek (H) [1]	**Functionally Independent**
Mad River [5]	**Functionally Independent**
Van Duzen River [E2]	**Functionally Independent**
South Fork Eel River [E3]	**Functionally Independent**
Larabee Creek	**Functionally Independent**
North Fork Eel River [E5]	**Functionally Independent**
(Upper Middle Mainstem Eel River [E6])**	**(Functionally Independent)**
Middle Fork Eel River [E7]	**Functionally Independent**
(Upper Mainstem Eel River [E8])***	**(Functionally Independent)**
Mattole River [14]	**Functionally Independent**

* All summer steelhead populations are considered functionally independent; see text for discussion. ** Summer steelhead have not been documented in this area; however, some of the watersheds that drain the north bank of the Eel River are environmentally similar to Larabee Creek and the major subbasins on the north side of the Eel River basin and might have harbored historical populations of summer steelhead. Such populations, if shown to exist, would be considered functionally independent, pending further analysis. ***The extent of habitat suitable for summer steelhead populations in the upper Eel River and its tributaries is unknown, and is likely to be restricted to the northwest corner of the basin (near the Middle Fork Eel River) where annual snowpack occurs.

evidence of which is based on neutral molecular markers, populations of summer and winter steelhead remain distinct and there is little evidence that exchanges have significant demographic consequences. Thus, it is very unlikely that dispersal among summer steelhead populations in separate basins will have demographic consequences. Indeed, if this hypothetical relationship between winter and summer steelhead is true, then summer steelhead populations are more likely to be dependent on sympatric winter run populations than on populations of summer steelhead in other basins.

4.8.3 Historical population structure of winter steelhead in the CCC-Steelhead ESU

Table 4.7 summarizes conclusions regarding population structure for the Central California Coast Steelhead ESU. Any smaller watersheds that are capable of supporting steelhead production that are not explicitly named are considered as dependent populations, and will be included as part of ESU viability criteria. As for the NC-Steelhead ESU, synthesis of results from analyses of genetic data and the connectivity-viability model are the primary basis for our conclusions. This holds true despite potential biases arising from our implementation of the IP model along this part of the coast (see §4.5, above).

Russian River

We conclude that winter steelhead in the Russian River historically existed as a single functionally independent population in roughly the upper half of the basin (above the confluence of Big Sulphur Creek, inclusive), and as potentially independent populations in a number of the larger tributaries to the lower mainstem (Table 4.8). Historical populations of steelhead in Dutch Bill and Sausal creeks occupied tributaries that barely satisfy our threshold for viability-in-isolation, and like other tributaries within the Russian River basin, the predictions from the IP model for these tributaries are likely to substantially exceed actual habitat. Therefore, we consider steelhead in Dutch Bill Creek and Sausal Creek to be dependent populations.

In reaching these conclusions, we considered a three issues. First, winter steelhead currently spawn or are thought to have historically spawned in most tributaries to and much of the upper mainstem of the Russian River, which is consistent with qualitative estimates of historical abundance (CDFG, 1965). Reports of relatively greater use of mainstem habitats by steelhead for spawning and rearing in the Russian River than we expect to be the case in the Eel River is consistent with the lower precipitation and smaller basin size of the Russian River. Second, although perhaps more subtle than what is observed in the other two large basins, the Russian River basin exhibits a substantial degree of environmental variability. Watersheds near the mouth are exposed to coastal climatic influences; watersheds in the central basin and upper basin experience warmer, drier conditions, yet still drain mountains of reasonably high elevation; watersheds in the southwest part of the basin experience much warmer, drier conditions overall (Plates 5, 4, and 6). Third, although population genetic structure of steelhead in the Russian River does not show concordance with geography, differentiation among populations is observed in the data (Deiner, 2004). We expect that differentiation among steelhead within the Russian River has been substantially influenced by the widespread transfer of hatchery steelhead *within* the basin (NRC, 1996). In summary, the combination of physical structure of the watershed, including both the distribution of spawning habitat and environmental variability support the existence of multiple populations of steelhead within the Russian River basin, and the genetic data, while not providing conclusive support for such an hypothesis, also do not argue against such a conclusion when considered in the context of historical and recent stocking practices.

Coastal basins: Russian River to the Golden Gate

We conclude that potentially independent populations of winter steelhead historically occupied Salmon Creek (Sonoma) [43], Americano Creek [45], Stemple Creek [46], and each of the two major tributaries to Tomales Bay [47]: Walker Creek [TB1] and Lagunitas Creek [TB2]. If considered as a single population, steelhead in Tomales Bay [47] might have existed as a functionally independent population, but environmental differences among the watersheds and their exposure to saltwater warrants considering them as separate populations. We further conclude that historical populations of steelhead in smaller basins existed as dependent populations[40]. Steelhead spawning along this entire stretch of coastline were influenced by immigration from both the Russian River and San Francisco Bay.

San Francisco Bay tributaries

Historical records show that winter steelhead occurred in almost every watershed tributary to San Francisco and San Pablo bays (Leidy et al., 2003). Under historical conditions, these fish formed at least

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[40] The IP model predicts that the Drakes Bay basin has sufficient IP-km to harbor a potentially independent population, but it is likely that much of this habitat is tidally influenced and thus unsuitable for spawning and rearing of early life history stages.

Table 4.7. Historical population structure of winter steelhead in the CCC-Steelhead ESU.

Population	**IP km**	**IP Bias Index**	**Self-recruitment**	**Historical Population Status**
Kolmer Creek [d]	3.86	moderate	0.517	dependent
Fort Ross Creek [d]	2.07	moderate	0.160	dependent
Russian Gulch (S) [d]	7.05	moderate	0.251	dependent
Russian River [42]	2348.83		0.999	**See Table 4.8**
Scotty Creek [d]	5.82	high	0.243	dependent
Salmon Creek (S) [43]	63.45	high	0.820	***Potentially Independent***
Bodega Harbor [44]	14.05	high	0.535	dependent
Americano Creek [45]	64.22	high	0.887	***Potentially Independent***
Stemple Creek [46]	73.11	high	0.921	***Potentially Independent***
Tomales Bay [47]	294.71	high	0.943	***Potentially Independent***
Walker Creek [TB1]	134.08	high		***Potentially Independent***
Lagunitas Creek [TB2]	160.63	high		***Potentially Independent***
Drakes Bay [48]	10.12	high	0.305	dependent
Pine Gulch [49]	12.90	high	0.302	dependent
Redwood Creek (M) [50]	10.37	high	0.212	dependent
San Francisco Bay [51]	3054.61		0.999	**See Table 4.9**
Pilarcitos Creek [52]	41.88	high	0.494	***Potentially Independent***
Canada Verde Creek [e]	4.27	high	0.232	dependent
Tunitas Creek [53]	16.40	high	0.668	dependent
San Gregorio Creek [54]	77.59	high	0.953	**Functionally Independent**
Pomponio Creek [55]	11.51	high	0.743	dependent
Pescadero Creek [56]	93.52	high	0.961	**Functionally Independent**
Arroyo de los Frijoles [e]	6.60	high	0.553	dependent
Gazos Creek [57]	16.10	high	0.846	dependent
Whitehouse Creek [e]	7.46	high	0.876	dependent
Cascade Creek [e]	5.88	high	0.900	dependent
Green Oaks Creek [e]	3.27	high	0.724	dependent
Ano Nuevo Creek [e]	4.22	high	0.699	dependent
Waddell Creek [58]**	16.24	high	0.862	***Potentially Independent***
Scott Creek [59]	23.51	high	0.938	***Potentially Independent***
Molino Creek [e]	2.90	high	0.602	dependent
San Vicente Creek [60]	7.99	high	0.843	dependent
Liddell Creek [e]	6.58	high	0.873	dependent
Laguna Creek [61]**	17.41	high	0.926	***Potentially Independent***
Baldwin Creek [e]	7.30	high	0.806	dependent
Wilder Creek [62]	14.12	high	0.855	dependent
San Lorenzo River [63]	215.25	high	0.994	**Functionally Independent**
Rodeo Creek Gulch [e]	6.10	high	0.733	dependent
Soquel Creek [64]***	66.41	high	0.979	***Potentially Independent***
Aptos Creek [65]	41.00	high	0.921	***Potentially Independent***

* The threshold for viability-in-isolation is set at 16 IP km. See text for how this value was selected. ** Conclusions for these watersheds reflect the high likelihood that lagoon habitats at least partly offset potential bias in the IP model. ***The historical status of Soquel Creek depends in part on whether substantial immigration from populations in the South-Central California Coast Steelhead ESU, especially the Pajaro and Salinas rivers, was substantial under historical conditions.

Table 4.8. Historical population structure of winter steelhead in the Russian River basin.

Watershed	IP km*	IP Bias Index	Self-recruitment	Historical Population Status
Lower Russian River**		high		dependent populations
Austin Creek [A]	111.85	high	0.981	***Potentially Independent***
Dutch Bill Creek [B]	17.38	high	0.973	dependent
Green Valley Creek [C]	61.67	high	0.988	***Potentially Independent***
Mark West Creek [D]	366.52	high	0.997	***Potentially Independent***
Dry Creek [E]	384.86	high	0.998	***Potentially Independent***
Maacama Creek [F]	106.91	high	0.991	***Potentially Independent***
Sausal Creek [G]	17.27	high	0.957	dependent
Upper Russian River [H]***	892.29	high	$>$0.999	**Functionally Independent**

* The threshold for viability-in-isolation is set at 16 IP km. See text for how this value was selected. **Unnamed tributaries downstream of the confluence of Big Sulphur Creek. ***The Upper Russian River population of winter steelhead occupies mainstem and tributary habitats upstream from the confluence of Big Sulphur Creek (inclusive).

five populations and possibly as many as fifteen that satisfy our threshold for viability-in-isolation. In part, the physical characteristics of the basin are what makes it difficult to reach a definitive conclusion. Environmental heterogeneity occurs at regional scales, such that geographically basins draining into one part of San Francisco Bay or San Pablo Bay tend to closely resemble one another (Figures 1.6 and 1.7). This is the basis for positing a minimum number of populations within the basin. Beyond this, it is not clear whether significant barriers to dispersal among basins historically existed. Of course, the bays themselves did not provide spawning or rearing habitat (at least not for young juvenile steelhead). However, the surface of the two estuaries was commonly covered by a substantial layer of freshwater, especially during periods of winter storms and subsequent spring-summer snowmelt in the Sierra Nevada. The widespread distribution of obligatory freshwater fishes among the tributaries to San Francisco and San Pablo bays provides evidence that freshwater layer was sufficient to allow dispersal among basins by fishes that are rather less mobile than juvenile or adult steelhead (Snyder, 1905). Moreover, in some parts of the estuary, the northern and southern regions especially, multiple watersheds historically drained into extensive, common wetlands. Whether this promoted dispersal among basins is not known, however, the potential fidelity to be reduced by mixing of run-off and perhaps even physical connections through distributaries can not be entirely overlooked. Unfortunately, we do not have sufficient genetic data or other forms of information to evaluate this continuum of hypotheses.

Despite the potential for substantial exchange among populations in environmentally similar watersheds, we consider steelhead in each major tributary as a distinct population, and evaluate the historical status of each separately. Although doing so means that we effectively defer consideration of environmental similarities among basins to our delineation of diversity strata within the ESU, we anticipate these results in Table 4.9. Since all of the tributaries to San Francisco and San Pablo bays, save one (Arroyo Corte Madera del Presidio [S1]), exceed our threshold for viability-in-isolation, analyzing these possibly composite populations in terms of their components is not likely to have serious consequences for the validity of ESU viability criteria.

Table 4.9. Historical population structure of winter steelhead in tributaries of San Francisco and San Pablo bays.

Population	IP km	IP Bias Index	Self-recruitment	Historical Population Status
Northwest Bay				
Arroyo Corte Madera del Presidio [S1]	12.75	high	0.294	dependent
Corte Madera Creek [S2]	31.74	high	0.527	***Potentially Independent***
Miller Creek [S3]	44.39	high	0.883	***Potentially Independent***
Novato Creek [S4]	78.58	severe	0.778	***Potentially Independent***
North Bay				
Petaluma River [S5]	225.39	severe	0.939	***Potentially Independent***
Sonoma Creek [S6]	268.70	high	0.955	**Functionally Independent**
Napa River [S7]	593.93	severe	0.978	**Functionally Independent**
East Bay				
San Pablo Creek [S8]	67.93	severe	0.754	***Potentially Independent***
San Leandro Creek [S9]	80.53	severe	0.954	**Functionally Independent**
San Lorenzo Creek [S10]	79.77	severe	0.985	**Functionally Independent**
Southeast Bay				
Alameda Creek [S11]	816.59	severe	0.975	**Functionally Independent**
Coyote Creek [S12]	498.29	severe	0.936	**Functionally Independent**
Southwest Bay				
Guadalupe River [S13]	157.25	severe	0.958	**Functionally Independent**
Stevens Creek [S14]	39.55	severe	0.775	***Potentially Independent***
San Francisquito Creek [S15]	59.22	severe	0.655	***Potentially Independent***
San Mateo Creek [S16]	57.41	severe	0.752	***Potentially Independent***
unnamed tributaries				dependent populations

In our evaluation of the historical role of population within the ESU, we considered the potential consequences of bias in our proxy measure of population carrying capacity. We expect that such bias affected most if not all of the watersheds in this basin, but is less severe in basins that drain the eastern slopes of the Santa Cruz Mountains than in basins in the southeastern and northern regions of the basin; however, sources of groundwater along major fault lines are likely to maintain the quality of summer rearing habitat in some basins (e.g., Napa River, Sonoma Creek, Coyote Creek, Guadalupe River, etc.). We also considered whether environmental differences among regions might limit effective dispersal among watersheds. Taking these issues into account, we concluded that a historical population in a watershed of intermediate size was more likely (albeit not certain) to act as functionally independent population if it was the largest population in its region or otherwise distinct from larger populations in its region, and have evaluated historical status accordingly (Table 4.9).

Coastal basins: Golden Gate to northern Monterey Bay

The geographical structure of this stretch of coastline is similar to that of the Mendocino coast, and our conclusions regarding historical population structure of steelhead are likewise similar (Table 4.7).

We conclude that functionally independent populations of steelhead historically spawned in Pilarcitos Creek [52], San Gregorio Creek [54], Pescadero Creek [56], Laguna Creek [61] and San Lorenzo River [63], and that steelhead in Waddell [58], Scott [59], Soquel [64], and Aptos [65] creeks acted as potentially independent populations under historical conditions. In support of these conclusions, we note that dispersal from populations in San Francisco Bay is likely to have been lower than modelled in the course of the connectivity-viability analysis, but that much of the immigration to the potentially independent and dependent populations along this coastline is predicted to originate from populations in the three largest watersheds (Figure 4.12).

Our conclusion regarding the status of Soquel Creek [64] is somewhat sensitive to the inclusion or exclusion of immigration from putative populations in basins just south of the ESU boundary (e.g., Pajaro River and Salinas River). Although it is possible that transfers of hatchery steelhead stocks among basins in this area have altered the historical population genetic structure of steelhead in this region (Table 4.2), we expect that substantial dispersal occurred in this region under historical conditions. Indeed, the lack of evidence for substantial barriers to gene flow in this region and elsewhere to the south suggests that such dispersal was relatively substantial.

4.9 Diversity strata

4.9.1 Diversity strata: NC-Steelhead ESU

Figure 4.18 summarizes our conclusions regarding the assignment of populations to diversity strata in the NC-Steelhead ESU. The clearest division is based on the life history differences between winter and summer steelhead. Within a life-history type, the structure presented in Figure 4.18 is based on environmental variability and is grounded in our initial multivariate analysis of basin-scale environmental and ecological characteristics for the NCCCRD. We also consider the spatial arrangement of populations in developing these strata.

Recall that diversity strata are not biological structures. A single population may therefore contribute to more than one diversity stratum if it occupies an environmentally heterogeneous watershed. For a population to be counted as contributing under multiple diversity strata, it is necessary for all components of that population to be extant and contributing to the spatial structure and diversity (and thus the viability) of that population as a whole. Populations with restricted distributions might not include the necessary diversity to represent all diversity strata to which they are thought to have contributed under historical conditions.

Winter: Northern Klamath Mountains

This stratum includes populations of winter steelhead that spawn in watersheds that drain relatively high elevation mountains in the Klamath Mountains ecoregion, many of which attain sufficiently high elevations for snowmelt to contribute significantly to the annual hydrograph. Most of these watersheds lie north of the mainstem Eel River. We include in this stratum larger minor mainstem tributaries of the Eel River whose watersheds include relatively high elevation mountains.

Winter: Southern Klamath Mountains

This stratum includes populations of winter steelhead that spawn in watersheds that drain lower elevation mountains in the Klamath Mountains ecoregion for which snowmelt contributes little to the annual hydrograph. Most of these watersheds lie south of the mainstem Eel River, but we also include in this stratum minor tributaries to the mainstem Eel River upstream of the confluence of the South Fork Eel River that drain smaller, somewhat lower watersheds lying on either side of the mainstem Eel River.

Winter: Northern Coastal

This stratum includes populations of steelhead that spawn in watersheds north of Punta Gorda that have relatively low elevation, receive relatively high amounts of precipitation, and are strongly influenced by coastal climate. Since the coastal regions of a number of watersheds from the two previously discussed strata exhibit these characteristics, we include these watersheds in this stratum as well. For example, Prairie Creek, a tributary to Redwood Creek (Humboldt) [1] is environmentally similar to nearby coastal basins that are not tributary to a larger watershed. The western portion of the South Fork Eel River watershed is exposed to coastal climatic influences, especially in terms of precipitation and coastally mediated temperature. We include the small basins of the Lost Coast in this stratum, largely based on the fact that these watersheds abut the Mattole River watershed, and receive high amounts of precipitation.

Winter: Central Coastal

This stratum includes populations of steelhead that spawn in watersheds south of the Lost Coast to Big Salmon Creek (inclusive). The division between this stratum and the one that follows reflects the geometry of and interior characteristics of the larger watersheds along this stretch of coast. The large watersheds in this stratum are more consistently affected by coastal climate, whereas those to the south exhibit a much stronger signature of interior climatic conditions. This division also coincides with one of the moderately pronounced breaks apparent in genetic analyses (Figure 4.7).

Winter: Southern Coastal

This stratum includes populations of steelhead that spawn in watersheds between the Navarro River and Gualala River, inclusive. These watersheds exhibit a narrower band of coastal influence than those to the north, and tend to be warmer and drier, particularly in the interior.

Summer: Interior

This stratum includes all populations of summer steelhead that ascend tributaries of the Eel River upstream of the North Fork Eel River, inclusive. These watersheds experience high summer temperatures with little or no coastal moderation. These populations have longer freshwater spawning migrations than do summer steelhead elsewhere in the NC-Steelhead ESU.

Summer: Coastal

This stratum includes all populations of summer steelhead that ascend the Van Duzen River, Larabee Creek, and other coastal basins in which summer temperatures are moderated by coastal climate. All but one of these basins receive substantial snowfall; the exception, the Mattole River, receives the largest amount of precipitation in the NCCCRD.

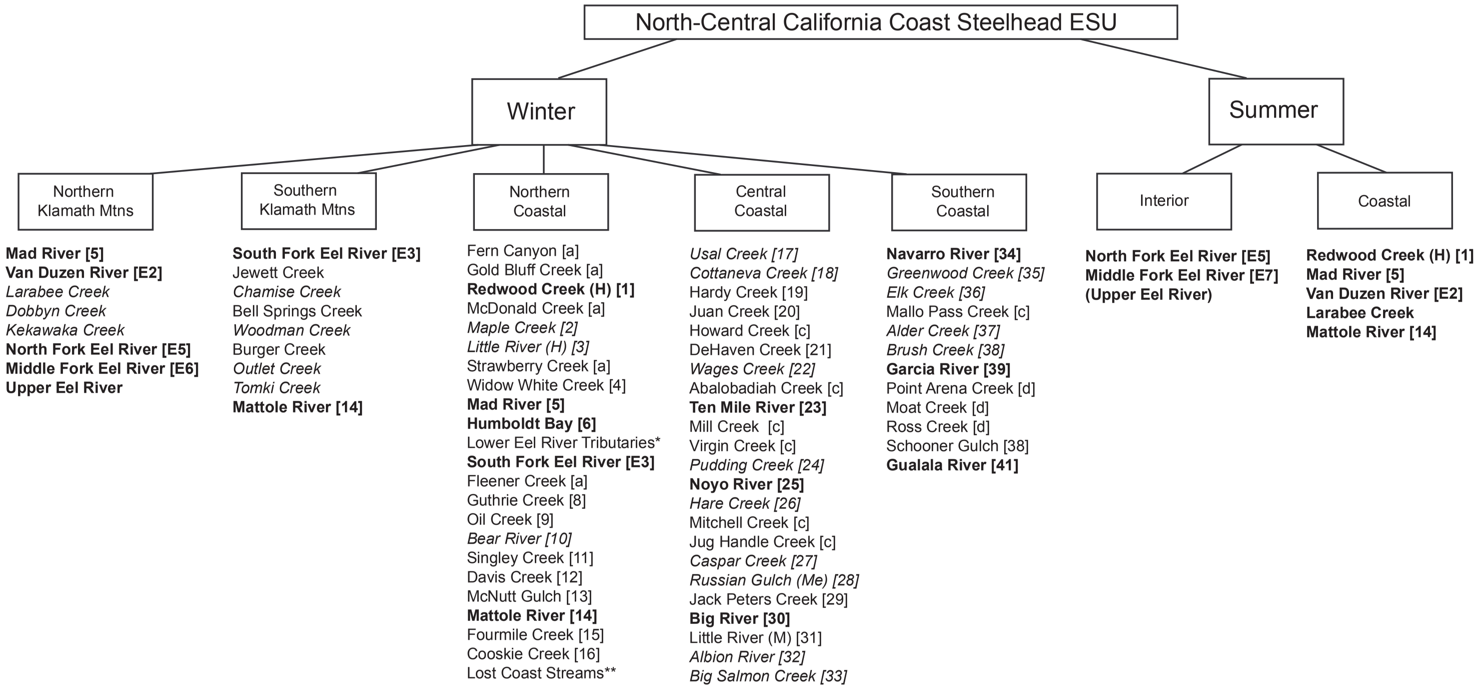

Figure 4.18. Arrangement of historical populations of the NC-Steelhead ESU into diversity strata. Functionally independent populations are listed in bold font. Potentially independent populations are listed in italic font. Dependent populations are listed in regular font. Not all dependent populations have been included in this figure.

4.9.2 Diversity strata: CCC-Steelhead ESU

Figure 4.19 summarizes our conclusions regarding the assignment of populations to diversity strata in the NC-Steelhead ESU. The clearest division is based on the life history differences between winter and summer steelhead. Within a life-history type, the structure presented in Figure 4.19 is based on environmental variability and is grounded in our multivariate analysis of basin-scale environmental and ecological characteristics for the NCCCRD. We also consider the spatial arrangement of populations in developing these strata. Note that only winter steelhead occur in the CCC-Steelhead ESU.

North Coastal

This stratum includes populations of steelhead spawning in direct tributaries to the Pacific Ocean north of the Golden Gate for which proximity to the coast strongly mediates climatic conditions, and tributaries of the Russian River exposed to coastally mediated climate.

Interior

This stratum includes populations of steelhead that spawn in interior watersheds that do not exhibit characteristics typical of coastal watersheds. These watersheds are typically warmer and drier in the summer due to the lack of coastal fog, and exhibit substantially different vegetation (e.g., oak savannahs and cottonwood riparian corridors, as opposed to redwood/conifer forests).

Santa Cruz Mountains

This stratum includes populations of steelhead that spawn in watersheds that drain the Santa Cruz Mountains and are direct tributaries to the Pacific Ocean.

San Francisco Bay: “Coastal”

This stratum includes populations of steelhead that spawn in tributaries to San Francisco Bay, but otherwise exhibit environmental characteristics more similar to coastal watersheds. These watersheds drain the eastern slopes of the coastal mountains that separate San Francisco Bay from the Pacific Ocean.

San Francisco Bay: “Interior”

This stratum includes populations of steelhead that spawn in tributaries to San Francisco Bay that exhibit the warmer, drier characteristics of basins that lie well inland of the coast.

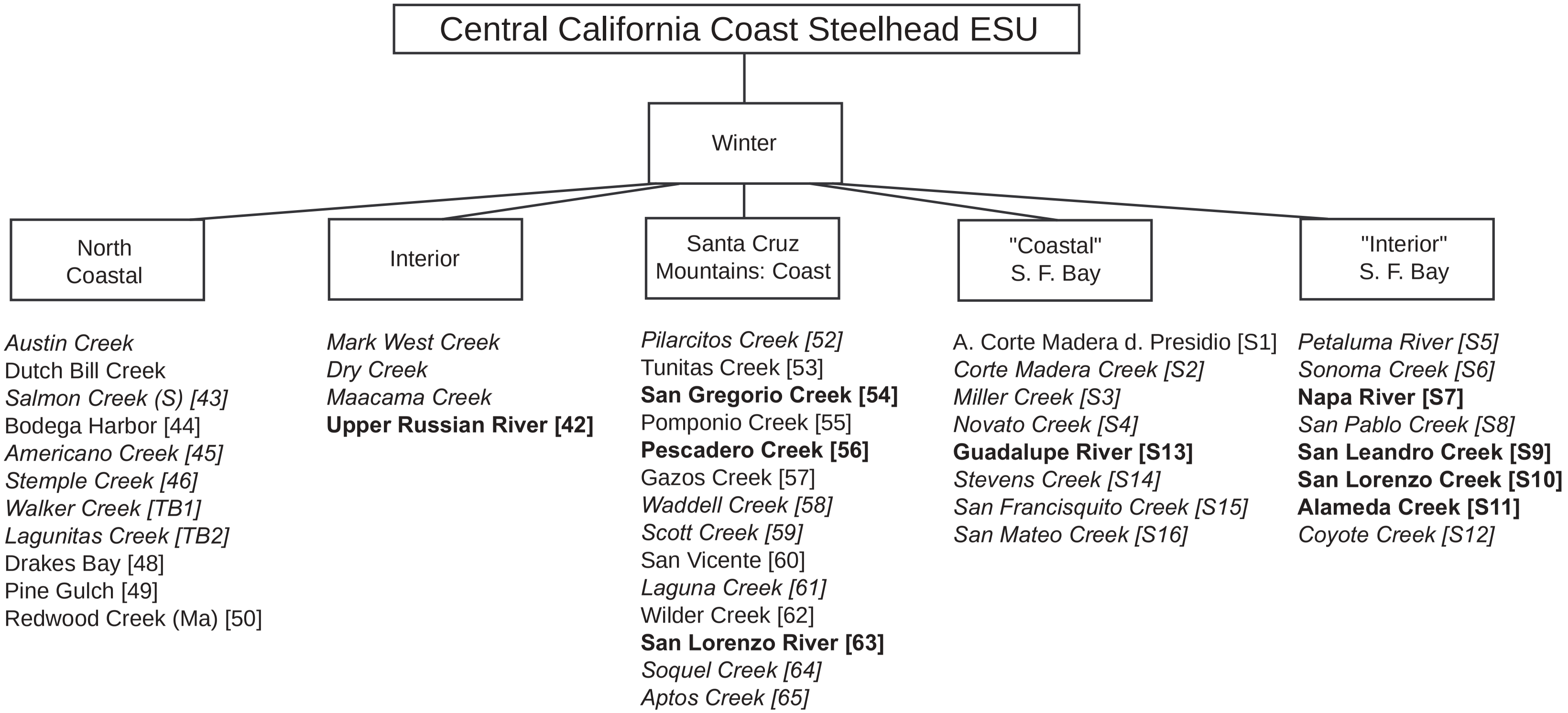

Figure 4.19. Arrangement of historical populations of the CCC-Steelhead ESU into diversity strata. Functionally independent populations are listed in bold font. Potentially independent populations are listed in italic font. Dependent populations are listed in regular font. Not all dependent populations have been included in this figure.

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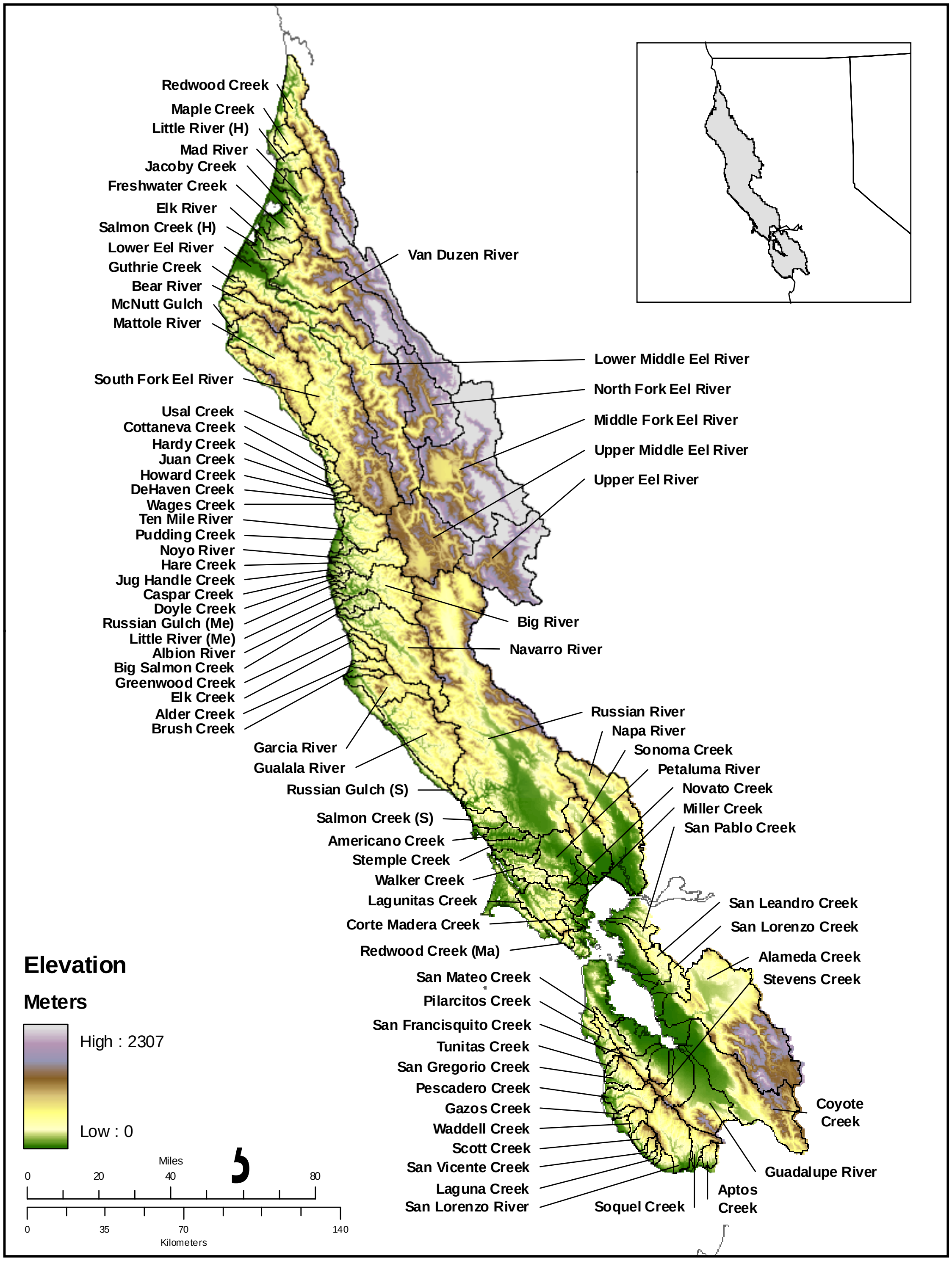

Plate 1. Elevation across the the NCCCRD.

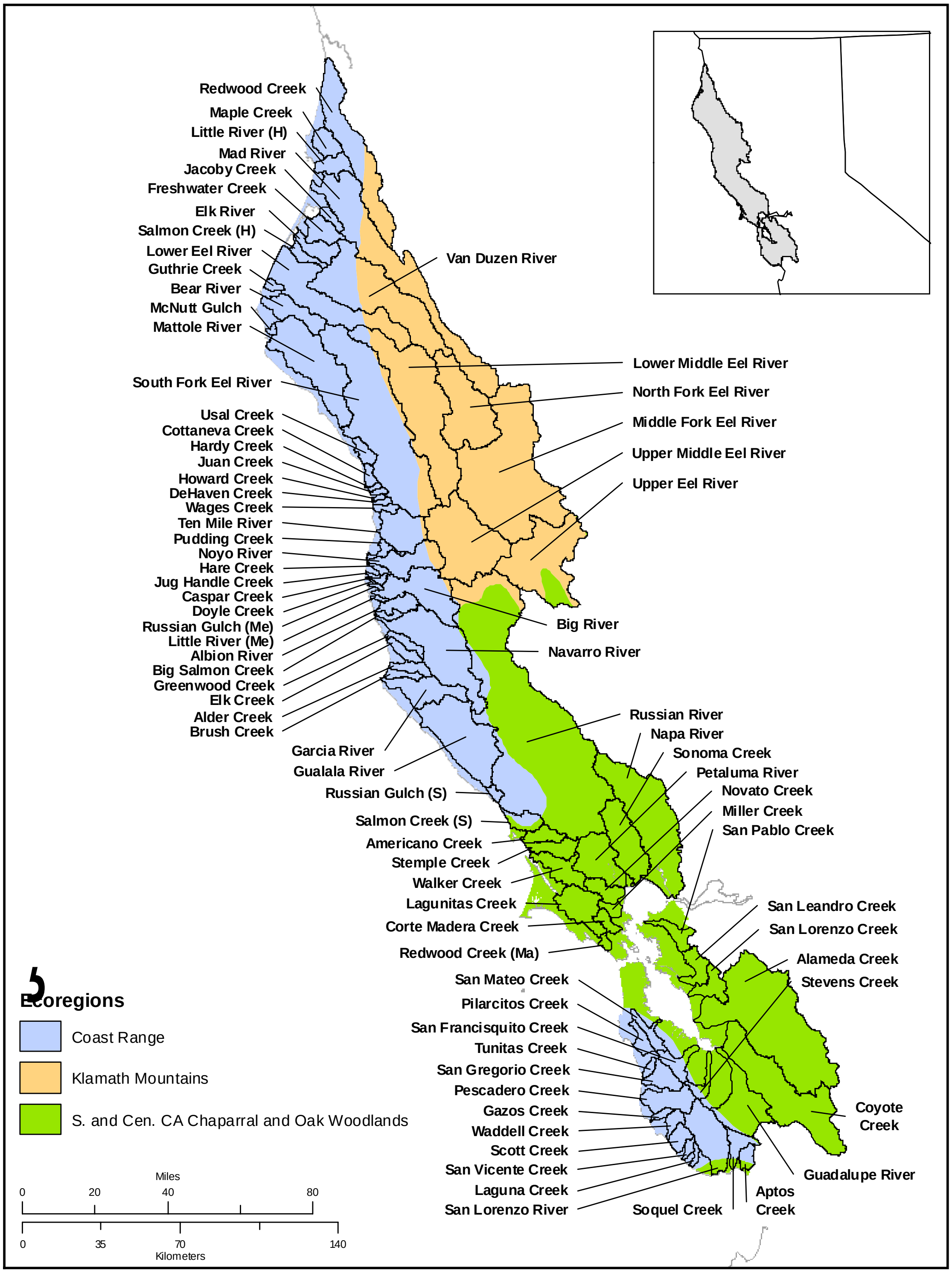

Plate 2. Ecoregions of the NCCCRD.

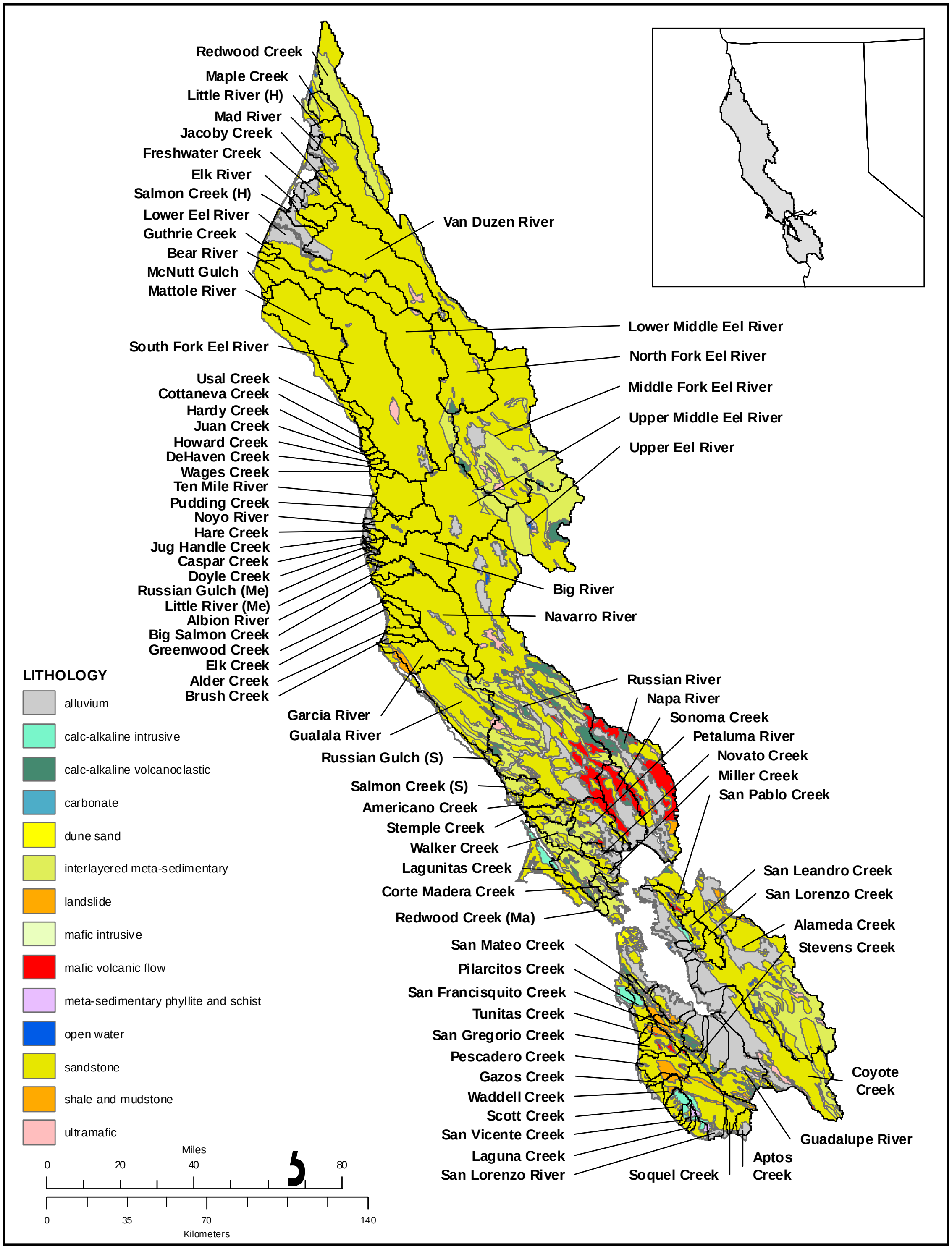

Plate 3. Geology across the NCCCRD (Jennings, 1977).

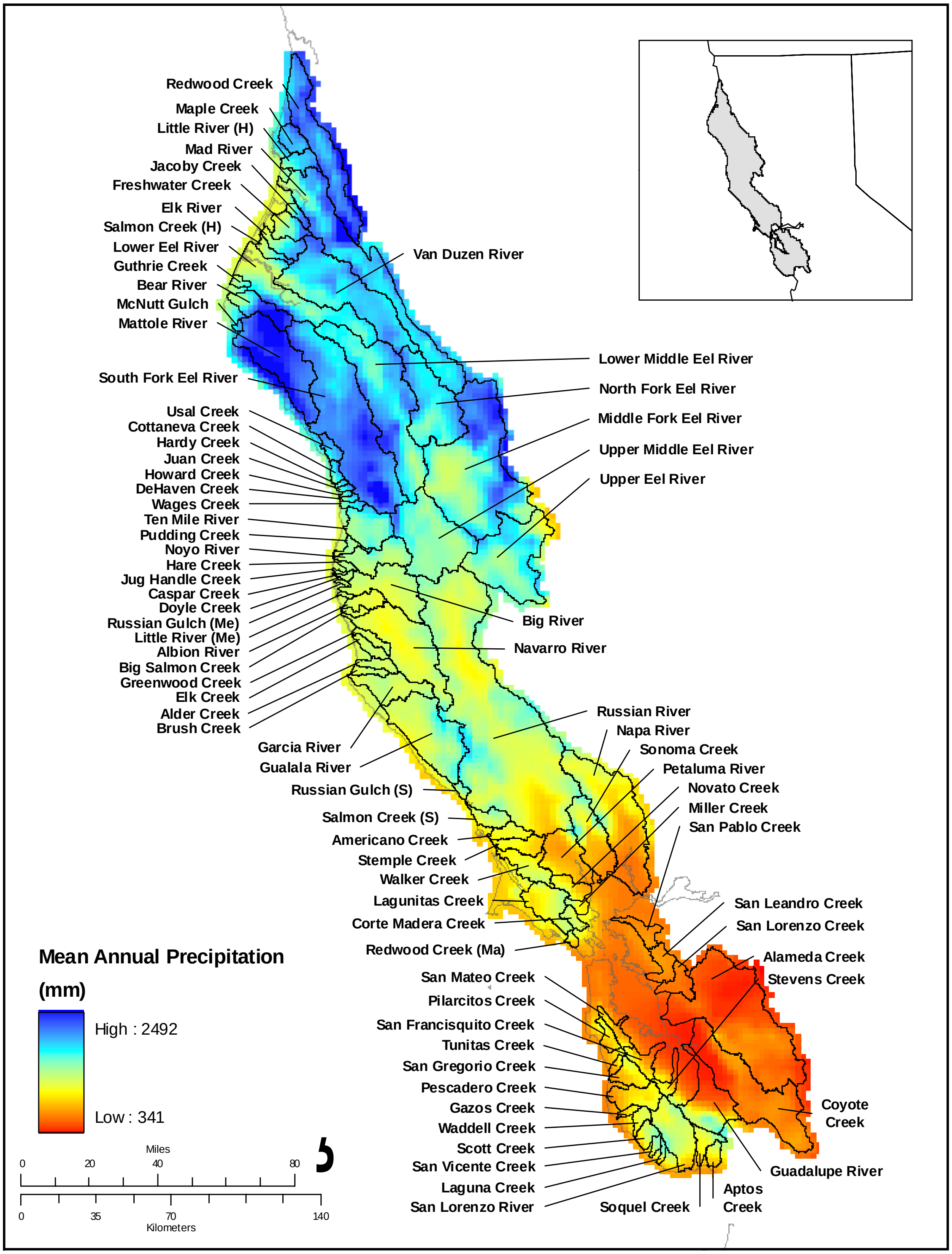

Plate 4. Mean annual precipitation across the NCCCRD.

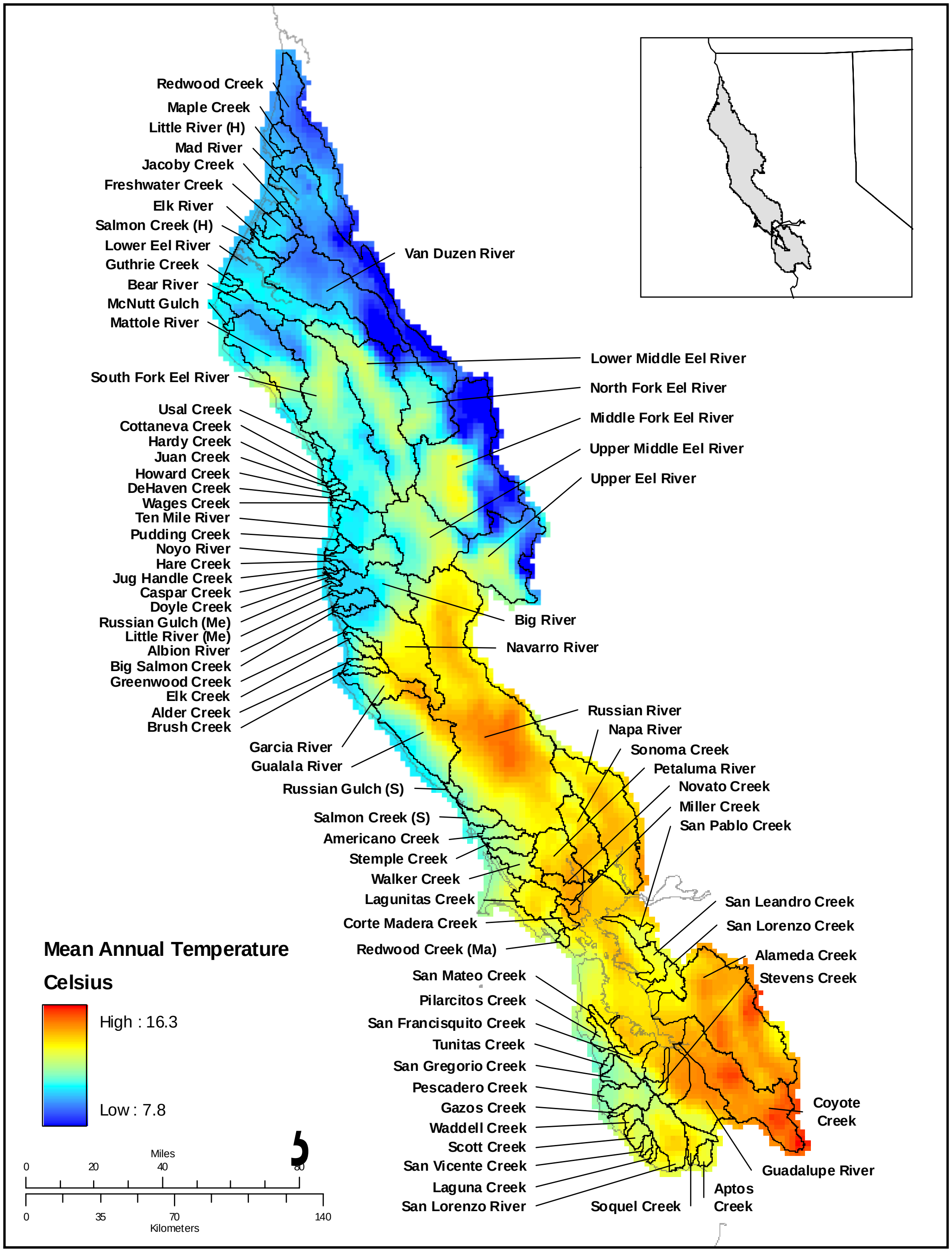

Plate 5. Mean annual temperature across the NCCCRD.

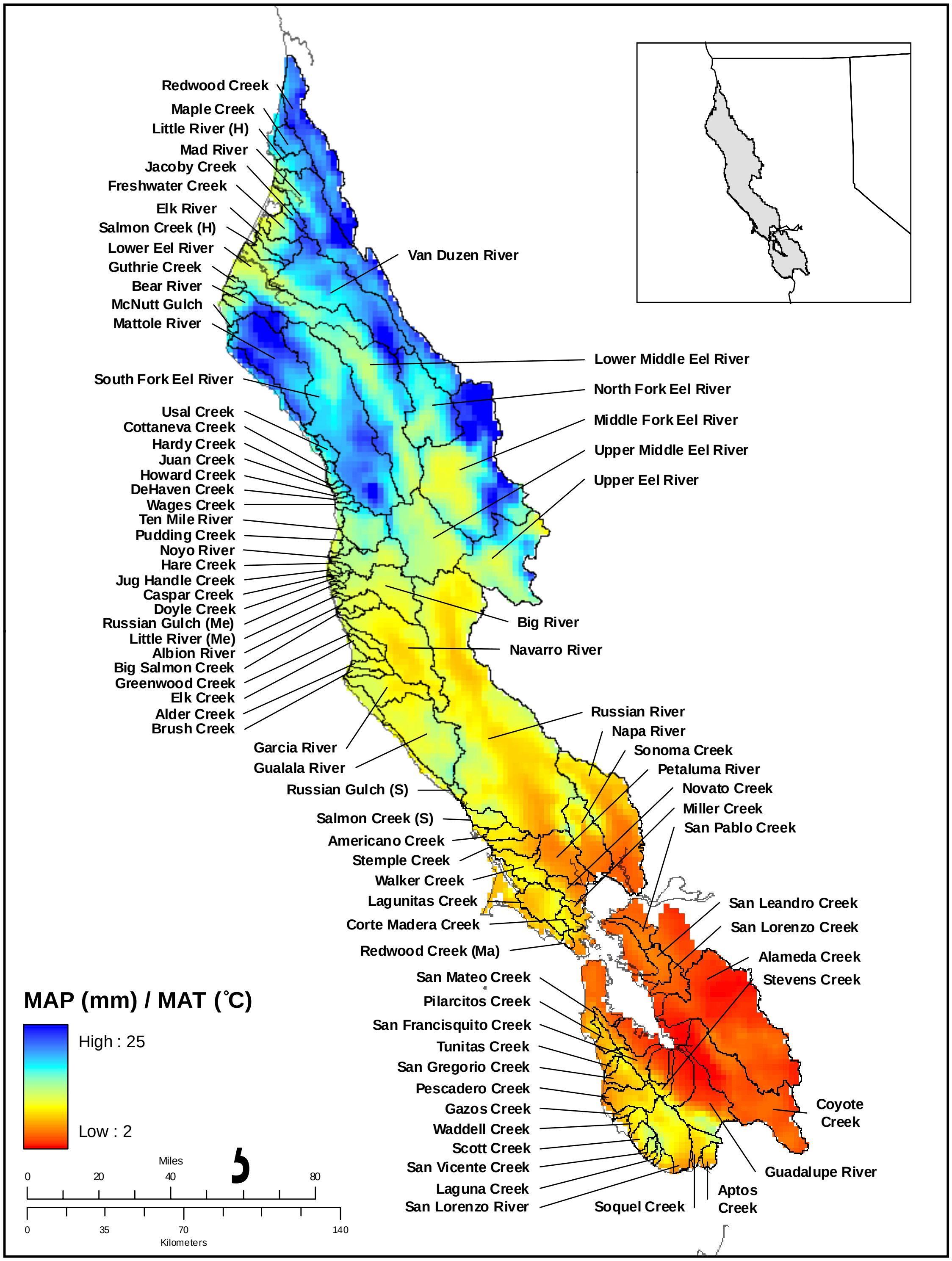

Plate 6. Ratio of mean annual precipitation to mean annual temperature across the NCCCRD.

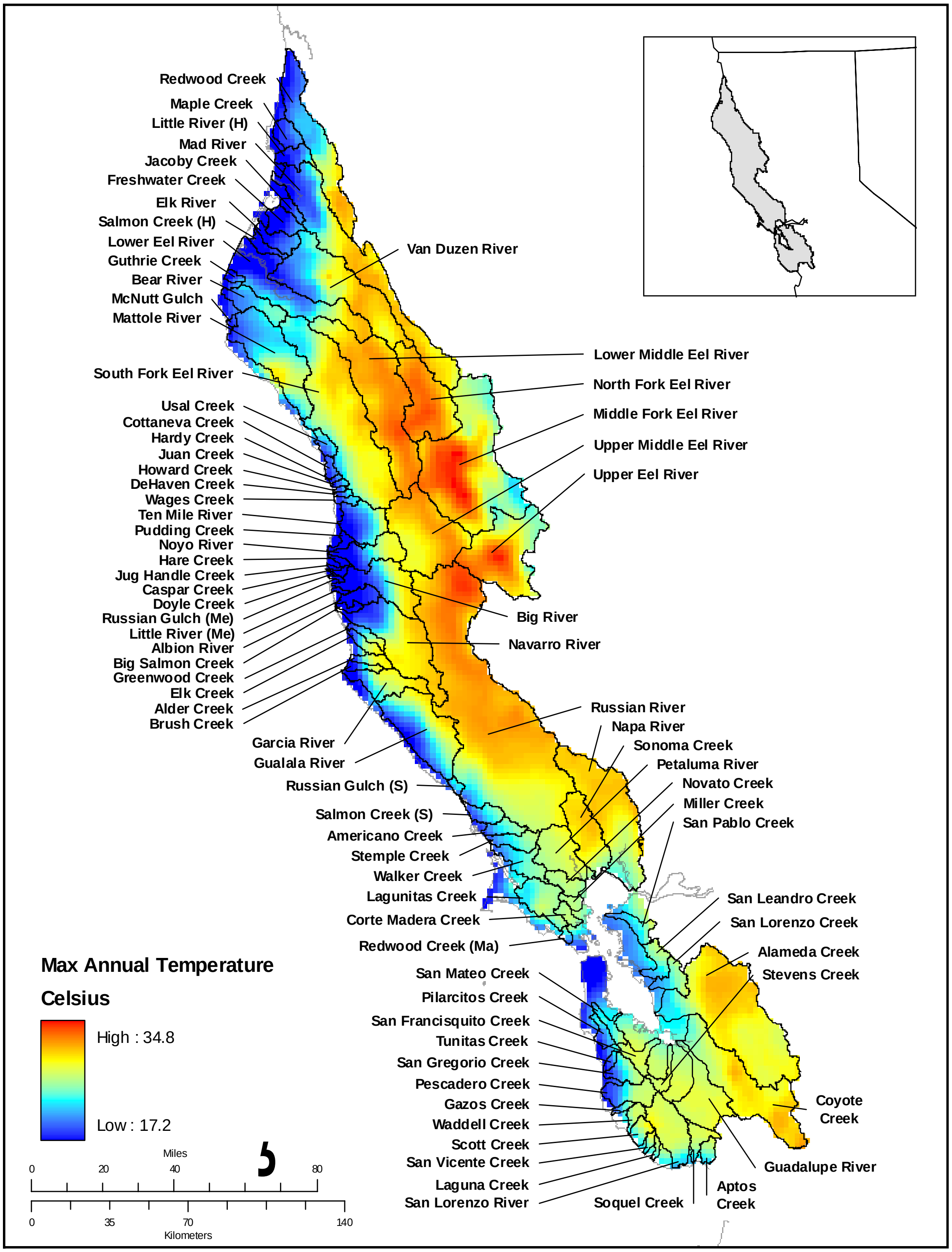

Plate 7. Maximum August temperature across the NCCCRD.

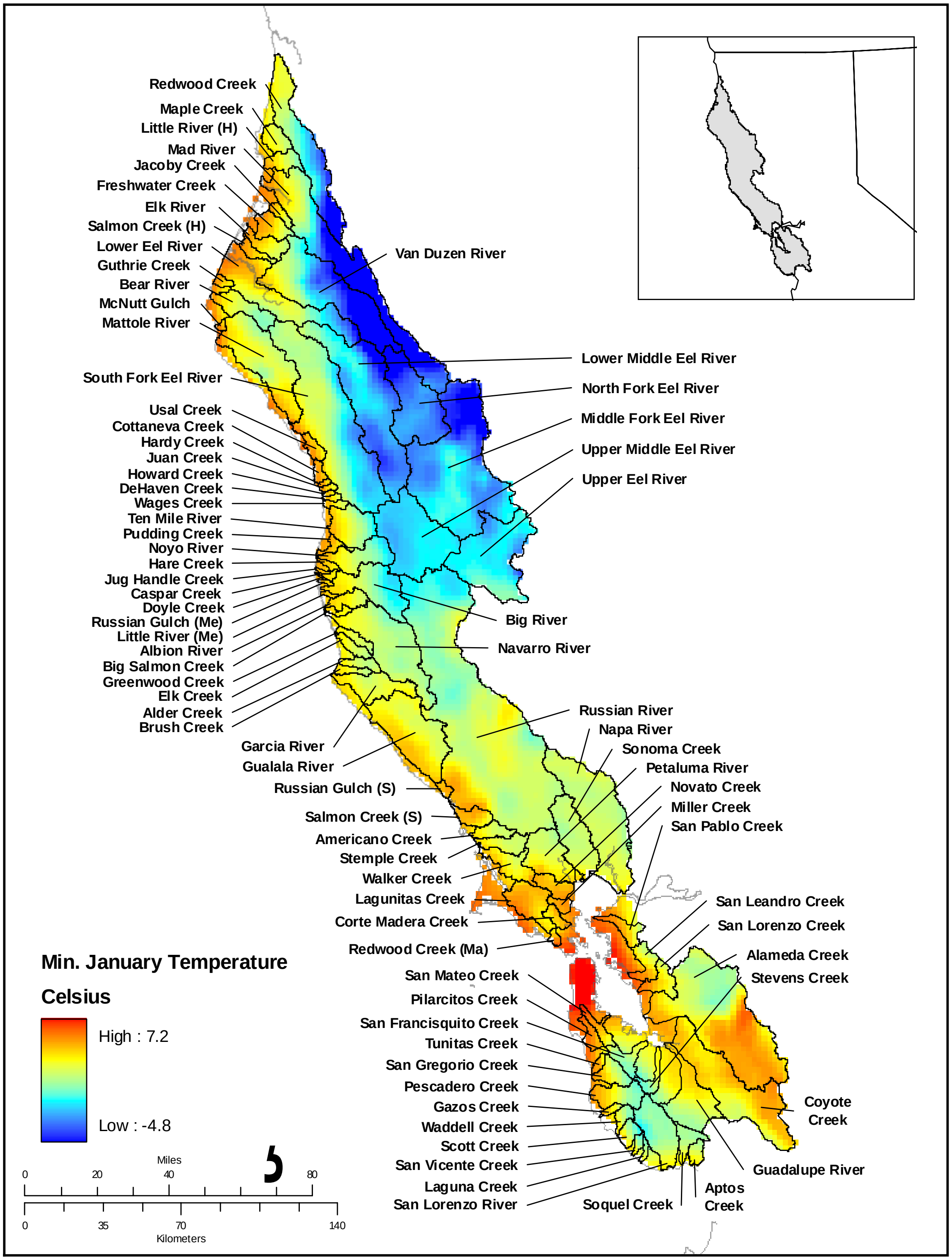

Plate 8. Minimum January temperature across the NCCCRD.

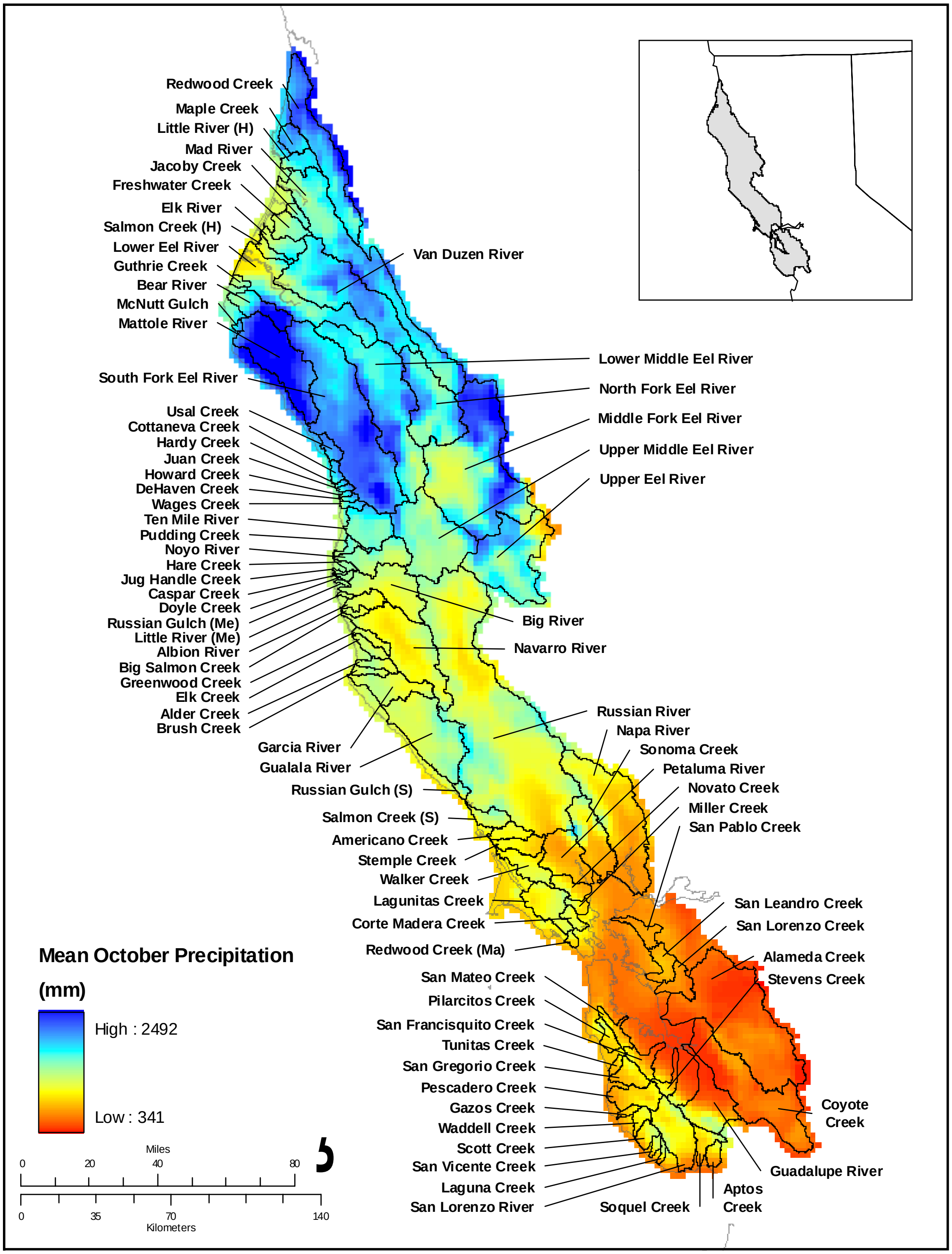

Plate 9. Mean October precipitation across the NCCCRD.

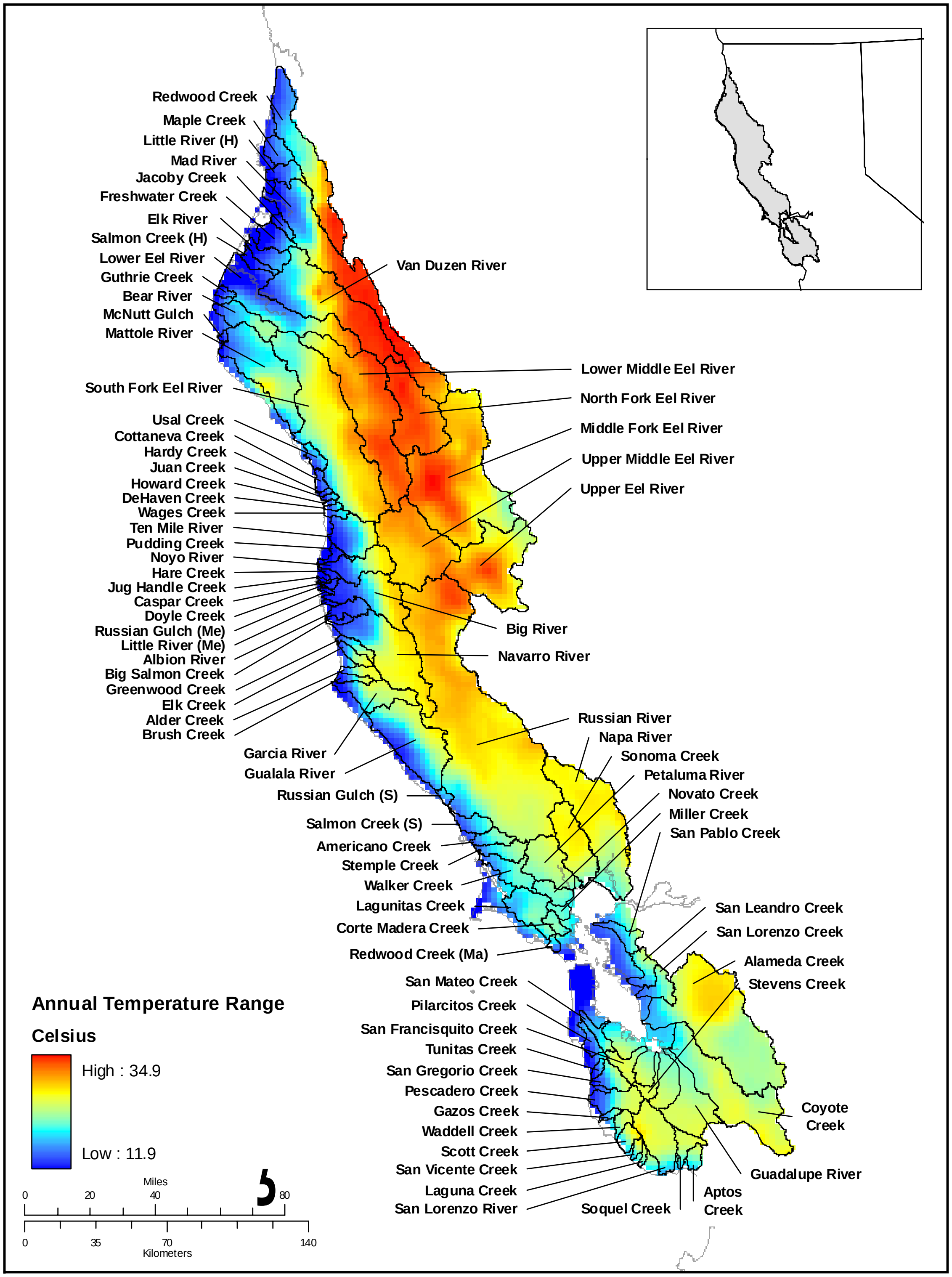

Plate 10. Annual temperature range across the NCCCRD.

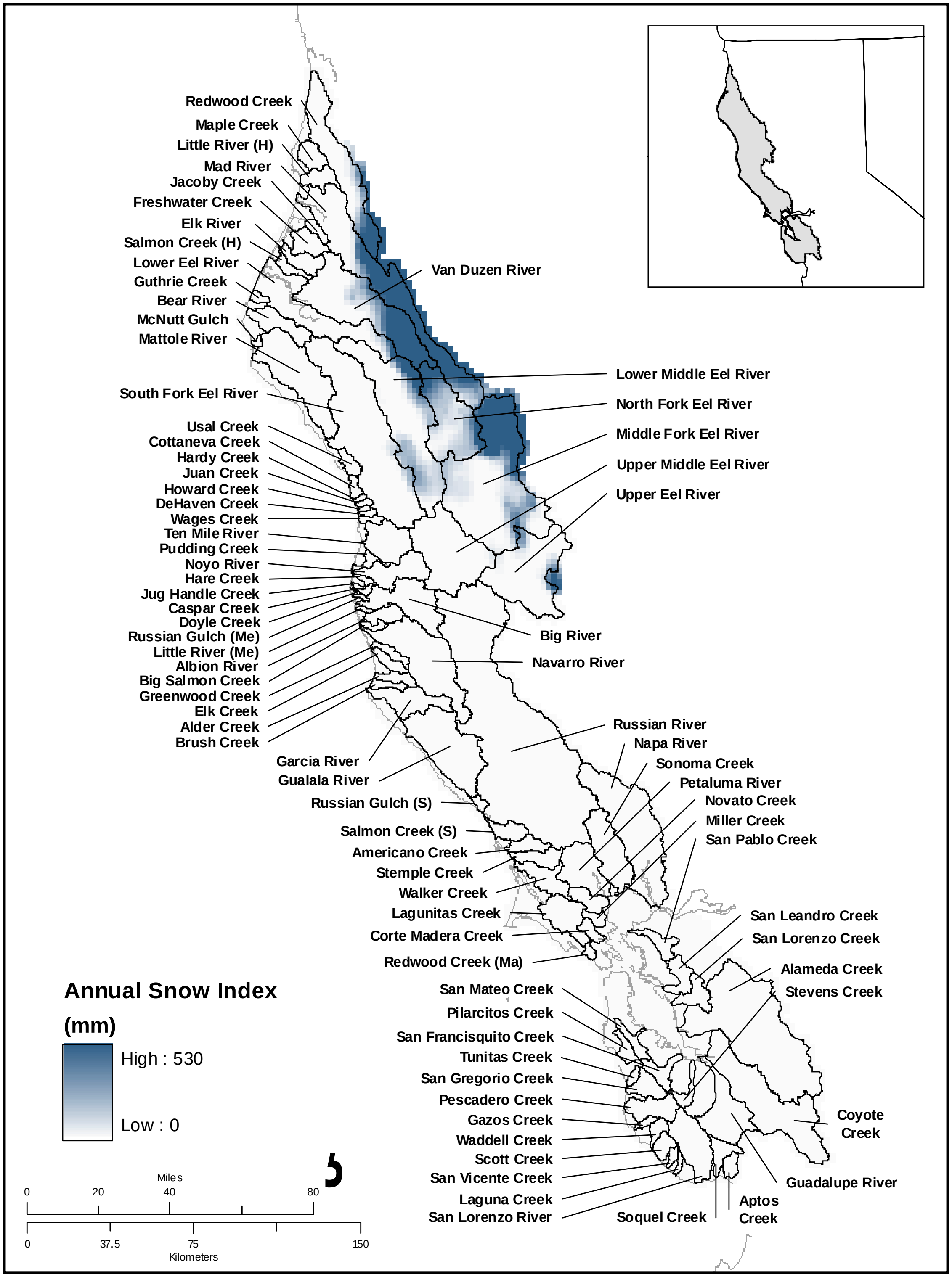

Plate 11. Snow index across the NCCCRD.

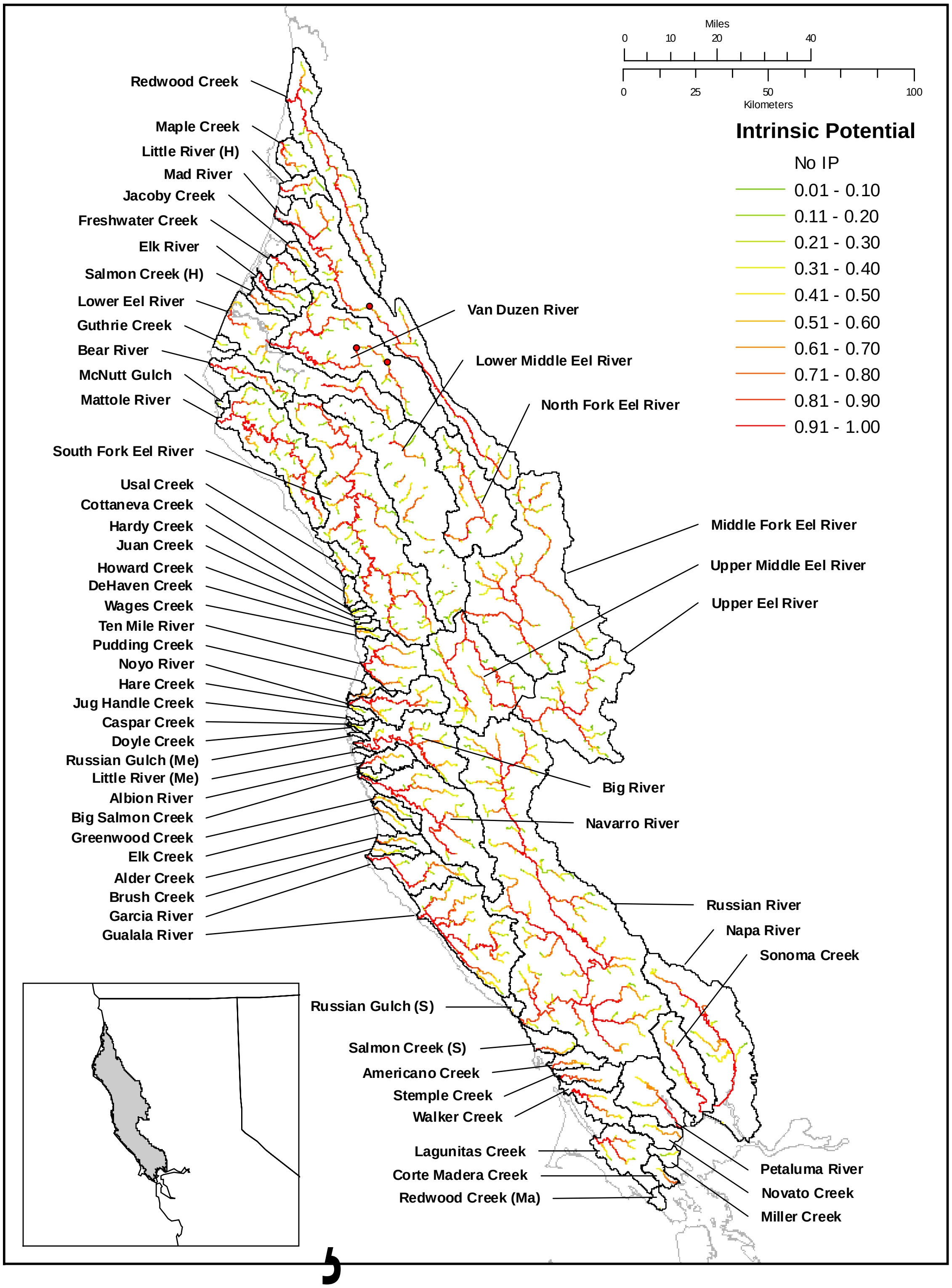

Plate 12. Intrinsic potential for Chinook salmon across the range of the CC-Chinook ESU.

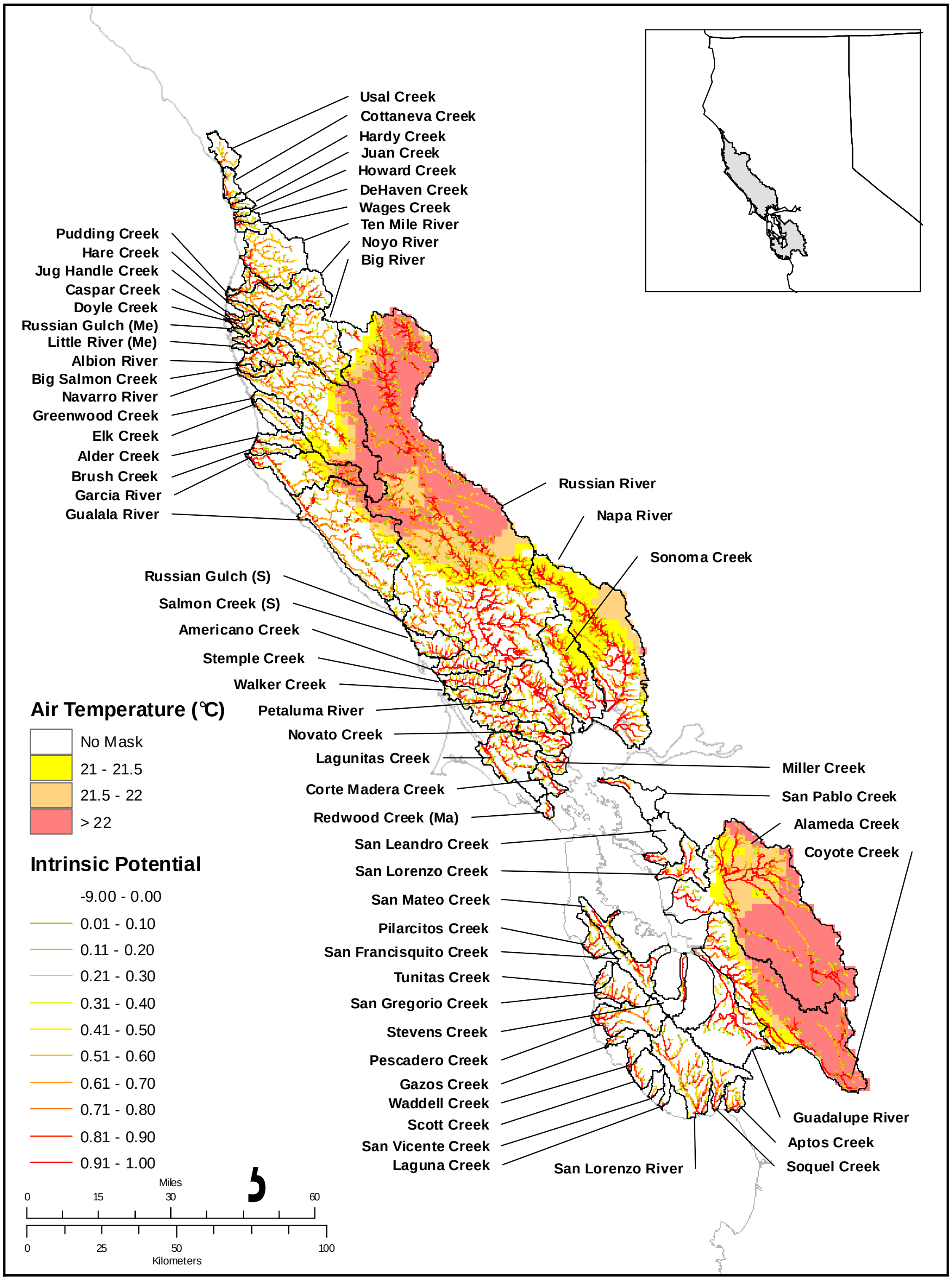

Plate 13. Intrinsic potential for coho salmon across the range of the CCC-Coho ESU, with temperature masks.

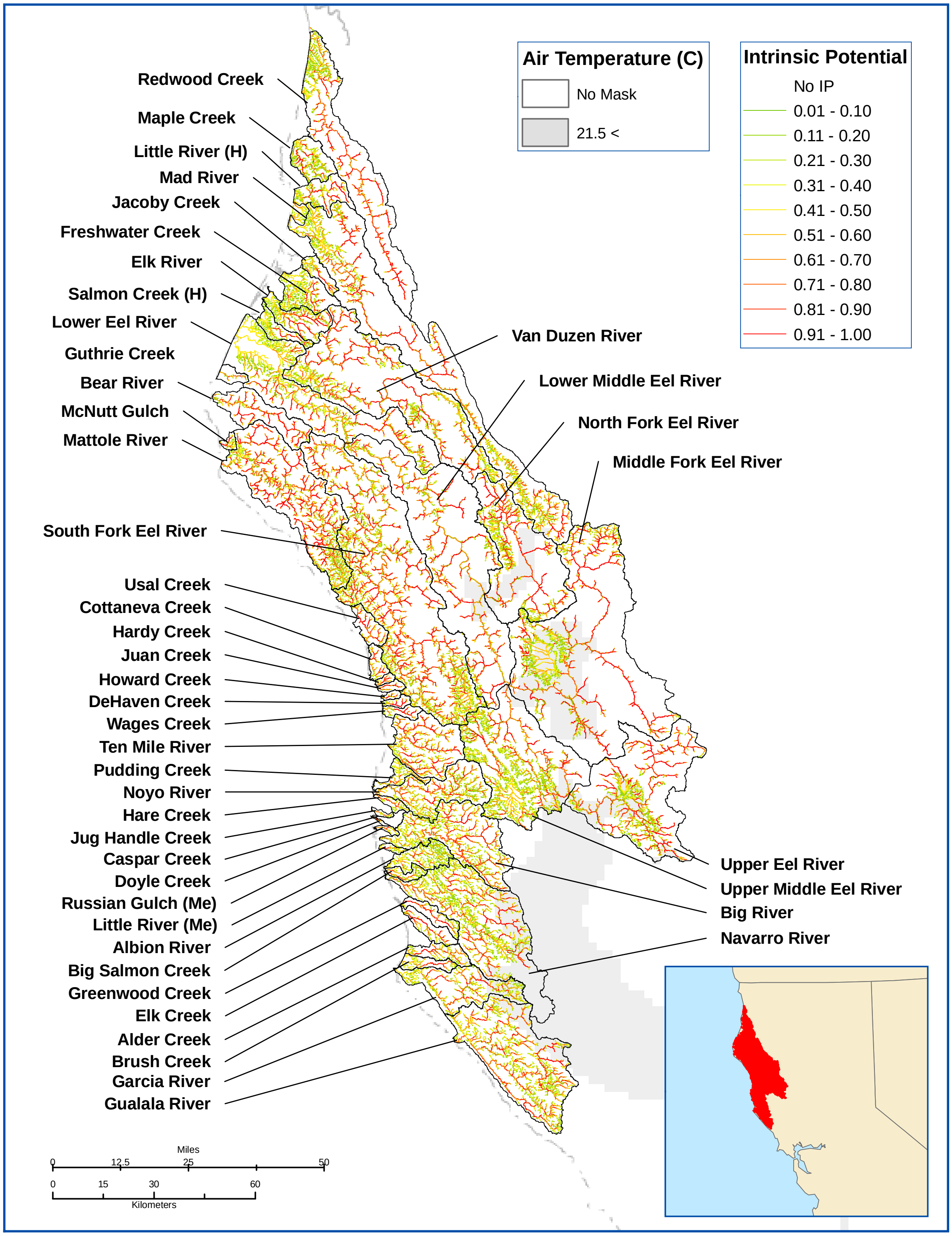

Plate 14. Intrinsic potential for steelhead across the range of the NC-Steelhead ESU, including areas where coho salmon are likely to be excluded by temperature.

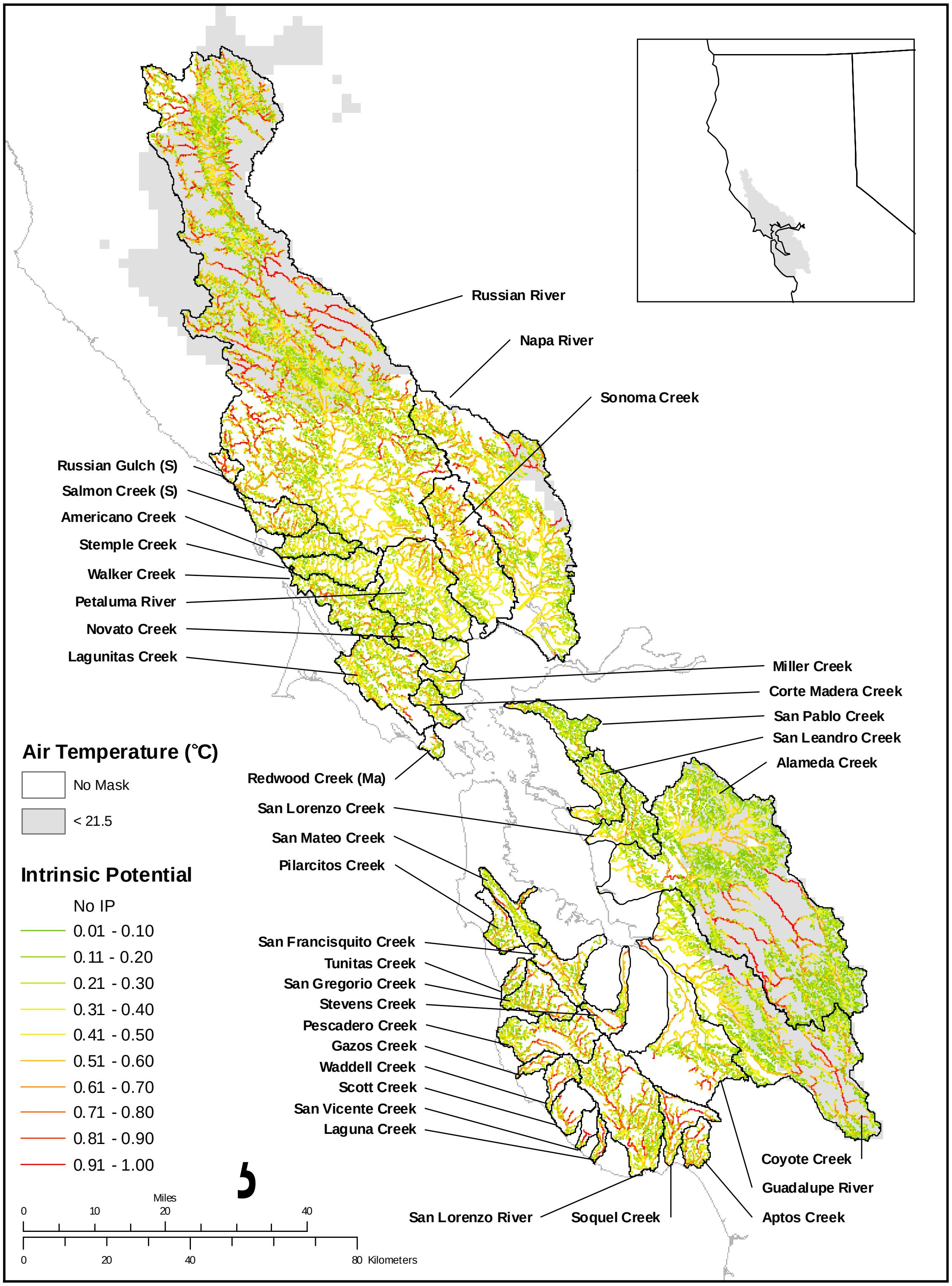

Plate 15. Intrinsic potential for steelhead across the range of the CCC-Steelhead ESU, including areas where coho salmon are likely to be excluded by temperature.

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