California WaterFix Hearing
Exhibit No. SWRCB-75

APPENDIX C

Central Valley Technical Recovery Team Reports

Technical Recovery Team Members

Steve Lindley, NMFS, SWFSC Fisheries Ecology Division (Chair)

Alice Low, California Department of Fish and Game

Dennis McEwan, California Department of Fish and Game

Bruce MacFarlane, NMFS, SWFSC Fisheries Ecology Division

Tina Swanson, Bay Institute

Jim Anderson, University of Washington

Bernie May, UC Davis

John G. Williams, consultant

Sheila Greene, California Department of Water Resources

Chuck Hanson, consultant

The Central Valley Technical Recovery Team has published five reports that provide scientific guidance for planning the recovery of listed Chinook salmon and steelhead in the Central Valley. Those five reports appear in this appendix in the following order:

- ☐ Population structure of threatened and endangered Chinook salmon ESU in California's Central Valley basin.
- ☐ Historical population structure of Central Valley steelhead and its alteration by dams.
- ☐ Monitoring and research needed to manage the recovery of threatened and endangered Chinook and steelhead in the Sacramento-San Joaquin basin.
- ☐ Framework for assessing viability of threatened and endangered Chinook salmon and steelhead in the Sacramento-San Joaquin Basin.
- ☐ Directed connectivity among fish populations in a riverine network.

NOAA Technical Memorandum NMFS

This TM series is used for documentation and timely communication of preliminary results, interim reports, or special purpose information. The TMs have not received complete formal review, editorial control, or detailed editing.

APRIL 2004

POPULATION STRUCTURE OF THREATENED AND ENDANGERED CHINOOK SALMON ESUs IN CALIFORNIA'S CENTRAL VALLEY BASIN

S. T. Lindley[1], R. Schick[1], B. P. May[2], J. J. Anderson[3], S. Greene[4], C. Hanson[5], A. Low[6], D. McEwan[6], R. B. MacFarlane[1], C. Swanson[7], and J. G. Williams[8]

[1] NOAA Fisheries, SWFSC, Santa Cruz Laboratory, 110 Shaffer Rd., Santa Cruz, CA 95060
[2] UC Davis, Department of Animal Science, One Shields Ave., Davis, CA 94920
[3] University of Washington, School of Aquatic and Fishery Science, Box 358218, Seattle, WA 98195
[4] California Department of Water Resources, 3251 S St., Sacramento, CA 95816
[5] Hanson Environmental, Inc., 132 Cottage Ln., Walnut Creek, CA 94595
[6] California Department of Fish and Game, Native and Anadromous Fish and Watersheds Branch, 1807 13th St, Suite 104, Sacramento, CA 95814
[7] The Bay Institute, 500 Palm Dr., Suite 200, Novato, CA 94949
[8] 875 Linden Ln., Davis, CA 95616

NOAA-TM-NMFS-SWFSC-360

U. S. DEPARTMENT OF COMMERCE
Donald L. Evans, Secretary
National Oceanic and Atmospheric Administration
VADM Conrad C. Lautenbacher, Jr., Under Secretary for Oceans and Atmosphere
National Marine Fisheries Service
William T. Hogarth, Assistant Administrator for Fisheries

Contents

List of Figures

List of Tables

List of Plates

Abstract

This report describes the historical structure of spring- and winter-run chinook salmon populations in the Sacramento-San Joaquin watershed based on historical distributional information, geography, hydrography, ecology, population genetics, life history information, and trends in abundance. For the purposes of technical recovery planning, there are potentially two levels of organization within the evolutionarily significant unit (ESU) that are of interest: populations and population groups. In future documents, we will describe ESU viability goals in terms of viable independent populations spread among population groups that will maintain the evolutionary potential and ensure the persistence of the ESU.

We divided the spring-run chinook salmon ESU into four geographic groups. Members of the groups inhabit similar environments, according to a principle components analysis of environmental variables. The groups are southern Cascades, northern Sierra, southern Sierra, and Coast Range. There were historically at least 18 independent populations of spring-run chinook salmon spread among these four groups, plus an additional seven spring-run chinook salmon populations that may have been strongly influenced by an adjacent population. Three of the 18 independent spring-run chinook salmon populations are extant (Mill, Deer and Butte Creek populations). Several of the seven dependent populations still have intermittent runs of spring-run chinook salmon, including Big Chico, Antelope, and Beegum creeks.

The winter-run chinook salmon ESU historically contained at least four independent populations. These populations all spawned in the southern Cascades, and have been extirpated from their historic spawning areas. The single extant population of winter-run chinook salmon spawns in habitat outside of this range (spawning below Keswick Dam on the floor of the Central Valley), and was founded by some unknown combination of fish from the original populations. The distribution and diversity of winter- and spring-run chinook salmon has been strongly altered by habitat modifications, especially the placement of impassable dams at low elevations throughout the Central Valley basin.

1 Introduction

1.1 Background

A major goal of the Central Valley Technical Recovery Team (TRT) is production of criteria that describe viable salmonid populations in terms of abundance, productivity, diversity and spatial structure (McElhany et al., 2000) for listed evolutionarily significant units (ESUs) in the Central Valley [1]. These viability factors can be assessed at various levels of biological organization, ranging from independent populations, through population groups experiencing similar environments and sharing life history traits, to the ESU. Viability assessments and viability criteria therefore require definition of population structure.

In this document, we delineate the historical population structure of the listed evolutionarily significant units of chinook salmon [2] in the Central Valley domain (Plate 1), based on available evidence. We seek to describe the historical structure of ESUs because we are relatively certain that these structures were viable, i.e., capable of persisting for long periods of time. An ESU may not need to be at its historical levels of abundance, productivity, diversity and spatial structure in order to be viable, but the further it is from its historical structure, the less likely it is to be viable. We describe the population structure in terms of geographically-based population groups composed of independent and dependent populations.

Population groups are components of an ESU that partition genetic diversity. These groups might share common life history traits (e.g., early run timing cued to snow melt) or reside in the same region (e.g., a certain mountain range with environmental conditions different from other regions with the ESU boundaries). Identifying these population groups may be useful for several reasons. The first is that such groups represent genetic diversity within the ESU, and maintenance of this diversity is important for ESU persistence (McElhany et al., 2000). Second, if it is necessary or desirable to reintroduce salmonids to areas where they were extirpated, it would be best to use a founder from the same group.

Population groups are composed of independent and dependent populations. In this report, we follow the independent population definition of McElhany et al. (2000):

> An independent population is any collection of one or more local breeding units whose population dynamics or extinction risk over a 100-year time period is not substantially altered by exchanges of individuals with other populations.

The focus on breeding units suggests that we define the boundaries of salmon populations by watershed boundaries, since salmon have high fidelity to the watershed where they were born. In most (but not all) cases, ESUs will be composed of multiple independent populations. Note that under *current* conditions, a population need not be viable to be considered independent.

1.2 Processes creating population structure

Geographic and behavioral isolation are major drivers of population divergence (Mayr, 1993; Barlow, 1995). Anadromous salmonids have a strong propensity to return to their natal stream upon maturation (Candy and Beacham, 2000; Hard and Heard, 1999; Pascual and Quinn, 1995; Quinn and Fresh, 1984; Quinn et al., 1991), and this homing isolates breeding groups. Isolation of breeding groups allows adaptation to local environmental conditions, creating phenotypic divergence and further reinforcing isolation (Healey and Prince, 1995; Quinn et al., 2001). The behavior and life history of winter-run chinook salmon and spring-run chinook salmon, in combination with the structure of the Central Valley stream network, make these mechanisms especially strong in our study area.

The life history of spring-run chinook salmon allows for exploitation of high-elevation spawning and rearing habitats. To reach these habitats, chinook salmon must migrate during high flow periods in the spring— later in the summer and fall, stream flows are too low for fish to pass higher gradient reaches. Once spring-run chinook salmon reach elevations high enough to maintain suitably cool water temperatures, they hold over the summer in pools. When temperatures drop in the fall, they move out of the pools (sometimes back downstream) and spawn. The low stream flows during the fall spawning season prevent fall-run chinook salmon from spawning with spring-run chinook salmon. Furthermore, eggs and juveniles of spring-run chinook salmon experience cooler waters than fall-run chinook salmon, which delays maturation such that some (possibly large) fraction of the juveniles do not emigrate from high elevation rearing areas until a full year of life has passed.

Winter-run chinook salmon, like spring-run chinook salmon, used to spawn at high elevations, but were restricted to the spring-fed headwaters of the southern Cascades. Winter-run chinook salmon were reproductively isolated from sympatric populations of spring-run chinook salmon because of their different spawning times.

---

[1] The endangered Sacramento River winter-run chinook salmon, threatened Central Valley spring-run chinook salmon and threatened Central Valley steelhead.

[2] Steelhead population structure will be described in a separate document.

Historically, winter-run chinook salmon entered freshwater in the winter and reached headwater areas in the spring. Rather than hold over the summer, as spring-run chinook salmon do, winter-run chinook salmon spawn during the summer (which isolates them reproductively from sympatric spring-run chinook salmon populations). This strategy is only successful in spring-fed streams with adequate summer flows and relatively low water temperatures. Fry emerge from the gravel in the late summer, and begin emigrating from upriver areas as water temperatures become suitable in the fall, entering the ocean the following spring.

The high elevation spawning areas used by spring-run and winter-run chinook salmon are isolated from each other by large distances, and during the summer, by low flows and high temperatures. Our initial assumption, on the basis of the isolation of spawning groups in different tributaries, and in the absence of other information, is that major basins (i.e., tributaries to the Sacramento and San Joaquin rivers) historically supported at least one independent population, and that larger basins may have supported several independent populations. In the following section, we review various kinds of information that might allow us to refine this hypothesis.

2 Conceptual approach to identifying populations

As discussed in the preceding section, population structure arises through isolation of breeding groups and adaptation to local conditions, which further reduces their tendency to breed with other groups. Clues to population structure therefore come from information about the physical isolation of spawning groups, environmental differences between habitats used by spawning groups, and evidence of reproductive isolation in the form of phenotypic and genotypic differences between populations. In this section, we discuss in detail the types of information that might provide insight into the population structure of Pacific salmonids.

2.1 Geography

We expect that the internal structure of an ESU will be related to the geography of that ESU because salmon usually spawn in their natal streams. The amount of straying between basins is inversely related to the distance between the basins (Candy and Beacham, 2000; Hard and Heard, 1999; Pascual and Quinn, 1995; Quinn and Fresh, 1984; Quinn et al., 1991). Geographic analysis can therefore provide insight into the population structure of Central Valley winter-run and spring-run chinook salmon. In order to more carefully examine the hypothesis that major basins supported at least one independent population, we considered the distances between watersheds (as the fish swims) that historically supported spawning and rearing of spring-run chinook salmon (as reported by Yoshiyama et al. (1996)). In the absence of detailed information on the distribution of spawners for most streams, we identified the intersection of streams and the 500 m elevation contour line, assuming that most spring-run chinook salmon spawning and rearing occurred above this elevation (Yoshiyama et al., 1996).

In addition to the spatial arrangement of basins, the basin size provides some information on whether a basin could have supported an independent population. Population ecology theory tells us that, due to demographic and environmental stochasticity, populations below a critical minimum size are unlikely to persist without immigration (Goodman, 1987). Because carrying capacity is related to habitat area, it is therefore plausible that watersheds smaller than some critical size are unable to support independent populations of chinook salmon. Currens et al. (2002) found that in the Puget Sound, the smallest watershed containing an independent population of chinook salmon is the Nooksack River, with an area of 477 km^2. The largest watershed containing a single independent population is the upper Skagit River basin, with an area of 2600 km^2; larger watersheds contained at least two independent populations. The Puget Sound results are of limited utility for the Central Valley due to the significant environmental differences between the regions, but nonetheless, provide a standard for comparison.

2.2 Migration rates

The extent to which adults move between sites affects the degree of reproductive isolation and, therefore, demographic independence between sites. Migration rate can be estimated in two ways: direct observation based on mark-recapture, and indirect inference based on population genetics. Mark-recapture estimates depend on few assumptions, but migrants may not necessarily contribute equally to reproduction (Tallman and Healey, 1994), and the estimates might vary over time. Genetic approaches are sensitive only to successful reproduction and integrate over longer time scales, but are dependent on several assumptions that are frequently violated in real studies.

2.3 Genetic attributes

The existence of genetic differences between reasonably large and stable populations indicates that these populations are independent, because low rates of gene flow between populations will rapidly erase such differences. There are many considerations that should be kept in mind when interpreting the results of population genetics studies, and these are described in detail Appendix A.

2.4 Patterns of life history and phenotypic characteristics

Chinook salmon have a remarkably flexible life history and variable phenotypes, and much variation has been observed among populations (Adkison, 1995; Healey, 1994; Healey and Prince, 1995). Some of this among-population variability is heritable, presumably reflecting adaptation to local conditions (Healey and Prince, 1995; Quinn et al., 2000, 2001) (although genetic drift and phenotypic plasticity lead to differences among populations (Adkison, 1995)). Because local adaptation is easily overcome by immigration, phenotypic differences between populations indicate that the populations are independent of one another, or at least that the selective environments of the populations are different.

2.5 Environmental and habitat characteristics

The distribution of lotic organisms is determined in part by their adaptation to their physical habitat "template," which is in turn created by biogeoclimatic processes (Poff and Ward, 1990). The life history characteristics that promote survival under one template may preclude survival under another, if the other template exceeds the tolerance or behavioral range of the organism. Poff and Ward (1990) emphasize substratum, thermal regime and streamflow pattern as minimal representations of the physical habitat template. Streams that differ markedly in these attributes are more likely to harbor populations that are independent of one another, because gene flow would be selected against. Chinook salmon have flexible life histories that can be tuned by adaptation to local conditions, presumably leading to optimal timing of adult entry to freshwater, migration to spawning areas, spawning, emergence, migration to rearing habitat, and emigration to the sea (but all within the constraints of development). Figure 1 illustrates some of the complex interactions among environmental effects and salmon life history events.

There is relatively abundant information on various aspects of the environment inhabited by chinook salmon in the Central Valley. In this report, we examine floristic ecoregions, geology, elevation, stream flow (magnitude, seasonal patterns, and interannual variation), and air temperature (a proxy for water temperature). There are strong correlations among these variables, leading us to use principle components analysis (PCA) to reduce the dimensionality of the information. PCA results can be potentially helpful in identifying population groups sharing similar environments (especially if they form discrete clusters) and in quantifying the similarity of environments experienced by different putative independent populations.

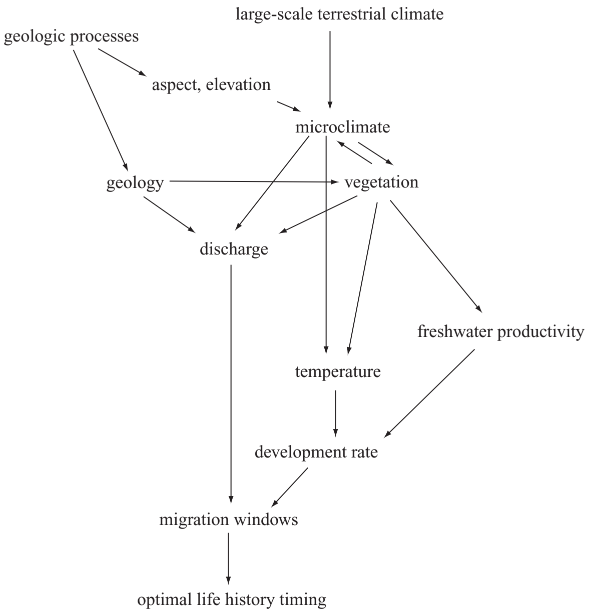

Figure 1. A simplified conceptual model of how aspects of the environment interact to influence the optimal timing of life history events such as spawning and juvenile emigration. Arrows indicate direct effects of one variable on another.

2.5.1 Ecoregional setting

Because the distribution of plants is controlled by climate, geology, and hydrology (among other factors), floristic regions are useful indicators of biogeography. Streams in different floristic ecoregions likely present chinook salmon with different selective environments, leading to local adaptation and reduction in gene flow between populations in different ecoregions.

2.5.2 Geology

Geology acts in several ways to determine characteristics of the environment faced by migrating and rearing salmon. Geologic processes determine many physical aspects of watersheds, including rock types, slope, aspect, and elevation. The interaction of these physical attributes with large-scale climate patterns determines the supply of water and sediments to stream channels on shorter time scales, and the nature of the stream channels themselves at longer timescales. We therefore expect that areas with different geological histories present salmonids with different selective regimes. However, geological attributes important to salmon habitats can be highly variable within as well as among different types of rock, depending on the extent of weathering and fracturing, particular chemical composition, and other factors.

2.5.3 Elevation

Except at extremes, elevation has little or no direct effect on organisms, but it strongly affects temperature and precipitation, and has been shown to be a primary determinant of ecological variability (Kratz et al., 1991). The elevation profile of a basin is therefore a useful proxy for streamflow and temperature. The effects of stream flow and temperature are discussed below.

2.5.4 Hydrography and thermal regime

By itself, stream flow variability has direct effects on stream-dwelling organisms as well as indirect effects on structural attributes of streams, and is therefore a useful indicator of environmental variability in lotic systems (Poff and Ward, 1989). Flow and temperature are often related in streams, and exert interacting effects on salmonids. The pattern of flow and temperature variation in rivers sets windows of opportunities for various stages of the salmonid life cycle, which combined with the developmental limits of salmonids, dictates when certain life history events and transitions must occur.

Fish that migrate to headwaters for spawning (e.g., Central Valley spring-run chinook salmon) tend to take advantage of high flows in the spring and summer while valley- floor spawners that migrate shorter distances tend to delay migration until after the peak flows (Healey, 1991). Adult upstream migration is thought to be blocked by temperatures above 21°C (McCullough, 1999), and temperatures below this level can stress fish, increasing their susceptibility to disease (Berman, 1990) and elevating their metabolism (Brett, 1979). The summer must be spent at high elevations to avoid negative impacts from high temperatures on egg viability (Hinze, 1959). Spawning can occur only when temperatures drop to acceptable levels (Murray and Beacham, 1987). The initiation of spawning is thought to be strongly influenced by temperature; spawning has been observed over a wide range of temperatures (2.2°C-18.9°C) but spawning of chinook salmon typically occurs below 13.9 °C (McCullough, 1999). Temperature controls the development rate of eggs in the gravel and the size of emerging alevins (Beer and Anderson, 1997; McCullough, 1999), and high temperatures reduce survival of eggs (Alderice and Velsen, 1978). Alevins must leave the gravel before scouring spring floods occur, or risk high rates of mortality (Montgomery et al., 1996; Beer and Anderson, 2001). Successful smolt emigration can occur only when temperatures are suitable (Brett, 1979). It is unlikely that chinook adapted to the hydrographic and thermal regime of a certain river can reproduce as effectively in a different stream with a substantially different regime.

Support for these ideas comes from comparing the results of model predictions and the observed pattern of adult migration and juvenile emergence in Mill Creek (Figure 2). Adults must move into the streams prior to the onset of high summer temperatures (> 21 °C) (Stage I in Figure 2). The adults hold over the summer either far upstream or in cool water refugia where the temperatures are below 16°C (Stage II in Figure 2). Cool water refugia are often several degrees cooler than the river temperature so fish might also hold over at lower elevations. If the fish are exposed to higher temperatures in this stage, high prespawning mortality is likely which can impact population productivity. Since temperatures above 14°C are generally lethal to the eggs, spawning should only begin below this level. We assume for illustration that spawning occurs between 12° and 14°C. Because isotherms move from high to low elevations in the autumn, the beginning of spawning can be protracted, beginning in August at the high elevations and in late October at low elevations (Stage III in Figure 2). However, as a result of the nonlinear relationship between egg development and temperature, the pattern of fry emergence with elevation does not necessarily match the pattern of spawning with elevation (Beer and Anderson, 2001). Because eggs deposited at lower elevations would experience higher incubation temperatures than eggs deposited at higher elevations, the low elevation fry could in fact emerge prior to high elevation fry that spawned two months earlier. The result is likely to protract the fry emergence period, with fish emerging at all elevations over the winter and spring. This is the pattern observed for spring-run chinook salmon in Mill, Deer and Butte creeks (Figure 24). A model-derived pattern of

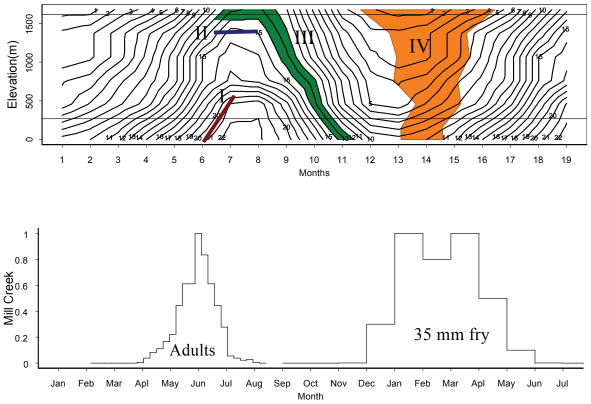

Figure 2. Effect of temperature on timing of spawning migration and fry emergence. Upper Panel shows the isotherm (°C) contours representative of northern Sierra Nevada streams. Line I depicts the thermal boundary for upstream adult migration. Line II depicts the thermally derived elevation where adults can safely hold prior to spawning, Area III depicts the 12 and 14°C isotherms, which are assumed to identify the spawning temperatures. IV depicts the resulting fry emergence distribution. Lower Panel: the relative upstream migrations of spring chinook adults and downstream migrations of 35 mm fry in Mill Creek.

emergence for fish spawning between 12° and 14°C is illustrated as Stage IV in Figure 2 using an egg development model (Beer and Anderson, 1997)[3]. Area IV depicts the fry emergence between maximum alevin weight and absorption of the yolk-sack. The observed patterns of adult immigration into Mill Creek in the spring and the downstream capture of their offspring as 35 mm fry eight months later (lower panel of Figure 2) comport with the modeled spawning and emergence pattern.

While there are reasonable flow data for Central Valley streams, water temperature data are not widely available. Studies have found that stream temperatures are closely related to air temperature. Langan et al. (2001) determined that the stream temperature from the Girnock burn in Scotland was 0.8°C warmer than the air temperature over a range 0° to 14°C. Mohseni et al. (1998) determined the air-water relationship from hundreds of streams could be described by an S-shaped function in which the river is warmer at air temperatures near freezing and is cooler than the air above 20°C. In between the extremes, water and air temperatures are essentially linearly related. Therefore, air temperature, in a linear function or S-function, can be used to estimate the water temperature and to a first approximation the water temperature is about equal to the air temperature. We therefore use the air temperature climatology to explore temporal and spatial variation in the thermal regimes at large scales.

2.6 Population dynamics

Abundance data can be used to explore the degree to which demographic trajectories of two groups of fish are independent of one another. All else being equal, the less correlated time series of abundance are between two groups of fish, the less likely they are to be part of the same population. Complicating the interpretation of correlations in abundance is the potentially confounding influence of correlated environmental variation. When groups of fish that are in close proximity are not correlated in abundance over time, it is likely that they are not linked demographically. The reverse is not always the case–when correlations in abundance between groups of fish are detected, more work is needed to rule out confounding sources of correlation.

2.7 Synthesis and decision making

2.7.1 Population groups

Other TRTs have identified groups of salmon within large (in the spatial sense) ESUs sharing common life history characteristics, environments, and genetics. It is assumed that conservation of the ESU depends on conservation of these groups becasue it is in these groups that significant gentic variation is contained. In the case of the Central Valley, such population groups might be defined largely on the basis of common environmental characteristics, because most populations are extirpated (making genetic analysis difficult) and run-timing differences were partitioned in the delineation of ESUs. We initially identified historical population groups through a qualitative analysis of geography, hydrography, and ecoregional information. The TRT quickly reached consensus on these groups, probably because the different types of information all seemed to point to the same conclusion. We performed a quantitative analysis (principle components analysis) of a wider suite of environmental information to check the reasonableness of the qualitative assessment.

2.7.2 Independent populations

The TRT followed a three-step process to identify independent populations:

1. identify watersheds that historically contained spawning groups of spring-run chinook salmon or winter-run chinook salmon.

---

[3] Available at http://www.cbr.washington.edu/egg_growth

2. group together watersheds within a critical dispersal distance (50 km) and in the same ecoregion to produce a list of hypothesized independent populations.

3. examine any other available data to test the population hypotheses.

3 Review of data

In the case of Central Valley spring-run chinook salmon and winter-run chinook salmon, we have at least some data on all of the above-described categories except direct estimates of migration rates among populations, although for many basins, only basic geographic and environmental information are available. In this section, we review the available data and discuss its implications for population structure. In the final sections of the report we list the independent populations of spring-run chinook salmon and winter-run chinook salmon and discuss how the data support the delineations.

3.1 Historical distribution

Yoshiyama et al. (1996) reviewed a variety of historical information, including reports by early fisheries scientists, journals of miners and explorers, and ethnographic sources, to reconstruct the historical distribution of spring-run chinook salmon and winter-run chinook salmon in the Central Valley. Plates 2 and 3 summarize this information. Spring-run chinook salmon appear to have occurred in all rivers with drainages reaching the crest of the Sierra Nevada (except for the Kern River) or southern Cascades, as well as some other streams draining the coast range and southern Klamath Mountains (Plate 2). With few exceptions, these watersheds have extensive areas above the 500 m elevation contour. Winter-run chinook salmon spawned only in the larger spring-fed streams of the southern Cascades region[4](Plate 3).

3.2 Geography

3.2.1 Distance among basins

We assume that most spawning of spring-run chinook salmon and winter-run chinook salmon occurred above 500 m elevation, and that the straying rate between spawning areas is inversely proportional to the distance along the streams separating the areas. Plate 4 shows the points where spring-run chinook salmon and winter-run chinook salmon streams cross the 500 m elevation contour. Figure 3 shows a neighbor-joining tree constructed from the distances among 500 m points. Distances to nearest neighbors among tributaries to San Joaquin and lower Sacramento rivers are longer than those of the upper Sacramento River.

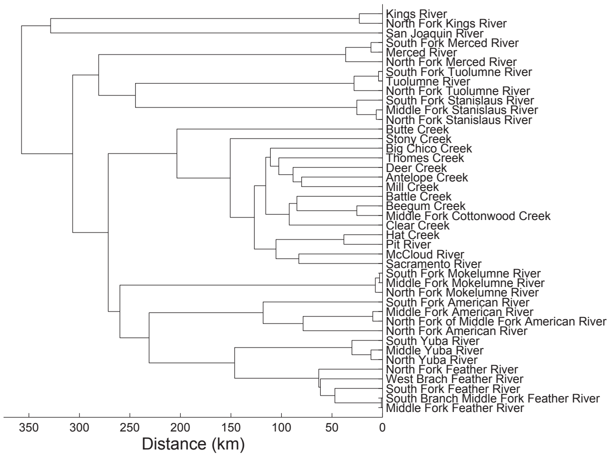

Figure 3. Neighbor-joining tree, based on distance along streams between 500 m elevation points, of watersheds that historically contained spring-run chinook salmon.

If distance between areas was the only information available, populations can be identified from Figure 3 by examining the population groups that form below a critical migration distance (x_c). Following the Interior Columbia Basin Technical Recovery Team (2003) and Quinn and Fresh (1984), we set x_c to 50 km, beyond which populations are probably independent. Other values of x_c might be reasonable, so we examined the sensitivity of the results to different values of x_c (Figure 4). The number of populations identified declines roughly exponentially with increasing x_c.

3.2.2 Basin size

Figure 5 shows the size of all basins in the Central Valley that historically supported spawning of spring- and winter-run chinook salmon, according to Yoshiyama et al. (1996). Of watersheds with extant spring-run chinook salmon spawning groups, Butte Creek is the largest at over 2000 km^2, although much of this area is of very low elevation. Deer and Mill creeks are 563 km^2 and 342 km^2, respectively. If we assume that the Puget Sound chinook salmon results (Currens et al., 2002) are roughly applica-

---

[4] CDFG suggested in several memos to their files (cited in Yoshiyama et al. (1996)) that winter-run chinook salmon were found in the Calaveras River, but given the lack of suitable spawning and rearing habitat in this low-elevation, rain-driven basin, it is most likely that the fish observed in the winter in the Calaveras were late-fall-run chinook salmon (Yoshiyama et al,1996).

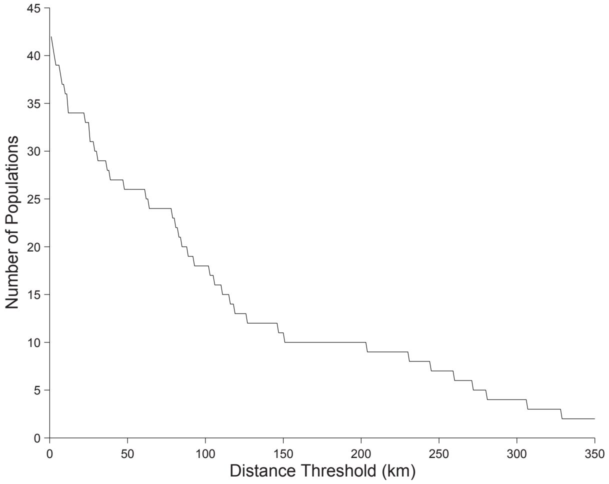

Figure 4. The number of population groups separated by dispersal distances. Distance measure is distance between 500 m elevation along the stream route.

ble to the Central Valley, then most river basins identified in Plate 2 contained at least one independent population, and most of the larger basins (e.g., Feather, American, Yuba, Stanislaus, Merced, Tuolumne, middle-upper San Joaquin rivers) may have contained two or more. As a rule of thumb, we assumed watersheds with an area > 500 km^2 to be capable of supporting independent populations, if other environmental attributes seemed suitable (especially the magnitude and variability of summer flow).

Other proxies for habitat area are available. Spring-run chinook salmon spawners are more directly limited by the amount of cool-water holding and spawning habitat than watershed area (although these measures are roughly correlated in the Central Valley). Cool-water habitat might be better measured by mean annual discharge or by the amount of high-elevation habitat. Figure 6 shows the relationship between elevation and area for watersheds that historically contained spring-run chinook salmon. Figure 7 shows the mean annual discharge rate for streams that historically supported spring-run chinook salmon or winter-run chinook salmon.

3.3 Population genetics

In this subsection we discuss the principle refereed papers and agency reports that provide molecular genetic data on Central Valley chinook salmon populations. Earlier works are cited in some of these papers. The results are structured by data type. Subsequently, we present a synthesis of these results and discuss their implications for the via-

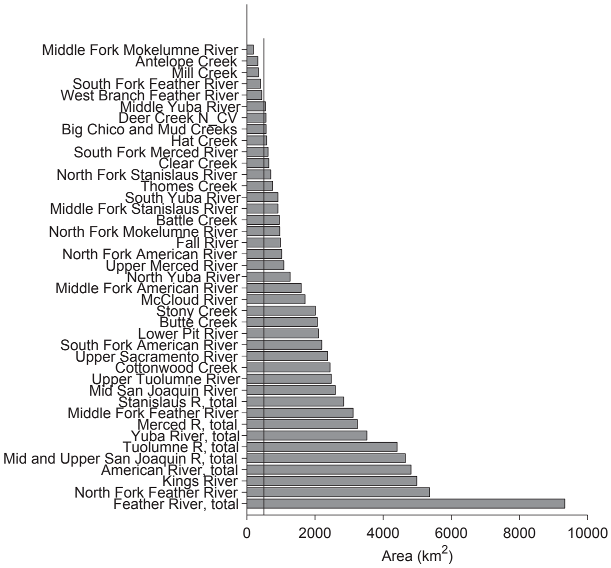

Figure 5. Area of Sacramento-San Joaquin watersheds that currently or historically contained spawning groups of spring-run chinook salmon, according to Yoshiyama et al. (1996). The vertical line marks 500 km^2.

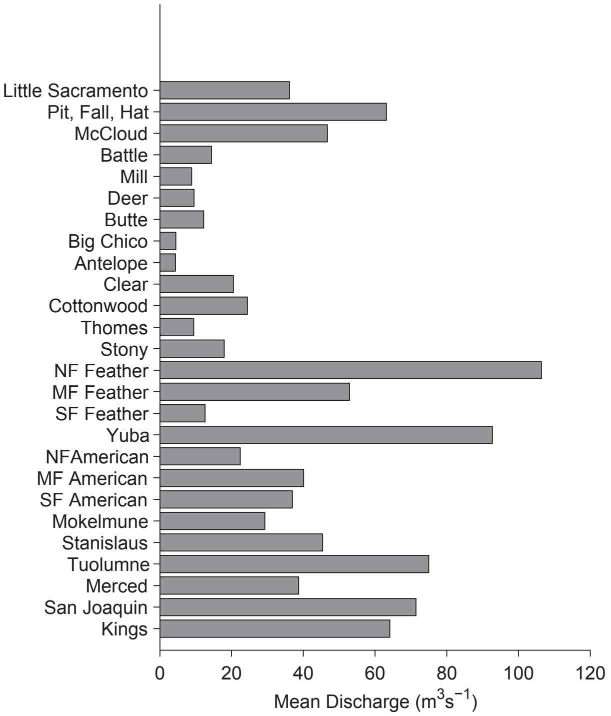

Figure 7. Mean annual discharge rate of Central Valley watersheds historically known to contain spring-run chinook salmon or winter-run chinook salmon.

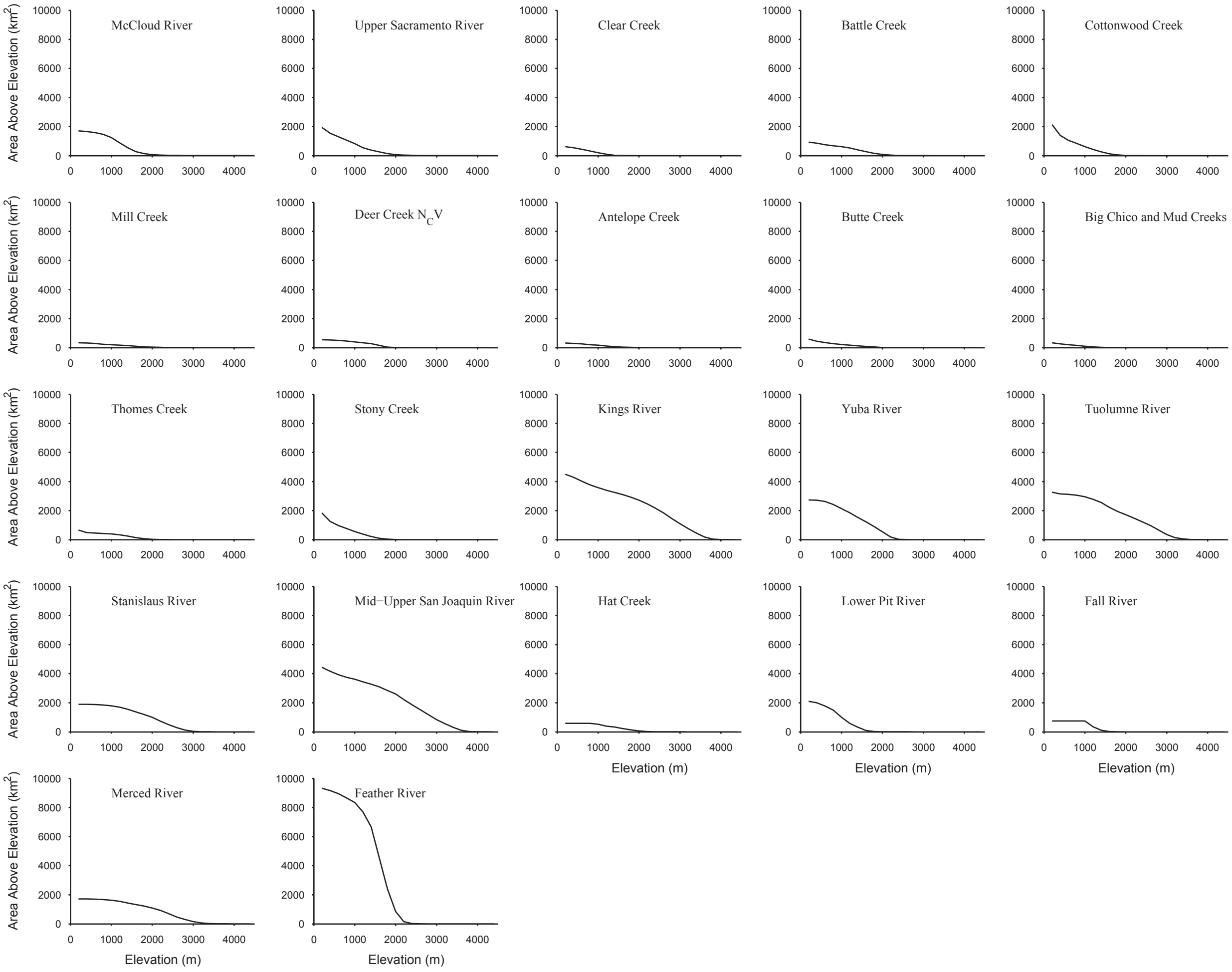

Figure 6. Area-elevation relationships of Central Valley watersheds historically known to contain spring-run chinook salmon or winter-run chinook salmon.

bility of Central Valley chinook salmon. See Appendix A for background information on population genetics.

3.3.1 Allozyme studies

Waples et al. (2004) examined patterns of genetic and life history diversity in 118 chinook salmon populations from British Columbia to California. The genetic data were derived from variation at 32 polymorphic allozyme loci. This comprehensive survey included 10 samples from the Central Valley representing fall, late-fall, spring, and winter runs. A salient feature of this study was that all Central Valley populations constituted a single taxonomic entity genetically distinct from all other populations, including those geographically proximate along the coast or in the Klamath/Trinity drainage (see Figures 8 and 9). This result indicates a more recent derivation of life history forms within the Central Valley or a greater recent gene flow rate among the Central Valley run types. Similar separation of Central Valley chinook from coastal populations was shown by Gall et al. (1991) using 47 polymorphic loci. An extension of the Waples et al. (2004) dataset has been used to show relationships among Central Valley chinook (Figure 10)[5]. Fall, late-fall, and Feather River spring-run chinook salmon formed one cluster, as did winter-run fish. Allele frequencies in Spring-run chinook salmon from Deer Creek, Butte Creek, Feather River hatchery, and Yuba River were not significantly different from each other.

3.3.2 Major histocompatibility complex (MHC) genes

Kim et al. (1999) describe results for MHC Class II exon variation among nine samples of spawning adults drawn from the Sacramento River (winter run (1991, N=18; 1992, N=27; 1993, N=9; 1994, N=23; 1995, N=33), spring run from the main stem (1995, N=13), spring run from Butte creek (1995, N=13), fall run (1993, N=19), and late fall run (1995, N=20)). The fish were taken at either the Red Bluff diversion dam or the Keswick dam. Four alleles were observed to be segregating at this locus. Figure 11 is a phenogram based on neighbor joining of Nei's genetic distance. The figure reveals the relationships among the samples with main clusters of winter-run chinook salmon samples, fall- and late-fall-run chinook salmon, and the spring-run chinook salmon samples. While the 1991 through 1994 winter-run chinook salmon samples show a high degree of temporal stability, the 1995 sample does not. The authors argue that this sample may have some admixture with spring-run chinook salmon. The limited number of populations sampled and the use of a single locus would urge some caution in drawing strong conclusions from these data.

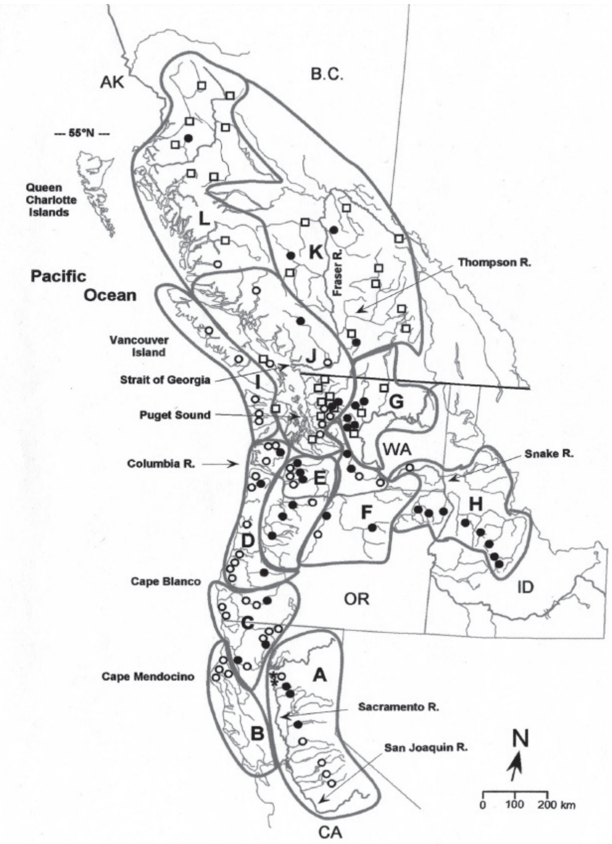

Figure 8. Populations sampled for genetic and life history data in Waples et al. (2004). Populations are coded by adult run time: closed circle = spring; open square = summer; open circle = fall; asterisk = winter. Twelve geographical provinces (A-L) used in the analysis of genetic and life history data are outlined in bold.

3.3.3 Microsatellites

Banks et al. (2000) used 10 microsatellite loci to examine the distribution of genetic variation within and among 41 wild and hatchery populations of Central Valley chinook salmon from 1991 to 1997, including representatives of winter, spring, fall and late fall runs. The number of loci examined in each of the 41 populations ranged from five to 10 loci. After initial genotyping of all individuals they adjusted their data sets in three ways. First, individuals were removed from the data set if they were missing one of five loci or two of eight or nine loci. Second, the four

---

[5] D. Teel, NWFSC, Seattle, WA, unpublished data.

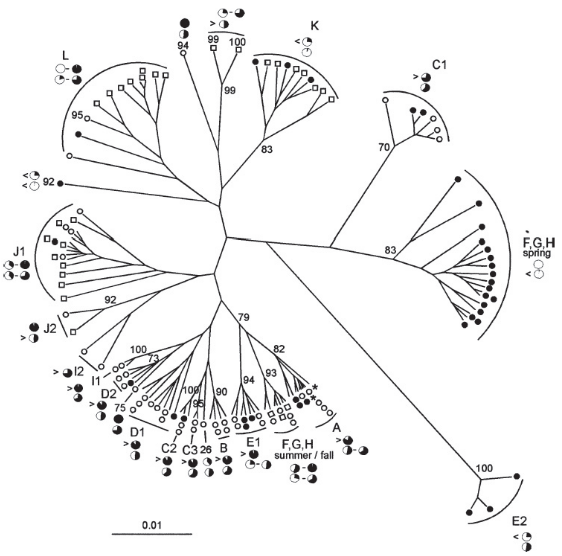

Figure 9. UPGMA phenogram of genetic distances (Cavalli-Sforza and Edwards) among 118 chinook salmon populations. Bold letters and numbers indicate provinces and areas, respectively, identified in Figure 8. Population symbols indicate adult run timing: closed circle = spring; open square = summer; open circle = fall; asterisk = winter. Genetic outliers (populations not closely affiliated with other nearby populations) are identified by their population identification number next to their symbol. Pie diagrams show the range of other life history trait values (upper: percent subyearling smolts; lower: marine harvest rate). Numbers at branch points indicate bootstrap support > 70%. Strong bootstrap support also exists for branch points within some labeled clusters but is not shown. From Waples et al. (2004).

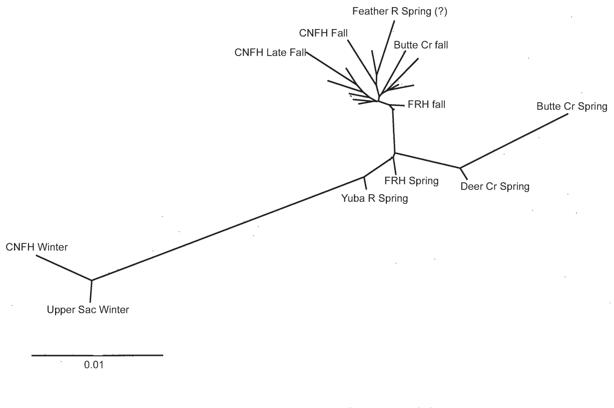

Figure 10. Neighbor joining tree (Cavalli-Sforza and Edwards chord distances) for Central Valley chinook populations, based on 24 polymorphic allozyme loci (unpublished data from D. Teel, NWFSC). Unlabeled branches are various fall-run chinook populations. CNFH = Coleman National Fish Hatchery; FRH = Feather River hatchery.

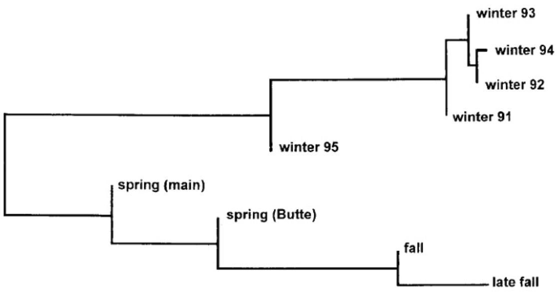

Figure 11. Phenogram based on Nei's genetic distance (D) demonstrating the relationships of Central Valley chinook runs.

populations from Butte, Mill, and Deer that involved juveniles were adjusted for apparent relatedness of individual genotypes. This procedure involved determining apparent full siblings and replacing them with putative parental genotypes. Third, winter run samples from 1991 through 1995 were determined to be admixtures of winter run and spring run. The suspect individuals were removed from the data set. After these adjustments were made, sample sizes varied from 11 to 144 with a mean of 64 individuals per population. An unweighted pair group method with arithmetic mean (UPGMA) dendrogram based on Cavalli-Sforza and Edwards chord distances from five loci showing the relationships of the 41 populations is shown in Figure 12. Four principle groupings are shown, winter run, Mill and Deer creek spring run, Butte creek spring run, and fall and late-fall. The three collections over two years of Upper Sacramento late fall run fish cluster closest to each other suggesting that they may constitute a distinct lineage.

While allele frequencies of spring-run chinook salmon in Deer, Mill, and Butte creeks appear statistically different from fall, late-fall, or winter-run populations, spring-run chinook salmon in the Feather and Yuba were not shown to be differentiated from fall-run chinook salmon by the allozyme data from Teel et al. (unpublished data) or the microsatellite data in Banks et al. (2000). A more detailed examination of putative spring-run chinook salmon adults using 12 microsatellite loci was conducted by Hedgecock (2002). Putative spring run hatchery samples from 1994, 1995, 1996 and 1999 and wild fish from 1996 and 2000 in the Feather were compared to Feather River fall run hatchery fish from 1995 and 1996, wild fish from Butte and Deer creeks, and a composite fall run sample from multiple locations. Eleven of fifteen pairwise comparisons among putative Feather River spring run samples were not significantly different from zero where only one

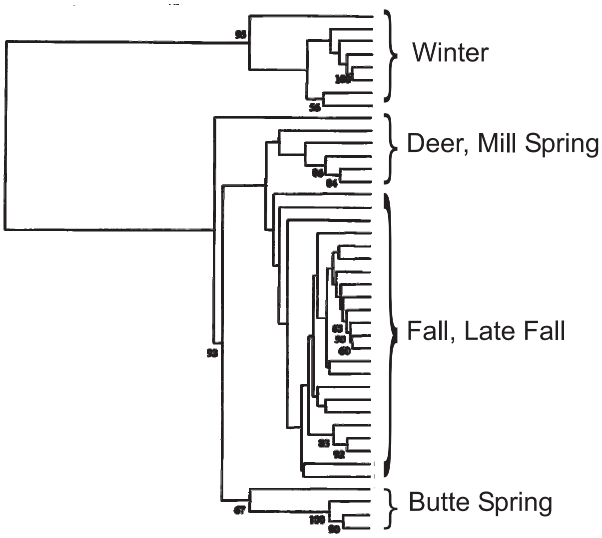

Figure 12. UPGMA dendrogram of Cavalli-Sforza and Edwards chord distances based on 5 microsatellite loci. Numbers at branch points indicate bootstrap percentages. Figure adapted from Banks et al. (2000).

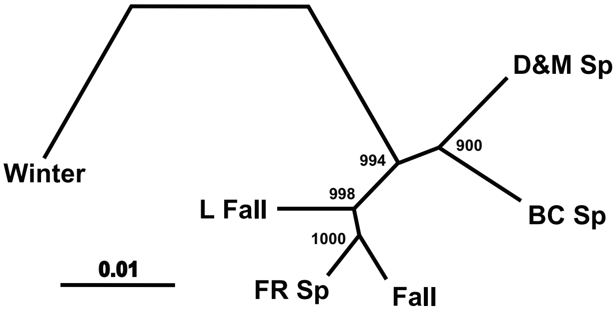

Figure 13. Neighbor joining tree (Cavalli-Sforza and Edwards chord distances) for Central Valley chinook populations, based on 12 microsatellite loci. D&M = Deer and Mill Creek; BC = Butte Creek; FR = Feather River; Sp= spring chinook; L Fall = late-fall chinook; Winter = winter-run chinook salmon. The tree was constructed using Cavalli-Sforza and Edwards measure of genetic distance and the unweighted pair-group method arithmetic averaging. The numbers at branch points indicate the number of times that these neighbors were joined together in 1000 bootstrap samples.

of twelve pairwise comparisons of these six samples with the two Feather River hatchery samples were not significantly different from zero. It should be pointed out that all but one of these twelve pairwise comparisons have F_{ST} values less than 0.01 (i.e., they are very similar). Also, the 1995 fall run hatchery sample is significantly different from the composite fall run sample and the F_{ST} for this comparison exceeds that for nine of the twelve comparisons between putative spring run and fall run samples within the Feather River. This latter point underscores how tenuous the significance levels are in these comparisons. That being said, all of these putative spring-run samples in the Feather River show a very close genetic similarity with the fall-run fish and little similarity to spring-run fish from Butte, Mill, or Deer creeks. In fact tagging studies of hatchery fish in the Feather River hatchery show that progeny from spring- and fall-run matings can return at either time and progeny from fall-run matings have been used in subsequent spring-run matings and vice versa (California Department of Fish and Game, 1998). Hedgecock (2002) show an UPGMA tree that combines related populations into six major groupings of Central Valley chinook salmon (Figure 13).

Williamson and May (2003) developed new microsatellite markers with more alleles per locus than those used previously in the Central Valley and used them to look for differences between fall-run chinook salmon from the Sacramento basin and fall-run chinook salmon from the San Joaquin basin. They used seven loci to examine variation within and among spawning adults from 23 samplings across three years, including four hatcheries and nine natural spawning populations. Seventeen to 75 alleles per locus were found supporting the view that a large amount of variation is present within these populations. However, limited differentiation was observed among the populations, far less than observed for chinook salmon in other regions of north America.

3.3.4 mtDNA

Nielsen et al. (1997) present data on the distribution of seven mitochondrial haplotypes among fall (nine locations, 479 individuals), late-fall (two locations, 56 individuals), spring (two locations, 113 individuals), and winter (one location, 46 individuals) runs of chinook salmon from 1992-1995. Fall- and late-fall-run fish revealed one rare and four common haplotypes. Of the four common haplotypes in fall-run fish, three were found in spring-run fish and only one in winter-run fish. The missing haplotype in the spring-run fish is the least common among the fall- and late-fall-run fish. Winter-run fish showed one rare haplotype as well. Nielsen et al. (1997) question whether several of the samples (1994 Deer Creek and both Butte Creek samples) were actually spring-run fish. If not, then the spring run may only possess two of the common fall and late-fall haplotypes. These results support the view of winter-run fish being differentiated from the other runs, and that Deer Creek spring-run chinook salmon are genetically distinct from spring-run chinook salmon in Butte Creek and the Feather River.

3.3.5 Synthesis and conclusions

How are we to interpret the above results? Each of the described studies suffers from various weaknesses in experimental design and violates several of the assumptions discussed in Appendix A. One common theme among many of the studies is probable violation of the sampling accuracy assumption. Whenever a juvenile sample is taken, there is the possibility of overlap of some run types and an overrepresentation of only a few families. Samples taken at weirs and fish ladders may represent multiple spawning populations. It is also doubtful that today's distribution of genetic variation within and among extant populations of chinook salmon in the Central Valley is very similar to the distribution 50, let alone 200, years ago. Nevertheless, a synthesis of the extant genetic data reveals the following picture.

1. Central Valley chinook salmon, including all run types, represent a separate lineage from other chinook salmon, specifically from California coastal chinook salmon (Waples et al., 2004).

2. Within the Central Valley and its currently available natural spawning habitat and hatcheries, there are four principle groupings that might form the basis of separate meta-population structures: (1) all winter-run chinook salmon, (2) Butte Creek spring-run chinook salmon, (3) Deer and Mill Creek spring-run chinook salmon, and (4) fall-, late-fall-, and Feather/Yuba spring-run chinook. The fourth group is represented by at least a dozen discrete spawning areas (i.e., major rivers). The first three groups are perilously close to extirpation since the first group (winter-run chinook salmon) is represented by only a single natural population and one hatchery population, the second (Butte Creek spring-run chinook salmon) is supported by a single spawning area and the third (Deer and Mill creek spring-run chinook salmon) is represented by just two discrete spawning areas. The data in Banks et al. (2000) suggest that the late fall run represents a fifth lineage.

3. Fall-run chinook salmon populations and spring-run chinook salmon in the Feather and Yuba rivers are very similar genetically to each other, probably because of the extensive movement of eggs among facilities and smolts to downstream areas (Williamson and May (2003), Teel, unpublished data; Hedgecock (2002)). This movement has included trucking of smolts downstream and transport of eggs from one hatchery to another. While the phenotype for early entrance into freshwater still persists in the Yuba and Feather rivers, the mixing of gametes of these fish with fall run fish has almost certainly led to homogenization of these runs. The genetic results from Hedgecock (2002), the existence of springtime freshwater entry, and the possible segregational natural spawning of spring-run fish in the Feather River system suggest that rescue of a spring run in the Feather may be possible, even though there has been extensive introgression of the fall run gene pool into that of the spring run. Further, the capacity of salmonid fishes to rapidly establish different run timings may make reestablishing discrete temporal runs in rivers possible if separate spawning habitats can be made available. It is doubtful that this phenotype will persist without immediate and direct intervention to preserve the genetic basis of spring run timing.

4. No data exist and therefore no conclusions are available for spring-run chinook salmon that exist in Big Chico, Antelope, Clear, Thomes, and Beegum creeks.

3.4 Life history diversity

While CDFG has recently been collecting life history information on spring-run chinook salmon in Mill, Deer and Butte creeks, limitations in the sampling prevent assessment of whether there are significant differences among spring-run chinook salmon in these streams. Interested readers can go to Appendix B, which summarizes the available data.

3.5 Population dynamics

Time series of population abundance are available only for the extant spring-run chinook salmon spawning groups in Butte, Deer and Mill creeks and the Feather River. Given the strong genetic divergence of Butte Creek spring-run chinook salmon from the Mill and Deer groups, and the close relationship of Feather River spring-run chinook salmon to Feather River fall chinook, the main question is whether Mill Creek and Deer Creek form a single population.

Inspection of the time series of spawner abundance (Figure 14) shows that spring-run chinook salmon in Deer and Mill creeks have had roughly similar patterns of abundance, with relatively high abundance in the late 1950s and 1970s (not shown), and a recent upturn in abundance

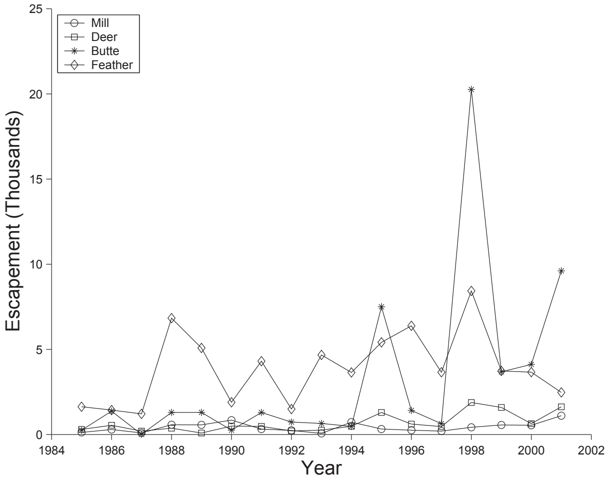

Figure 14. Estimated escapement of spring-run chinook in Mill, Deer, Butte creeks and the Feather River.

in beginning in the late 1990s. Big Chico creek has shown a similar pattern, but the extended periods of no spawners indicates that this is not an independent population. Butte Creek also had peaks of abundance around 1960, but abundance was low throughout the 1970s and the recent increase in abundance has been much larger than in the other streams. A major caveat in interpreting the spring-run chinook salmon spawning escapement data is that population estimation techniques were not standardized until the 1990s.

The population dynamics of Mill and Deer creeks can be compared quantitatively in several ways. The simplest way is to compare estimates of the parameters that describe the population time series. The simplest model that can capture the observed dynamics is the random-walk-with-drift (RWWD) model (Dennis et al., 1991). In the RWWD model, population dynamics are governed by exponential growth (drift) with random variation (the random walk). Measurement error in the population estimates can be accounted for by recasting the RWWD model as a state-space model (Lindley, 2003), which reduces the bias in estimates of the process error variation. Table 1 shows the parameter estimates of the state-space RWWD model when applied to the spawner escapement data. Parameter estimates for both populations are similar, with broadly overlapping probability intervals for parameter estimates.

A potentially more informative approach is to fit models that describe various levels of interaction among populations, and evaluate the relative performance of the models with some metric, such as Akaike's information criterion (AIC) (Burnham and Anderson, 1998). We fit three models: the simple RWWD model where Mill Creek and Deer Creek are independent, a model where there is no migration between the populations but there is correlation in the environment (expressed as covariation in the process variation), and a model where migration is allowed between the populations. The models are described in more detail in Appendix C.

The best model, in terms of AIC, is the model with no migration and uncorrelated process variation. The other models do fit the data slightly better, but not enough to justify their additional parameters. The model with correlated errors is not very compelling— AIC is higher and the estimate of the covariance is biologically insignificant. The migration model is more compelling— while it had the highest AIC (and was thus the least supported by the data), the estimates for migration rates were biologically significant, with a little more than half of the probability mass below the 0.10 migration rate thought to indicate demographic dependence (McElhany et al., 2000). In summary, the population trends in Mill and Deer creeks suggest that these populations have independent dynamics, although the evidence for independence from this analysis of population dynamics is not overwhelming.

3.6 Environmental characteristics

3.6.1 Ecoregional setting

The Sacramento-San Joaquin basin spans several major floristic ecoregions (as defined by Hickman (1993)), including the Great Central Valley, the Sierra Nevada, the southern Cascades, northwestern California, and the Modoc Plateau (Plate 5). Spring-run chinook salmon pass through the alluvial plains of the Great Valley during their migrations to and from the ocean. Spring-run chinook salmon spawning and rearing occurred mainly in the southern Cascades and the Sierra Nevada ecoregions, with some populations using basins in the Modoc plateau and northwestern California ecoregions.

3.6.2 Hydrographic variation

Precipitation generally declines from north to south along the Central Valley, but orographic effects are an extremely important source of variation in precipitation[6] (Plate 6). West-facing, high-elevation basins generally receive more total precipitation and more precipitation as snow. The basins draining into the Sacramento River are generally

---

[6] Precipitation climatology data obtained from The Climate Source Inc., Corvallis, OR.

Table 1. Parameter estimates for random-walk-with-drift model. Numbers in parentheses are 90% central probability intervals.

Stream	population growth rate	variance of growth rate
Deer Creek	0.112 (-0.097, 0.307)	0.346 (0.122, 0.699)
Mill Creek	0.042 (-0.200, 0.273)	0.439 (0.197, 0.730)

lower in elevation than those draining into the San Joaquin, and are more driven by rainfall than the snow-melt driven San Joaquin basin streams. Stream discharge is further influenced by the geology of the basin (shown in Plate 7). Highly fractured basalts and lavas found more commonly in the southern Cascades can store water and release it through springs, dampening variation in discharge and maintaining relatively high and cool flows during summer months.

Spring-run chinook salmon evolved in the pre-dam period, and we must therefore examine the unimpaired[7] hydrography of the Central Valley to understand how hydrographic variation might have driven population differentiation. Fortunately for the Central Valley TRT, the U. S. Army Corps of Engineers and State of California Reclamation Board estimated the unimpaired hydrography of the Central Valley as part of a comprehensive study of Central Valley hydrography (USACOE, 2002). As described by California Department of Water Resources (CDWR) (1994), "unimpaired" flow (the flow that would have occurred if dams and major diversions were not in place) was computed from various flow gauges. Prehistoric conditions were probably somewhat different, since other anthropogenic factors also influence flow, and these were not accounted for the in the calculation of unimpaired flow. Such effects include consumptive use of water by riparian vegetation that is no longer present, reduced groundwater accretion due to groundwater withdrawals, the effects of floodplains that are no longer connected to channels, and the episodic outflow from the Tulare Lake basin.

Figure 15 shows the mean monthly unimpaired discharge for 28 hydrologic units, and Figure 16 shows the month of peak discharge for these same units. In general, Sacramento River tributaries draining lower elevation basins of the southern Cascades (e.g., Sacramento Valley eastside tributaries such as Mill, Deer and Butte creeks) have peak discharges in February, and Sacramento and San Joaquin tributaries draining high elevation basins in the Sierra Nevada (e.g., Feather, Yuba, Tuolumne rivers) have peak discharges in May. Tributaries to the Sacramento arising in the Cascades ("Sac. Valley E. Side Streams" and "Sac. R. Near Red Bluff" in Figure 15) maintain relatively high flows with low interannual variability over the late summer compared to streams that historically supported spring-run chinook salmon in the southern Sierra (e.g., Stanislaus River).

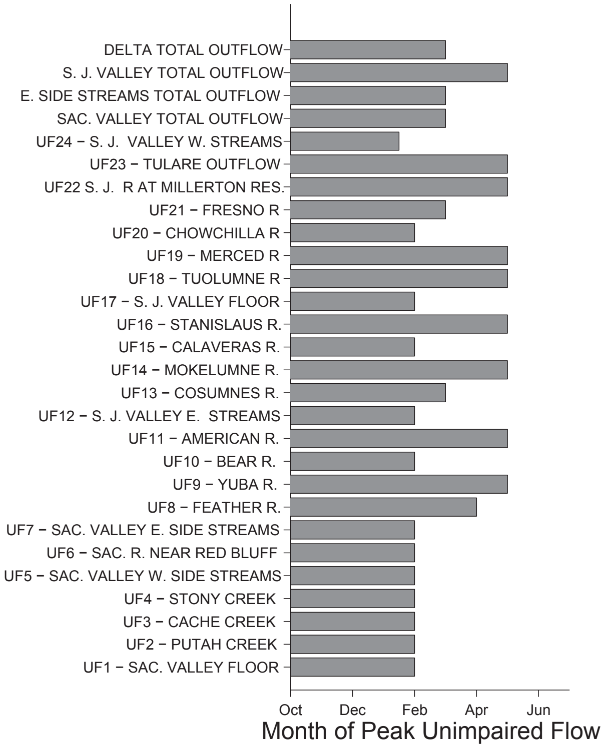

Figure 16. Month of peak discharge for the Sacramento and San Joaquin rivers and assorted tributaries, prior to development of on-stream reservoirs.

3.6.3 Thermal variation

There are some major differences in thermal regime among Central Valley subbasins. Plate 8 shows the average high air temperature in August in the Sacramento-San Joaquin basin, Plate 9 shows the average low temperature in January, and Plate 10 shows the range between

---

[7] "Unimpaired" in the sense of USACOE (2002).

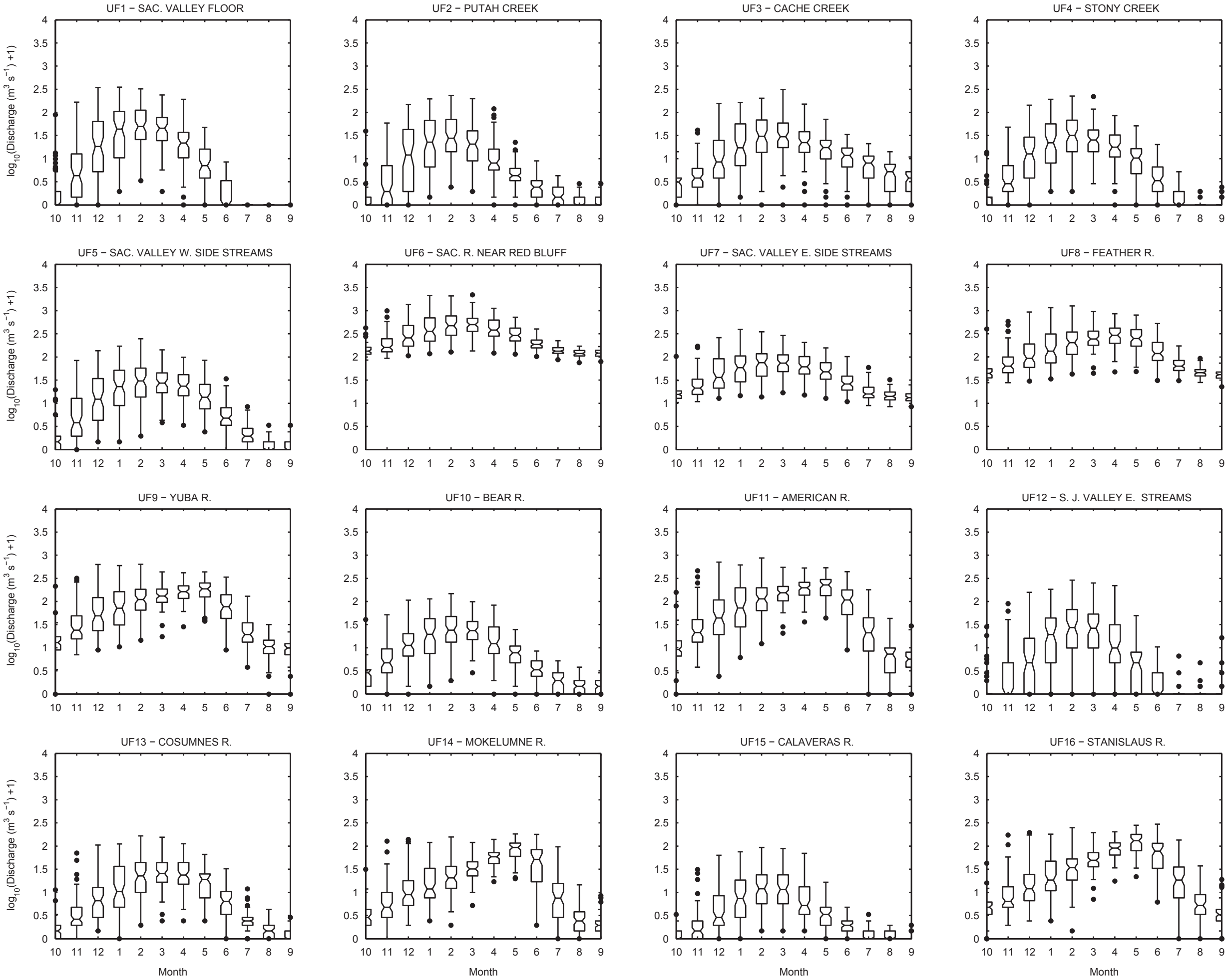

Figure 15. Estimated monthly discharge of the Sacramento and San Joaquin rivers and assorted tributaries, prior to development of on-stream reservoirs. Center of notch indicates median; notch represents standard error of median; box covers interquartile range; whiskers cover 1.5 × interquartile range; outliers are represented by dots. Year of record is water year, 1 October-30 September, and discharge is $\log_e \mathrm{m}^3\mathrm{s}^{-1}$.

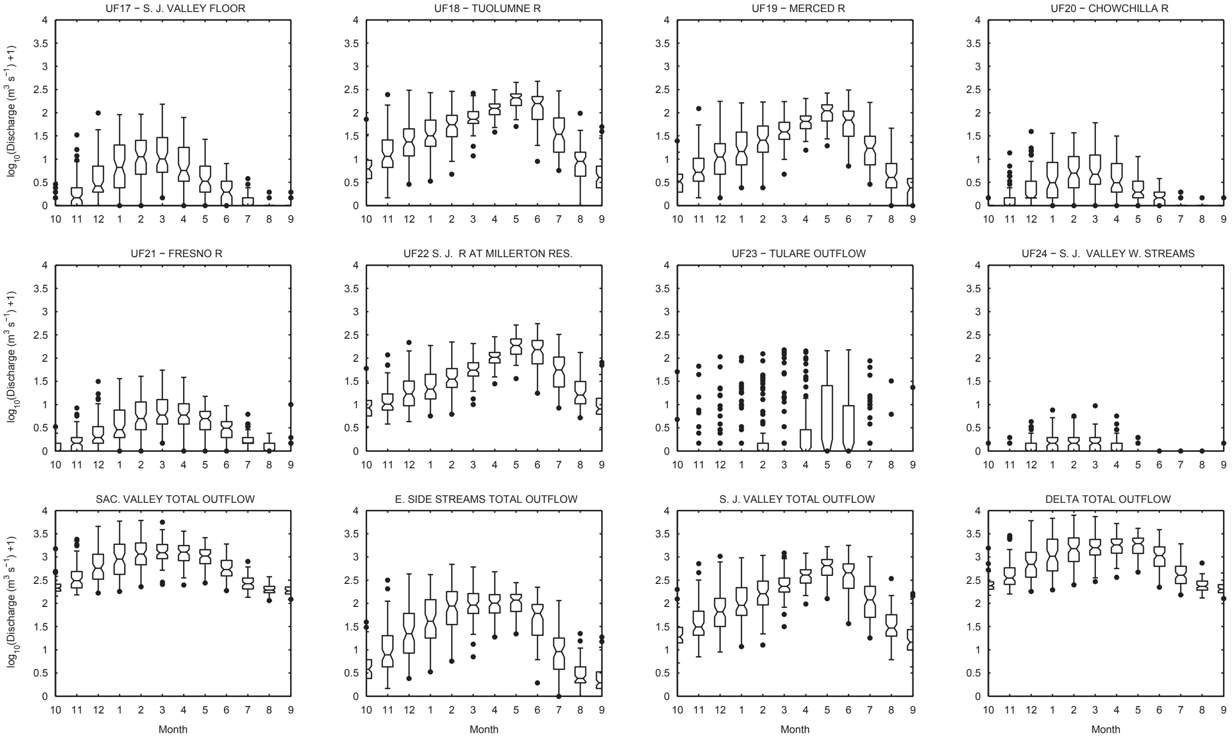

Figure 15. Continued. Estimated monthly discharge of the Sacramento and San Joaquin rivers and assorted tributaries, prior to development of on-stream reservoirs. Center of notch indicates median; notch represents standard error of median; box covers interquartile range; whiskers cover 1.5 × interquartile range; outliers are represented by dots. Year of record is water year, 1 October-30 September, and discharge is $\log_e \mathrm{m}^3\mathrm{s}^{-1}$.

these values[8]. Not surprisingly, temperature decreases with increasing elevation and latitude. Among drainages that historically supported spring-run chinook salmon, the Feather and Pit drainages stand out as being particularly warm in summer and highly variable over the year. This contrasts with the central and southern Sierra drainages, which are cool in the summer and show minimal seasonal variation.

3.7 Synthesis of environmental information

We conducted a principle components analysis of the environmental data described above to see how watersheds relate to each other in multivariate space and to identify common patterns of variation. The analysis is described in detail in Appendix D; the most important results are presented here.

The first two principle components, describing 55% of the variance, strongly delineate the upper Sacramento basins (southern Cascades and Coast Range drainages) from the lower Sacramento-San Joaquin basins (Sierra Nevada drainages), largely on the basis of their different geology, ecoregion, timing of peak flow, elevation, and temperature (Figure 17). The PCA does not reveal a strong split between northern and southern Sierra drainages, but with the exception of Butte Creek, the southern Cascades and Coast Range basins are well-separated. Butte Creek clusters with Coast Range streams due to its relatively low altitude and warm temperature. Some pairs of watersheds group very closely together in both the multivariate space defined by the PCA and actual geographic space, including Mill-Deer, Pit-McCloud, North and Middle Fork Feather, North and Middle Fork American, and Mokelumne-Stanislaus.

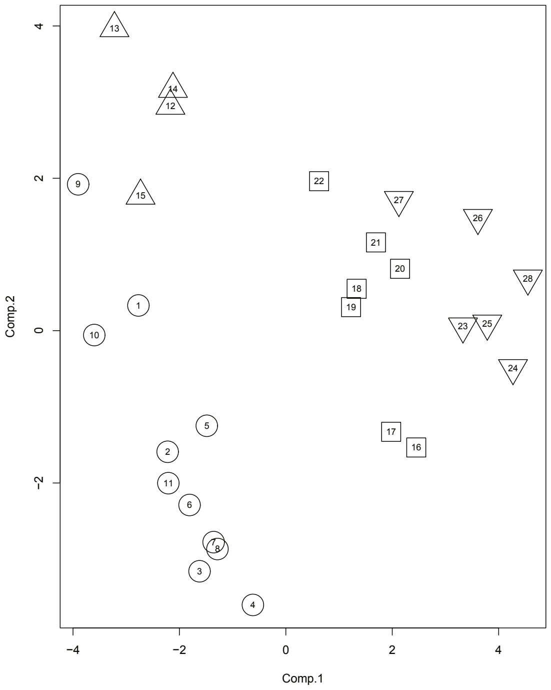

Figure 17. Principle components analysis of environmental attributes. Symbols denote regions: ◯–Southern Cascades; □–Northern Sierra; △– Coast range; ▽– Southern Sierra. Numbers indicate stream: 1–Upper Sacramento; 2–Lower Pit; 3–Fall; 4–Hat; 5–McCloud; 6–Battle; 7–Mill; 8–Deer; 9–Butte; 10–Big Chico; 11–Antelope; 12–Clear; 13–Cottonwood; 14–Thomes; 15–Stony; 16–NF Feather; 17–MF Feather 18–SF Feather; 19–WB Feather; 20–Yuba; 21–N&MF American; 22–SF American; 23–Mokelumne; 24–Stanislaus; 25–Tuolumne; 26–Merced; 27–San Joaquin; 28–Kings.

4 Structure of the Central Valley spring-run chinook ESU

In this section, we describe the structure of the Central Valley spring-run chinook salmon ESU in terms of geographic groups, independent populations, and dependent populations. Although there are differences in physical habitat among streams within the groups there are also general similarities regarding climate, topography and geology that make them useful categories for discussion of the spatial structure of Central Valley spring-run chinook. These groups should be considered in the assessment of ESU-level viability, because spatial diversity is directly related to these units, and genetic diversity is likely to be so as well.

4.1 Population groups

We initially delineated population groups on the basis of geography as defined by mountain ranges (Coast Range, southern Cascades, northern Sierra and southern Sierra) and associated thermal and hydrographic conditions (Figure 18). The geographically-based grouping is well-supported by the PCA results (Figure 17). We retained the split between the northern and southern Sierra because these basins drain into different major rivers and because although they did not form well-separated groups in multivariate space, the groups did not overlap.

---

[8] Temperature climatology data obtained from The Climate Source Inc., Corvallis, OR

The geology, elevation and aspect of the basins in the different groups causes hydrology to vary among the regions. Streams in the southern Cascades group are influenced by springs that maintain relatively high summer flows and lower interannual variability in summer flow. The Coast Range group encompasses streams that enter the Sacramento River from the west. These streams originate in the rain shadow of the coast range, and appear to be marginally suitable for spring-run chinook salmon under current climate conditions. These streams are strongly influenced by rainfall, with relatively small annual discharge and high interannual variability. The northern Sierra group is composed of the Feather and American River drainages, which are tributaries to the Sacramento with high annual discharge and predominately granitic geologies. Rivers in the southern Sierra group drain into the San Joaquin River (or directly into the delta, in the case of the Mokelumne River), and have hydrologies dominated by snowmelt.

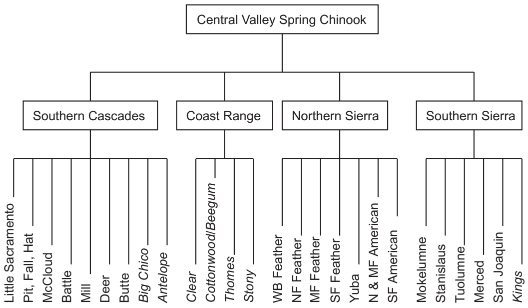

Figure 18. Historical structure of the Central Valley spring-run chinook salmon ESU. Independent populations are in regular type; dependent populations are in italics. In this figure, Mill and Deer creek spring-run chinook salmon populations are indicated as independent, although the TRT will also consider the possibility that spring-run chinook salmon in these two streams form a single population.

4.2 Independent populations

If we assume that spawning groups in different geographic groups are independent, the question then becomes which populations or groups of populations within these groupings formed independent populations. Several characteristics were used to decide whether populations were independent: distance from a basin to its nearest neighbor (at least 50km), the basin size (generally at least 500 km^2), and significant environmental differences between basins inside of the distance criterion. It is likely that historically there was significant population structure within these basins associated with various tributaries. Contemporary data on population genetics and dynamics were also used directly, where available, and indirectly to substantiate the isolation rule of thumb. Table 2 summarizes the independent and dependent populations of spring-run chinook salmon that historically existed in the Central Valley. The remainder of this section consists of discussions of these populations.

4.2.1 Little Sacramento River

The Little, or Upper, Sacramento is a spring-fed river draining Mt. Shasta. The river itself divides the volcanic southern Cascades ecoregion from the granitic northwestern California ecoregion. It is a moderate-size basin (2370 km^2), well-isolated from its nearest neighbor, the McCloud River (83 km between 500m points). It, unlike the McCloud, is not known to have supported bull trout (Moyle et al., 1982), but did support winter-run chinook salmon as well as spring-run chinook salmon (Yoshiyama et al., 1996). We concluded the the Little Sacramento was large enough and well-isolated enough to have supported an independent population of spring-run chinook salmon. Access to the Little Sacramento is presently blocked by Keswick and Shasta dams.

4.2.2 Pit River–Fall River–Hat Creek

It is not clear whether the middle Pit River itself actually supported spawning spring-run chinook salmon, but the Fall River and Hat Creek (its major tributaries) are documented to have contained spring-run chinook salmon (Yoshiyama et al., 1996). The middle and upper Pit is relatively low gradient, meandering across a flat valley floor, and is warm and turbid (Moyle et al., 1982). Large falls block access shortly above the confluence of the Fall River (Yoshiyama et al., 1996). The Fall River arises from springs at the edge of a lava field, and subsequently has a fairly large discharge of clear water. Hat Creek is similar to the Fall River. The whole region is above 500 m, and Hat Creek and the Fall River are within 50 km of each other. Based on the similarity and proximity of Hat Creek and the Fall River, and the fairly short lengths of accessible habitat within the tributaries, we decided that this area probably was occupied by a single population that had significant substructure. Access to this watershed is presently blocked by Keswick and Shasta dams.

Table 2. Historical populations of spring-run chinook salmon in the Central Valley. Criteria for independence include isolation (I), minimum basin size (S), and substantial genetic differentiation (G). See text for detailed discussion.

Independent Populations	Criteria met	Notes
Little Sacramento River	I, S	
Pit–Fall–Hat rivers	I, S	
McCloud River	I, S	only basin to support bull trout
Battle Creek	I, S	
Butte Creek	I, S, G	
Mill and Deer creeks	I, S, G	TRT will analyze as one or two populations
NF Feather River	I, S	
WB Feather River	I, S	
MF Feather River	I, S	
SF Feather River	I, S	
Yuba R	I, S	relationship between historical and current populations unknown
N & MF American River	I, S	
SF American River	I, S	
Mokelumne R	I, S	
Stanislaus River	I, S	
Tuolumne River	I, S	
Merced River	I, S	
San Joaquin River	I, S	
Dependent Populations		
Kings River		basin frequently inaccessable to anadromous fish
Big Chico, Antelope, Clear, Thomes, Cottonwood, Beegum and Stony creeks		not enough habitat to persist in isolation

4.2.3 McCloud River

The McCloud River, a spring-fed tributary to the Pit River, drains Mt. Shasta, and was swift, cold and tumultuous before hydropower development (Moyle et al., 1982). The McCloud River is the only Central Valley river known to have supported bull trout (*Salvelinus confluentus*), extirpated from the McCloud in the 1970s (Moyle et al., 1982)), and it also supported winter-run chinook salmon salmon. The area above 500 m elevation is isolated from other areas historically used by spring-run chinook salmon, being over 100 km from Hat Creek, Battle Creek, Fall River, and the mainstem Pit River. We concluded that the McCloud River was large enough and well-isolated enough to have supported an independent population of spring-run chinook salmon. Access to this watershed is now blocked by Keswick and Shasta dams.

4.2.4 Battle Creek

Battle Creek is a spring-fed stream draining Mt. Lassen, a Cascadian volcano. It is known to have supported winter-run, spring-run, and fall-run chinook salmon. Its nearest neighbors are rather distant (>80 km) west-side streams (Clear and Beegum creeks) that have quite different hydrologies and offer marginal habitat for spring-run chinook salmon. The more ecologically-similar McCloud and Little Sacramento rivers are well over 100 km away. We concluded that Battle Creek historically contained an independent population of spring-run chinook salmon. It is possible, however, that Battle Creek received significant numbers of strays from the major upper Sacramento River tributary populations. Very large numbers of spring-run chinook salmon migrated past Battle Creek, and if only a small fraction strayed into Battle Creek, this might have had a significant impact on the Battle Creek population. Presently, hydropower operations and water diversions prevent access to areas suitable for spring-run chinook salmon spawning and rearing, but there are no large impassable barriers in Battle Creek.

4.2.5 Butte Creek

Butte Creek and its spring-run chinook salmon appear to be unique. The fish are genetically distinct from spring-run chinook salmon from Mill and Deer creeks. Banks et al. (2000) and Hedgecock (2002), using microsatellites, Kim et al. (1999), using MHCII, and Teel (unpublished), using allozymes, found Butte Creek spring-run chinook salmon to be quite distinct from spring-run chinook salmon in Mill and Deer creeks as well as spring-run chinook salmon from the Feather River and other chinook salmon groups in the Central Valley. Such genetic distinctiveness indicates nearly complete isolation from other chinook populations. Butte Creek spring-run chinook salmon have an earlier spawning run timing than other extant Cascadian populations. Physically, the Butte Creek watershed is unusual for a spring-run chinook salmon stream, being low elevation (all spawning occurs below 300 m) and having rather warm summer water temperatures (exceeding 20°C in 2002 in the uppermost and coolest reach). Such warm temperatures are observed only in the lower reaches of Mill and Deer creeks. It appears that Butte Creek spring-run chinook salmon regularly survive temperatures above the incipient lethal limit reported for chinook salmon, suggesting that they may be adapted to warmer temperatures that most chinook stocks, although spring-run in Beegum Creek apparently survive in similar temperatures[9], and spring-run in the San Joaquin River were reported to do so as well (Clark, 1943; Yoshiyama et al., 2001). While the headwaters of Butte, Deer and Mill creeks are close together, Butte Creek joins the Sacramento River quite far downstream from Mill and Deer, having a long run across the valley floor. We concluded that Butte Creek contains an independent population of spring-run chinook salmon. Access to Butte Creek is presently adequate, although during drought years in recent decades, water diversions have caused the lower reaches to run dry during the spring-run chinook salmon migration period (California Department of Fish and Game, 1998).

4.2.6 Mill and Deer creeks

The question of whether Mill and Deer creeks support two independent populations or a single panmictic population of spring-run chinook salmon is a thorny one. Evidence supporting the panmictic hypothesis includes information on population genetic structure, life history, and habitat attributes. The frequencies of microsatellite alleles in Mill and Deer creeks are not significantly different (Banks et al., 2000; Hedgecock, 2002), although the small sample sizes in these studies provide limited statistical power. Habitat attributes of these adjacent basins are remarkably similar in terms of watershed area, elevation, precipitation, and geology, and the two streams clustered closely together in the PCA. Basin areas are small— the Mill Creek watershed is smaller than any watershed occupied by an independent chinook population in the Puget Sound (Currens et al., 2002). The best available information suggests that Mill and Deer creek spring-run chinook salmon populations were never very large historically; (Hanson

---

[9] public communication, D. Killam, CDFG, Red Bluff, CA.

et al., 1940) estimated that Mill Creek could support about 3000 and Deer Creek about 7500 spring-run chinook salmon spawners. Furthermore, large numbers of spring-run chinook salmon once migrated past Mill and Deer creeks on their way to upper Sacramento tributaries, and Mill and Deer creeks may have received significant numbers of strays, causing their dynamics to be linked to that of the up-river tributary populations.

Evidence supporting the independent populations hypothesis includes spatial isolation and population dynamics. The distance between the 500 m isopleths in Mill and Deer creeks is 89 km, longer than the 50 km cutoff used to distinguish independent chinook populations in the upper Columbia domain (Interior Columbia Basin Technical Recovery Team, 2003). The mouths of the two creeks, however, are much closer together, roughly 25 km. Analysis of contemporary spawning escapement trends supports the independence hypothesis, but not overwhelmingly so (See Appendix C for the analysis).

We could reach no conclusion as to whether Mill and Deer creeks are independent of one another, although we did conclude that spring-run chinook salmon in these streams are currently independent from other spring-run chinook salmon populations. The TRT will conduct viability analyses that consider the streams as independent populations and as a panmictic population. Given that these two streams represent a significant lineage within Central Valley chinook and are a major component of the extant ESU, we suggest that parties implementing recovery actions choose results from the more precautionary alternative.

4.2.7 North Fork Feather River

The North Fork Feather River is well-isolated from other higher-elevation areas of the Feather River, and is in the southern Cascades while the other subbasins of the Feather are in the Sierra Nevada ecoregion. The headwaters are fed by rainfall and by snowmelt from Mt.L̃assen, and rocks are predominately of volcanic origin. Spring-run chinook salmon could ascend quite high in this river (Yoshiyama et al., 1996). The TRT concluded that the North Fork Feather River likely contained an independent population of spring-run chinook salmon. Access to this watershed was blocked by Oroville Dam in the 1968; habitat above Oroville is thought to be in good condition[10].

4.2.8 West Branch Feather River

The West Branch of the Feather River is a tributary to the North Fork of the Feather River that drains a fairly small basin (430 km^2), but according to Yoshiyama et al. (1996), spring-run chinook salmon moved quite far up into the basin. The 500-m contour crossing of the West Branch is about 63 km from the 500-m crossing of the North Fork and 69 km from the Middle Fork of the Feather. The West Branch of the Feather River, unlike other tributaries of the Feather, is completely within the southern Cascades ecoregion. Given the large amount of the west branch that was historically used by spring-run chinook salmon, its position in the Cascades ecoregion, and its isolation from other systems, the TRT concluded that the West Branch of the Feather River contained an independent population of spring-run chinook salmon, in spite of the small area of the basin. An alternative hypothesis is that the West Branch and North Fork together supported an independent population with significant internal structure. Like other tributaries of the Feather River, access to the West Branch is presently blocked by Oroville Dam.

4.2.9 Middle Fork Feather River

The Middle Fork Feather River is a large basin (> 3000 km^2), and is quite different than the adjacent North Fork Feather River. The Middle Fork is entirely within the Sierra Nevada ecoregion, although the watershed is lower in elevation compared to more southerly Sierra basins. The Middle Fork is over 100 km from it nearest neighbor, the South Fork Feather River. Such a distance between suitable spawning and rearing environments suggests that migration between these rivers was low in demographic terms. The TRT concluded that the Middle Fork Feather River historically contained an independent population of spring-run chinook salmon. Access to this watershed is blocked by Oroville Dam.

4.2.10 South Fork Feather River

As discussed in the preceding section, the South Fork of the Feather River probably was home to an independent population of spring-run chinook salmon. Access to this watershed is blocked by Oroville Dam.

4.2.11 Yuba River

The Yuba River is a tributary to the Feather River, joining the Feather River on the floor of the Central Valley. The Yuba River basin as a whole is fairly large (3500 km^2) and well-isolated from the American and Feather rivers

---

[10] E. Thiess, NOAA Fisheries SWRO, Sacramento, CA, personal communication.

(≈ 250 km and 150 km, respectively). Peak discharge in the Yuba River occurs somewhat later than in the Feather River. Within the basin, the north, middle and south forks of the Yuba River cross the 500 m elevation line within 11-37 km of each other, suggesting that some exchange among these basins was likely, but that there may have been significant structuring of the population within these tributaries. In the absence of further information, we will treat the entire Yuba River as a single independent population, while recognizing that there may have been significant population structure within the Yuba River basin. Access to much of the areas historically utilized for spawning and rearing is now blocked by Englebright Dam.

4.2.12 North and Middle Fork American River

The American River basin, as a whole, is the third largest sub-basin in the Central Valley that historically supported spring-run chinook salmon, and its spawning areas are well-isolated from the adjoining Yuba and Mokelumne rivers. Clearly, spring-run chinook salmon populations in the American River would have been independent from those in other basins; the question then is whether sub-basins within the American might have contained independent populations.

The North Fork of the American River has an area of roughly 1000 km^2 and the Middle Fork's area is about 1600 km^2. Both basins extend to the crest of the Sierra Nevada. Yoshiyama et al. (1996) documents the presence of spring-run chinook salmon in both basins. The 500-m crossings of the two rivers are only 10 km apart. Following the isolation rule of thumb, we concluded that together, the North and Middle Forks of American River supported an independent population of spring-run chinook salmon. It is possible that each of the basins may have contained independent populations. Access to these watersheds is blocked by Nimbus Dam.

4.2.13 South Fork American River

The South Fork of the American is the largest sub-basin in the American (area = 2200 km^2), and it is fairly isolated from the other American River tributaries, being about 120 km from the North and Middle forks. We concluded, from the large size and relative isolation, that the South Fork of the American River contained an independent population of spring-run chinook salmon. Access to this watershed is blocked by Nimbus Dam.

4.2.14 Mokelumne River

The Mokelumne River is unique among historical spring-run chinook salmon basins in that it drains directly into the Delta rather than into the Sacramento or San Joaquin rivers. The basin as a whole is of moderate size (2700 km^2) and it is well isolated from adjacent rivers– the Mokelumne's nearest neighbor, the American River, is about 280 km away. According to Yoshiyama et al. (1996), spring-run chinook salmon were present in the Mokelumne River, but only in the mainstem below the confluence of the various forks. The upstream limit was thought to be near the present-day location of the Electra Powerhouse (elev. 205 m). The actual amount of accessible spawning habitat was probably relatively small compared to other Sacramento and San Joaquin tributaries. We concluded that the Mokelumne River contained an independent population of spring-run chinook salmon. Access to much of this watershed is now blocked by Camanche Dam.

4.2.15 Stanislaus River

The Stanislaus River is the northernmost spring-run chinook salmon-bearing tributary to the San Joaquin River. It has an area of 2840 km^2, and is about 250 km from its nearest neighbor, the Tuolumne River. According to Yoshiyama et al. (1996), spring-run chinook salmon entered all of the forks of the Stanislaus for "considerable" distances (reaching as high as 1030 m elevation on the Middle Fork). The forks themselves enter the mainstem Stanislaus not far below the 500-m contour (distances among 500-m crossings range from 6 to 28 km). We concluded that the Stanislaus contained at least one independent population, and may have had substantial structure within the basin. Access to this watershed is presently blocked by New Melones and Tulloch dams.

4.2.16 Tuolumne River

The Tuolumne River basin has an area of nearly 4900 km^2, with much of this area at high elevation. It is 250 km from the Stanislaus River and 320 km from the Merced River. Yoshiyama et al. (1996) state that spring-run chinook salmon had access to over 80 km of the mainstem Tuolumne River, reaching nearly to the boundary of Yosemite National Park. Access to the major tributaries to the Tuolumne River, such as the Clavey River and South and Middle Forks, may have been limited by steep sections near their mouths. We concluded that the Tuolumne River contained an independent population of spring-run chinook salmon. Access to habitat suitable for spring-run chinook salmon spawning and rearing is currently blocked by La Grange and Don Pedro dams.

4.2.17 Merced River

The Merced River basin, as a whole, has an area of roughly 3250 km^2. The major tributaries join in above the 500-m contour line, suggesting little barrier to movement among spawning and rearing locations within the basin. The lowest major tributary is the North Fork, which has a substantial falls 2 km upstream from its mouth and drains a low-elevation area. According to Yoshiyama et al. (1996), spring-run chinook salmon could access at least the lower 11 km of the South Fork, and possibly significantly more if spring-run chinook salmon could pass the waterfall near Peach Tree Bar. In the mainstem, spring-run chinook salmon reached to the area of El Portal (elev. 700 m) and perhaps nearly to Yosemite Valley (Yoshiyama et al., 1996). The Merced's nearest neighbor is the Tuolumne River, over 300 km away. We concluded that the Merced River contained at least one independent population of spring-run chinook salmon, and probably had significant structure corresponding to the mainstem and South Fork. Access to habitat suitable for spring-run chinook salmon spawning and rearing is now blocked by McSwain and New Exchequer dams.

4.2.18 Middle and Upper San Joaquin River

The Middle and Upper San Joaquin basin (area above the valley floor) is a large basin (4700 km^2) and it is more than 300 km from its nearest neighbors, the Merced and Kings rivers. According to Yoshiyama et al. (1996), spring-run chinook salmon ascended as far as Mammoth Pool (elev. 1000 m), which is well below the confluence of the North, Middle and South forks. Anecdotal accounts reported by Yoshiyama et al. (1996) suggest that the population in the San Joaquin was quite large, perhaps exceeding 200,000 spawners per year. Additionally, San Joaquin spring-run chinook salmon may have been adapted to warm temperatures, like those in Butte Creek and perhaps Beegum Creek; Clark (1943) reported spring-run chinook salmon successfully holding over the summer at temperatures of 22°C. We concluded that the middle and upper San Joaquin River contained an independent population of spring-run chinook salmon. Access to habitat suitable for spring-run chinook salmon spawning and rearing is now blocked by lack of flow below Friant Dam, by Friant Dam itself, and above that, by a series of hydroelectric dams. Access to the San Joaquin had already been greatly reduced by various weirs and diversions prior to the construction of Friant Dam.

4.3 Dependent populations

In this section, we describe groups of spring-run chinook salmon that we believe were not historically independent of other populations in the Central Valley. We term them "dependent" populations because they probably would not have persisted without immigration from other streams (either because they are sink populations or part of a metapopulation). Note that dependent populations may play a role in ESU viability, and populations labeled dependent are not necessarily expendable.

4.3.1 Kings River

Yoshiyama et al. (1996) presents information indicating that spring chinook salmon spawned in the Kings River, and the Kings River basin is quite large, with substantial high-elevation areas. The Kings River drains into the Tulare Lake Basin, which in turn drains episodically into the San Joaquin basin. According to the calculations of California Department of Water Resources (CDWR) (1994), if the water storage and diversion system had not been in place during the 1921-1994 period, outflow from the Tulare Lake basin would have happened in only 38 of the 74 years, with stretches of up to 8 years without outflow. It seems that an independent population of spring-run chinook salmon would not be able to survive by spawning in the Kings River, since in many years, neither juveniles or adults could complete their migrations. However, details of the historical connection between the Kings River and San Joaquin River are not well documented (The Bay Institute, 1998), and passage for salmon may have been possible. We hypothesize that under favorable flow conditions, spring-run chinook salmon from the San Joaquin and its tributaries spawned in the Kings River, and therefore we concluded the the Kings River did not contain an independent population of spring-run chinook salmon. On the other hand, it is hard to reconcile the reports of large abundances of spring-run chinook salmon in the Kings River with its extreme isolation and its frequent inaccessibility. Perhaps, in actuality, the Kings River may have been connected to the San Joaquin basin frequently enough to support an independent spring-run chinook salmon population. Access to the Kings River is now blocked by frequently dry streambed upstream of the confluence of the Merced and San Joaquin rivers, the now-dry Tulare Lake bed, a series of irrigation weirs, and Pine Flat Dam.

4.3.2 Big Chico, Antelope, Clear, Thomes, Beegum and Stony creeks

All of these streams appear to offer habitat of marginal suitability to spring-run chinook salmon, having limited area at higher elevations and being highly dependent on rainfall. Records reviewed by Yoshiyama et al. (1996) do not suggest that spring-run chinook salmon were historically abundant in these streams. We acknowledge that the sparse historical record of fish in Beegum Creek may reflect its extreme remoteness. However, the small area of available habitat argues against the existence of an independent population.

We hypothesize that the persistence of spring-run chinook salmon population in these streams is dependent on the input of migrants from nearby streams, such as Mill, Deer and Butte creeks, and historically, spring-run chinook salmon from the extirpated populations in the upper Sacramento basin. An alternative hypothesis is that this group of streams operates as a metapopulation (Hanski and Gilpin, 1991), i.e., member populations may not be viable on their own, but migration among members of the group maintains persistence of the whole group.

The classification of these populations as dependent does not mean that they have no role to play in the persistence or recovery of the Central Valley spring-run chinook salmon ESU. If these populations are adapted to their unusual spawning and rearing habitats, they may contain a valuable genetic resource (perhaps being more tolerant of high temperatures than other spring-run chinook salmon). These habitats and populations may also serve to link other populations in ways that increase ESU viability over longer time scales.

4.4 Other spring-run chinook salmon populations

In this subsection, we discuss the status of extant spring-run chinook salmon stocks that we believe do not represent historical entities.

4.4.1 Feather River below Oroville Dam

Historically, spring-run chinook salmon probably did not spawn below the location of Oroville Dam. The dam releases cold water from its base, and this creates conditions that support an early run of chinook salmon, which are called spring-run chinook salmon by CDFG (although CDFG does not consider this population to be true spring-run chinook salmon (California Department of Fish and Game, 1998)). Presumably, this run-timing attribute is a legacy from spring-run chinook salmon populations that once spawned above Oroville Dam.

Spring-run chinook salmon currently in the Feather River are clearly independent from the spring-run chinook salmon populations in southern Cascade streams, as indicated by several genetic studies (Banks et al., 2000; Kim et al., 1999; Hedgecock, 2002). What is less clear is whether this population is independent from the Feather River Hatchery spring-run chinook salmon, or Feather River fall-run chinook.

Hedgecock (2002) found small but statistically significant allele frequency differences between Feather River spring-run chinook salmon and fall-run chinook salmon, suggesting minimal exchange between these groups (certainly much less than 10%). Hedgecock (2002) found that spring-run chinook salmon captured in the river formed a homogeneous group with spring-run chinook salmon captured in the hatchery, which suggests that the naturally-spawning population may not be independent from the hatchery spawners. California Department of Fish and Game (1998), however, reported that fish released as spring-run chinook salmon returned in the fall run at high rates, and vice-versa, suggesting that the two groups are integrated. The TRT, while perplexed by this information, believes that *F*eather River spring-run chinook salmon should be conserved because it may be all that is left of an important component of the ESU, and we will continue to consider this population in future analyses.

4.4.2 Mainstem Sacramento River, below Keswick Dam

It is highly doubtful that spring-run chinook salmon historically used the mainstem of the Sacramento River for spawning. Spring-run chinook salmon apparently began using the mainstem Sacramento River below Keswick Dam following the construction of Shasta and Keswick Dams. Recently, very few spring-run chinook salmon have been observed passing RBDD. There is no physical or obvious behavioral barrier to separate fall-run chinook from spawning with spring-run chinook below Keswick. CDFG biologists believe that serious hybridization has occurred between the runs (California Department of Fish and Game, 1998), and that spring-run chinook salmon have nearly disappeared from this stretch of the Sacramento River.

5 Structure of the Sacramento River winter-run chinook ESU

The population structure of winter-run chinook salmon was probably much simpler than that of spring-run chinook salmon. Winter-run chinook salmon were found historically only in the southern Cascades region, and the TRT found no basis for subdividing the ESU into units other than independent populations (Figure 19, Table 3). Following the logic and evidence laid out for spring-run chinook salmon in the southern Cascades region, we reached parallel conclusions: there were historically four independent populations of winter-run chinook salmon (Little Sacramento, Pit-Fall-Hat, McCloud River, and Battle Creek). The first three of these areas are blocked by Shasta and Keswick dams, and access to Battle Creek has been blocked by the Coleman National Fish Hatchery weir and various hydropower dams and diversions. Currently, there is one independent population of winter-run chinook salmon inhabiting the area of cool water between Keswick Dam and Red Bluff. Unlike spring-run chinook salmon, winter-run chinook salmon have persisted in this area due to their temporal isolation from the highly abundant fall-run chinook salmon. This area was not historically utilized by winter-run chinook salmon for spawning.

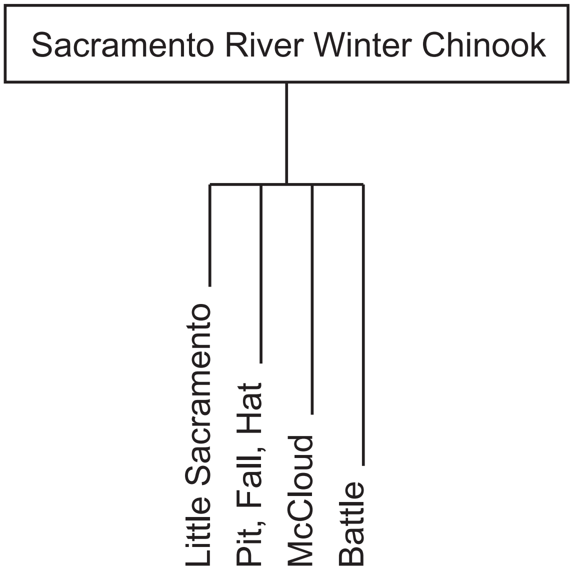

Figure 19. Historical structure of the Sacramento River winter-run chinook salmon ESU.

6 Acknowledgments

We thank Colleen Harvey-Arrison, Tracy McReynolds and Paul Ward for life history information and data on Mill, Deer and Butte Creek spring-run chinook. Arwen Edsall, Aditya Agrawal and Matthew Goslin provided GIS support. Qinqin Liu, Tracy McReynolds, Mike Lacy, Colleen Harvey-Arrison, Tommy Williams and David Boughton reviewed earlier drafts of the manuscript.

Table 3. Historical populations of winter-run Chinook salmon in the Central Valley. Criteria for independence include isolation (I), minimum basin size (S). See text for detailed discussion.

Independent Population	Criteria met	Notes
Little Sacramento R.	I, S	
Pit–Fall–Hat Cr.	I, S	
McCloud R.	I, S	only basin to support bull trout
Battle Cr.	I, S	

A The use of population genetics for determining population structure

In this Appendix, we review common methods and concerns that should be considered in the interpretation of the results. More thorough explanations of some of this material can be found in Hallerman (2003) and references therein.

A.1 Quantitative trait loci vs. Mendelian markers

Most of the molecular markers used in population genetic studies are inherited in a simple Mendelian fashion and, with exception of the major histocompatibility complex (MHC) loci, are essentially selectively neutral. They have little or no effect on successful reproduction, and therefore the frequency of these markers does not change as a result of natural selection. Quantitative trait loci (QTLs) are those loci which code for phenotypic characters (e.g., growth rate, behavior, swimming speed, etc.). Many quantitative traits are under natural selection, and can be expected to change frequency when the population is exposed to different selective forces.

A.2 Types of molecular data

Below we discuss some of the principle types of molecular variation that have been used to gather data for chinook populations. These data come from two principle forms of analysis, separation of DNA sequences in matrices or gels (e.g., starch, agarose, acrylamide; Figure 20) or direct determination of DNA sequences (Figure 21).

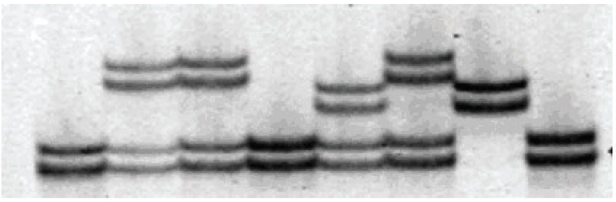

Figure 20. Microsatellite variation where each allele is portrayed by two bands, each representing one of the two strands of a DNA molecule. Vertical sets of bands are derived from single individuals. Individuals with two bands are homozygous for the same allele, receiving the same from both parents and individuals with two sets of bands are heterozygous receiving different alleles from each parent. Starting on the left side, the first individual is homozygous and the second is heterozygous, both sharing one allele in common. Three alleles are revealed on this gel.

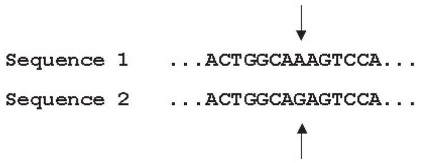

Figure 21. DNA sequence variation. The principle type of DNA variation is in the sequence of nucleotides found at some location (locus) in the genome. Mutations give rise to the replacement of one of the four nucleotides (guanine - G, adenine - A, cytosine - C, and thymine - T) with another. In this case the two DNA sequences or alleles differ in having an A or a G (at point of arrow).

A.2.1 Allozymes

Allozymes are different forms of protein (usually catalytic enzymes, e.g., lactate dehydrogenase) encoded by a single Mendelian locus. Variation in DNA sequence (e.g., substitution of a G for a T) leads to changes in the DNA triplet code for the amino acids that make up enzymes. Thirty percent of these changes in amino acids involve a change in charge of the amino acid (e.g., a negatively charged amino acid is replaced with one with a neutral charge). These changes in charge may lead to the change in overall charge on the enzyme molecule. This change in charge can lead to differences in mobility in an electric field. One can detect these differences in migration by staining for specific enzymes, employing their substrate specificity.

A.2.2 MHC

The major histocompatibility complex (MHC) consists of several classes of genes that encode proteins involved in the immune response. Each class may consist of several loci. MHC genes are highly polymorphic and under intense selective pressure. MHC genes have been implicated in mate selection (Aeschlimann et al., 2003), such that individuals choose mates with divergent MHC types thereby maintaining variation at these loci in populations that go through bottlenecks. MHC variation is usually detected as sequence variation, either through direct sequencing or some form of gel separation that can detect changes in sequence rather than length of sequence (e.g., single strand conformational polymorphism, denaturing gradient (DGGE) or temperature gradient gel electrophoresis (TGGE)).

A.2.3 Microsatellites

Microsatellites are a class of repetitive DNA, consisting of variable numbers of 2-6 bp repeats (e.g., TATATATATATA). The repeating units may be simple repeats of the same unit, a complex of several repeats (e.g., TATATATA-CATCATCATCATCAT), or an interrupted sequence (e.g., TATATATATA-GAATAC-CATCATCAT-CAT). Surrounding the repeat are anonymous DNA sequences from which primers are designed to amplify the repeat region. These surrounding or flanking sequences evolve slowly and can often permit primers from a related taxon to amplify (e.g., chinook salmon primers will often work in cutthroat trout).

A.2.4 mtDNA

Mitochondrial DNA is found in tens to hundreds of copies in each mitochondrion and a given cell can have hundreds of mitochondria. The mitochondrial genome in fish ranges from 15 to 20 kbp (Billington and Hebert, 1991). The principle features of this type of DNA are (1) relatively strict maternal inheritance, (2) no recombination, and (3) a higher rate of mutation than most nuclear DNAs. Usually all mtDNA molecules in an individual are identical. Occasionally paternal leakage can occur and lead to sequence heteroplasmy (presence of different types of mtDNAs in the same individual) and some instances of length heteroplasmy may occur. Mitochondrial DNA molecules that differ in sequence are considered haplotypes (only one form per individual). In reality mtDNA can be thought of as a single locus that experiences no recombination. Each haplotype is a single allele at the mtDNA locus.

A.3 Allele frequencies

The principle data for use in studying populations are the frequencies of alleles at individual genetic loci. Evolutionary similarity of populations is judged based on similarities in allele frequencies, that is two populations with very dissimilar sets of frequencies for a group of loci are said to be reproductively isolated and to have been isolated for a longer time than populations with more similar allele frequencies.

A.4 Mutations and mutation rates

Changes in DNA sequence (mutations) are constantly occurring over time. Most mutations are lost from a population in the first few generations, while a few increase in frequency, even to the point of completely replacing other forms (alleles) of that sequence (allelic substitution). Different types of DNA experience substantially different rates of mutation or substitution. Mutation rate is often directly related to the number of alleles segregating in the population. For the markers used in work on chinook salmon, allozymes exhibit the lowest level of mutation, MHC and mtDNA intermediate (five to 10 times that of most nuclear genes) and microsatellites the highest (100 fold increase over allozymes).

A.5 Populations and gene pools

Populations are collections of individuals that have the potential to reproduce with each other and not to reproduce with individuals from other populations. The distinction of populations is easy to understand for fish in two lakes with no corridors for migration. The distinction is harder to draw for anadromous fish that inhabit rivers with many sub-drainages.

Gene pools consist of all of the genetic variation held by a population. In essence, a gene pool can be described by the allele frequencies of a given population over the entire genome. Gene pools under assumptive models of no selection, no immigration or selective emigration, large population size, no mutation, and random mating are expected to remain constant: one generation passes its gene pool intact on to the next generation. Obviously, reality violates many of the assumptions of the model and these violations must be weighed in interpreting the results from molecular genetic studies.

A.6 Genetic drift

A common assumption in population genetic studies is that a gene pool stays the same from generation to generation, that is, the same allele frequencies at each locus will be observed in the spawning adults each generation (or each year assuming overlapping generations). This assumption is based on having thousands of spawners that have an equal probability of mating with each and producing the same number of offspring per family. Obviously, reality shows there are uneven family sizes and often small numbers of spawners in many tributary streams. Thus, there is some variation in allele frequencies from one generation to the next, termed "genetic drift." Genetic drift is expected to be greatest for those loci with larger numbers of alleles and those populations with the smallest number of breeders.

A.7 Gene flow

While salmonid fish are noted for their fidelity to return to their natal streams (homing), they do at times stray to other streams. This straying is often called migration from one population to another and not to be confused with the migration pattern of salmonids to the ocean and back to their natal stream. There are two types of straying, emigration (out of the population) or immigration (into the population). Straying/migration is not equivalent to gene flow or introgression. It only matters for competition for habitat resources whether a fish simply enters or immigrates into a non-natal population. For that immigrant to effect evolutionary change it must leave its gametes in the non-natal population. That a non-natal fish appears in a population is not in and of itself sufficient for gene flow; however, transferring eggs from one hatchery to another likely is. We usually term this exchange of genes *gene flow* for intraspecific exchange, and *introgression* where the flow is across a species boundary from hybridization and subsequent backcross events.

A.8 Data analysis

A.8.1 Is this a single population and is it genetically stable?

There are several tests that can be done to establish the genetic integrity and genetic health of a population. The first test is whether the population is in Hardy-Weinberg equilibrium. If the mutation, selection, genetic drift, and immigration are minimal and mating is basically random, then there is an expectation of frequencies of single locus genotypes based on the allelic frequencies at that locus. Departures from Hardy-Weinberg equilibrium at multiple single loci imply deviations from the aforementioned basic assumptions. Non-random mating within the presumptive population (e.g., mating between native and out-of-basin hatchery fish or multiple sub-populations within the drainage system) is often the cause of departure from Hardy-Weinberg equilibrium.

A more sensitive measure of genetic integrity of a population is the test for linkage disequilibrium. This test examines pairs of loci at a time and seeks to determine if the observed gamete frequencies in the population fit the expected distribution of gametes based on allele frequencies. Again, departures from the basic population assumptions can be detected by linkage disequilibrium and more importantly the signature from past generational disruptions in equilibrium last for multiple generations, unlike Hardy-Weinberg equilibrium which can be returned in a single generation.

A.8.2 Are these populations reproductively isolated?

Once allele frequencies are calculated for sample sets, they can be compared to determine if the allele frequency arrays for two populations are significantly different. Alternatively, could the samples be drawn from a common population? Determination that the samples could not come from a single random mating population implies that there must be at least two populations and that they should be managed separately. There are a variety of means of testing for significantly different allele frequency arrays (Hallerman, 2003).

A.8.3 How is the diversity partitioned among the populations?

The distribution of allelic variation within and among populations can be evaluated with the genetic statistic F_{ST}. This statistic compares the levels of heterozygosity found in component populations relative to an imaginary pooled population of all the component populations. An F_{ST} of 0.07 for a pair of populations would suggest that 7% of the total variation is between the populations. Values below 0.005 are often not significant, such that the populations might not in fact be reproductively isolated.

A.8.4 Pairwise genetic distance values

Arithmetic measures of the similarity of allele frequencies between a pair of populations can be calculated using a number of different algorithms. Today most of these measures give dissimilarity measures (termed “genetic distance”) rather than similarities. Thus, a pair of populations with a lower genetic distance value is considered more related than a pair of populations with a higher genetic distance value. Some common measures used today include Nei (1972, 1978), Goldstein’s $(du)^2$, and Cavalli-Sforza and Edwards chord distances (1967).

A.8.5 Clustering or ordination - putting the genetic distance values together

Gaining a feel for the overall relationships for a group of populations can be accomplished by combining the information from the pairwise population comparisons into an overall graphical representation. Many approaches are available including: unweighted pair-group method using arithmetic averages (UPGMA), multidimensional scaling (MDS), principal component analysis (PCA), minimum spanning tree, neighbor joining, etc. Some of these methods ordinate the populations in two or three dimensions, some draw lines of linkage with shortest lines indicating those pairs of populations with the most similarity, while others position the populations in space without any lines linking populations.

Several methods are available to test the robustness of particular ordinations. Maximum likelihood compares probabilities for different trees to choose the best tree. Bootstrapping generates pseudo replicates of the original data set by random sampling with replacement.

A.8.6 Concerns in interpreting the results

The clarity in scoring of Mendelian loci coupled with a rich history of theoretical population genetics can lead to overconfidence in accepting the seemingly obvious conclusions from interpreting the results. However, in the following paragraphs we discuss a number of concerns or cautions that should be addressed because they may alter the meaning of the results. Most of these concerns cannot be overcome and we tend to ignore them based on assumptions that may be erroneous. There are obvious overlaps among these concerns.

A.8.7 Sampling accuracy

Assumption: The sample of fish analyzed reflect the population being examined.

Discussion: While we often use the mouths of rivers to designate major populations from one another, the complexity of each individual river will dictate how the fish that spawn in that river are broken into subsets of populations that have varying levels of gene flow among them. Temporal and spatial spawning separations may lead to reproductive isolation of populations within rivers. We need to know how a sample was taken in order to feel confident that the sample is a true reflection of the population in question? This assumption of sampling accuracy is probably often violated and the literature is rife with statements that apparently aberrant samples may be combinations of populations (e.g., “The wild population . . . from Butte Creek that may have been contaminated with a few fall-run fish” (Hedgecock et al., 2001) or “It seems likely that the spring run is mixed into the 1995 winter run because the run is most similar to spring” (Kim et al., 1999).)

A.8.8 Temporal stability

Assumption: The results for one year will be replicable in the next year.

Discussion: While evolutionary change is expected, relatively stable gene pools over several generations are a requisite to comparisons of data sets taken in different years. Admixture, low spawner, and sampling inaccuracy can lead to temporal variation that may equal spatial variation (see Williamson and May (2003)).

A.8.9 Historical reflection

Assumption: The population in the stream today is nearly the same as the population 200 years before.

Discussion: We know that populations are constantly changing due to new mutations, random drift, changes in environment, and immigration. These changes would be expected to be relatively small over 200 years. However, there have been drastic anthropogenic changes in the environment, and immigration from transplants and straying has increased many fold. Contaminants may have increased mutation rates. Small numbers of spawners in some years have led to gross change in allele frequencies from random drift.

A.8.10 Admixture

Assumption: The population has not experienced admixture of genes from other populations (e.g. transplants or straying leading to hybridization with out-of-basin stocks or other temporal runs).

Discussion: The current population is a reflection of the contributions of previous generations. Since most wild spawning goes unobserved, the number of nonnatal fish that spawn is unknown. While data suggest that hatchery fish contribute less to a gene pool, any contribution of gametes to the gene pool will alter the composition of that gene pool over time. The data for fall-run chinook salmon in the Central Valley strongly support the conclusion that admixture from transplants and straying has reduced an historical tapestry of different populations to essentially one panmictic population (Williamson and May, 2003).

A.8.11 Genetic uniqueness

Assumption: Statistical differences in molecular markers among populations are reflective of substantial gene pool differences among the populations.

Discussion: Are these fish sufficiently different from other geographically proximate runs to warrant independent status? Beyond run timing what quantitative traits distinguish one population from another such that each should be managed separately?

A.8.12 Genetic variability

Assumption: The molecular marker variability rates are reflective of the variability in important survival traits.

Discussion: Can we ascertain whether the levels of variability for a few dozen molecular markers are predictive of the genetic health of a population for 100 years?

B Life history diversity of Central Valley spring-run chinook salmon

Life history information is available for the spring-run chinook salmon spawning groups in Mill, Deer and Butte creeks. Biologists at CDFG have collected and compiled information on adult migration timing, the size distribution of spawners, the timing of juvenile emigration, and the size of juvenile emigrants. In general, periods of high flow cause gaps in the sampling, and it is likely that significant numbers of fish move during these high-flow periods. No attempt has been made to account for the effects of these gaps on the information presented here.

B.1 Adult migration

The Butte Creek spring-run chinook salmon enter their natal stream roughly six weeks earlier, on average, and have a more protracted migration than spring-run chinook salmon in Mill and Deer creeks (Figure 22). Run timing in Mill and Deer creeks looks quite similar. This size distribution of spawners looks quite similar in all three streams, with perhaps fewer < 60 cm fish (typically two-year-old) in Butte Creek (Fig 23), although this difference may an artifact of sampling differences rather than the result of biological differences.

B.2 Juvenile emigration

In all three streams, the peak of juvenile emigration occurs in January or February (Figure 24). Emigration of young-of-the-year (YOY) juveniles appears to be somewhat later, and yearlings somewhat earlier, in Mill and Deer creeks than in Butte Creek, consistent with the latter spawning timing and colder water temperatures in Mill and Deer creeks. Figure 25 shows the size distribution of emigrants from all three streams. In October, all outmigrants are yearlings. In November, YOY begin to be observed, but only in substantial numbers in Butte Creek. YOY migrants are abundant in all three streams from December through May. In the December through April period, the modal size of migrants is constant at around 40 mm, presumably reflecting the prolonged emergence of fry from the gravel. As the outmigration season progresses, the upper tail of the distribution broadens, reflecting the growth of juveniles in areas above the traps. Modal size increases in May and June. Overall, the patterns look very similar among the streams, with only the early and prolonged emigration from Butte Creek standing out as different (and this may be an artifact of the different sampling regimes in the streams).

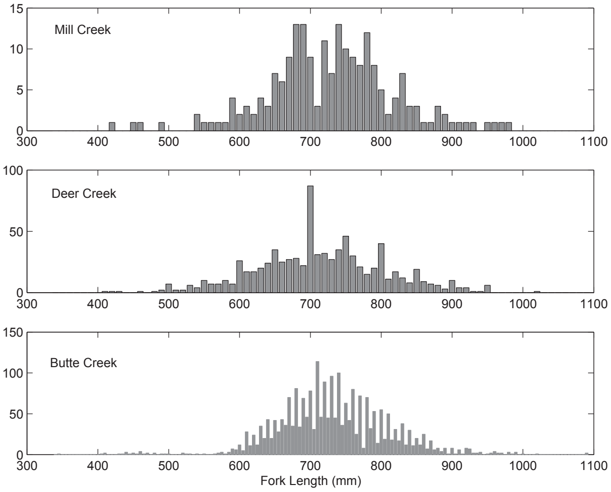

Figure 23. Size distribution of spawning adult spring-run chinook salmon in Mill, Deer and Butte creeks.

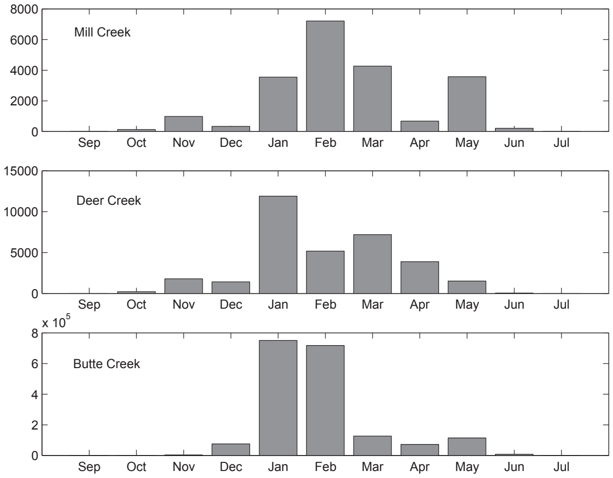

Figure 24. Mean monthly catches of juvenile spring-run chinook salmon in rotary screw traps in Mill, Deer and Butte creeks.

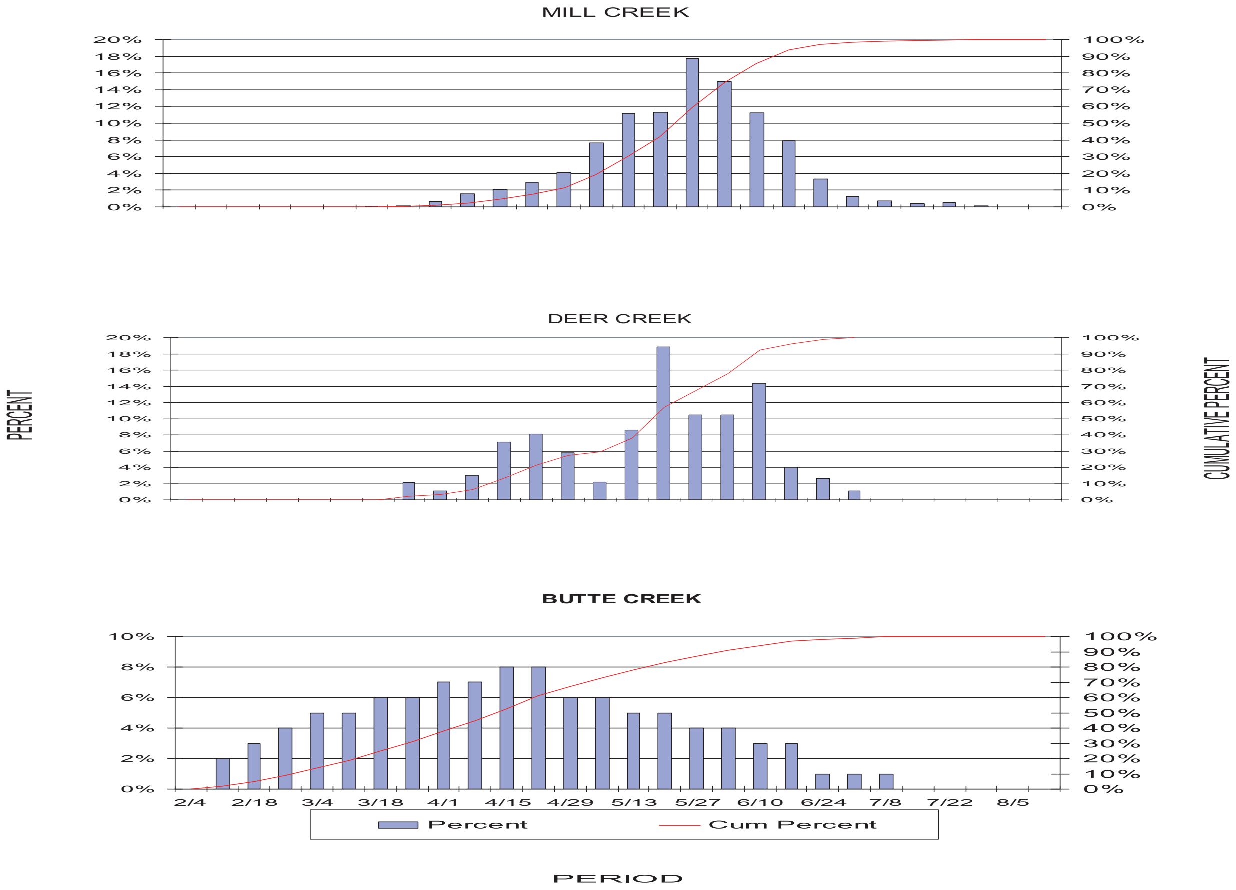

Figure 22. Weekly migration of spring-run chinook salmon into Mill, Deer and Butte creeks. Bars show the percentage of migrants migrating in that week; the line shows the cumulative percent migration.

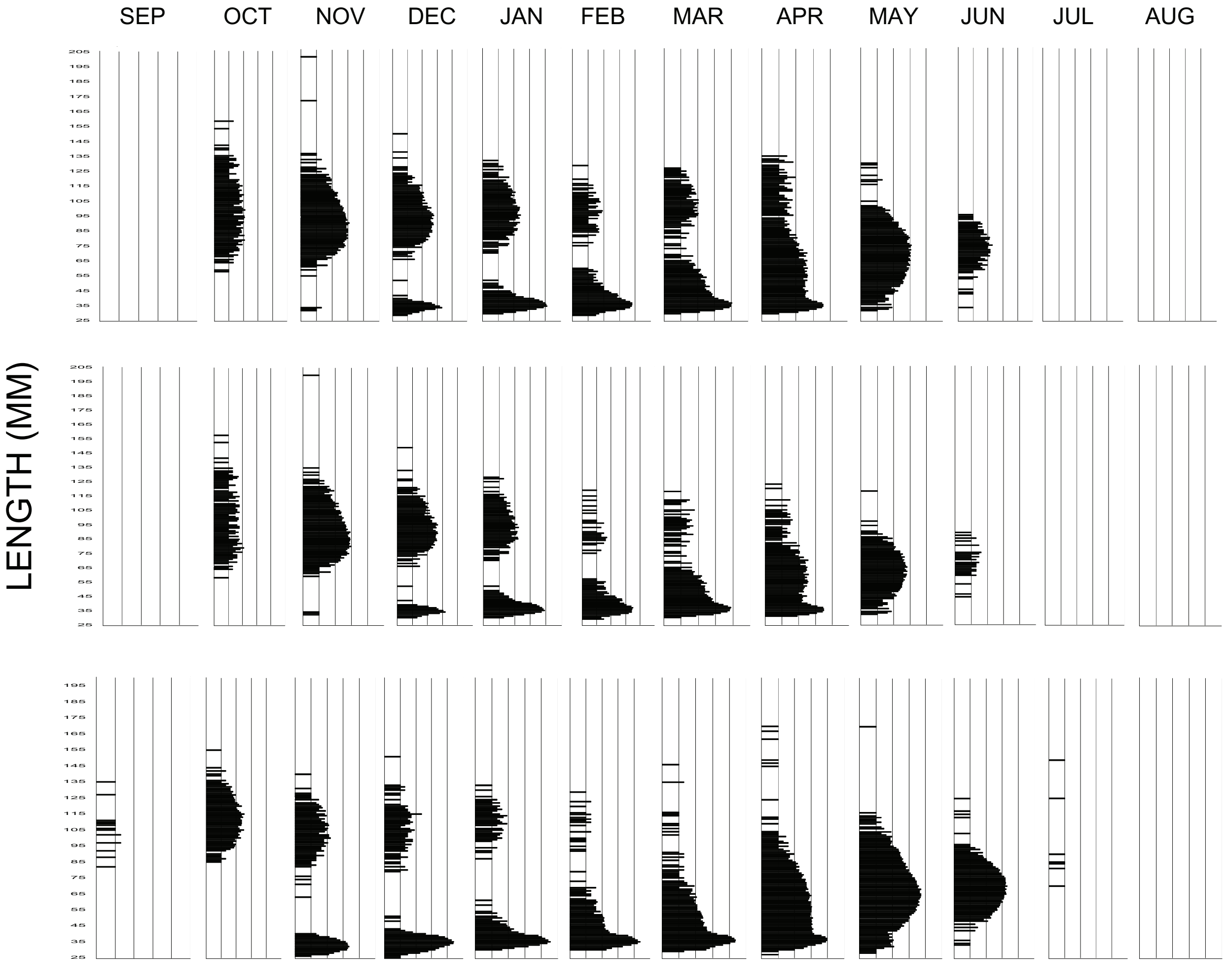

Figure 25. Size distribution of juvenile spring-run chinook salmon migrants in Mill (top), Deer (middle) and Butte (bottom) creeks. The x-axis is on the $\log_{10}$ scale. Data from C. Harvey-Arrison and T. McReynolds, CDFG.

C Population dynamics of Mill and Deer Creek spring chinook

Summary: A model comparison approach is used to test whether Mill and Deer creek spring-run chinook form a single population. Three models, based on random-walk-with-drift dynamics, are compared: completely independent dynamics, correlated process variation, and a simple metapopulation model allowing for migration between populations. According to Akaike's Information Criterion, the model ignoring correlated process variation and migration is the most parsimonious explanation for the observed time series of abundances. The metapopulation model is not implausible, however, and the estimated rates of migration are biologically significant.

C.1 Model formulations

Three hypotheses describe the possible relationship between two spawning groups:

1. completely independent dynamics
2. correlated environment causing correlations in abundance
3. migrations between populations causing correlation in abundance

These hypotheses can be tested by fitting corresponding models to population abundance data and comparing the fits with Akaike's Information Criterion (AIC) (Burnham and Anderson, 1998). The model with the lowest AIC is the most parsimonious model of the data. Three models are sketched below, corresponding to the three hypotheses above. models are cast in state-space form to account for observation error in abundance.

Let N_t denote the size of a population of chinook. Total population size is not typically measured in salmon populations, rather, only mature individuals are available for counting in freshwater. N_t is therefore estimated from a running sum of spawning escapements:

$$N_t = S_t + S_{t+1} + S_{t+2}. \tag{1}$$

The summation is taken over three years because most chinook salmon spawn by age 3 in the Central Valley. A similar approach to estimating population size from observations of breeding adults has been used in studies of a variety of vertebrates (Dennis et al., 1991; Holmes, 2001).

C.1.1 Model 1: independent populations

A state-space model for two independent populations is described by

$$\begin{aligned} N_{t+1,a} &= \alpha_a N_{t,a} + \eta_{t,a} && (2)\\ N_{t+1,b} &= \alpha_b N_{t,b} + \eta_{t,b} && (3)\\ y_{t,a} &= N_{t,a} + \epsilon_{t,a} && (4)\\ y_{t,b} &= N_{t,b} + \epsilon_{t,b}, && (5) \end{aligned}$$

where α_a is the population growth rate of population a, $\eta_{t,a}$ is a random change in population size caused by the environment, $y_{t,a}$ is the observation of population size at time t, and $\epsilon_{t,a}$ is an observation error. Both η_t and ϵ_t are assumed to be normal and independent, with means = 0 and standard deviations proportional to N_t^2. This is an approximation to lognormal errors, which could easily be used for this model but not for the migration model described below without leaving the normal linear setting (which allows use of the Kalman filter, greatly simplifying computations).

C.1.2 Model 2: correlated environment

Model 1 can be extended to incorporate correlated environmental variation simply by treating the η_ts as arising from a bivariate normal distribution with mean = 0 and with covariance Σ:

$$\Sigma = \begin{bmatrix} c_p N_{t,a}^2 & c_{a,b} N_{t,a} N_{t,b} \\ c_{a,b} N_{t,a} N_{t,b} & c_p N_{t,b}^2 \end{bmatrix}, \tag{6}$$

where c_p and c_{ab} are proportionality constants (roughly, coefficients of variation).

C.1.3 Model 3: migration between populations

Model 1 can also be extended by adding movement between populations to the state equations, creating a simple metapopulation model:

$$\begin{aligned} N_{t+1,a} &= (1-s_{ab})\alpha_a N_{t,a} + (1-s_{ab}))\eta_{t,a} && (7)\\ &\quad + s_{ba}\alpha_b N_{t,b} + s_{ba}\eta_{t,b} \\ N_{t+1,b} &= (1-s_{ba})\alpha_b N_{t,b} + (1-s_{ba})\eta_{t,b} && (8)\\ &\quad + s_{ab}\alpha_a N_{t,a} + s_{ab}\eta_{t,a}, \end{aligned}$$

where s_{ab} is the fraction of group a moving into spawning area b.

C.2 Model fitting and comparison

Maximum likelihood estimates of unknown parameters were obtained by minimizing the negative loglikelihood with the Nelder-Mead algorithm for multidimensional unconstrained minimization. Variances and probabilities were log and logit transformed, respectively, so that they would fall on the real line. The likelihood of the data was found with the Kalman filter (Harvey, 1989; Lindley, 2003). To explore the issue of parameter uncertainty, a Bayesian approach was taken by simulating from the joint posterior distribution of the parameters using the Metropolis-Hastings algorithm (Metropolis et al., 1953; Hastings, 1970).

C.3 Results and discussion

Table 4 summarizes parameter estimates and the AIC of the three models as applied to Mill (a) and Deer (b) Creek spawner data. According to AIC, Model 1 is the best approximation to the data, followed by Model 3 and Model 2. This means that there is no *need* to invoke migration between populations or correlated environments to explain the population dynamics of Mill and Deer Creek spring-run chinook salmon. AIC differences of $< 2 - 3$ relative to the best model, however, indicate that models 2 and 3 are not unreasonable approximations to the data. The estimate of the covariance of process errors for Model 2 is positive but small, indicating that most of the variation in population size is independent: even though the covariation is statistically significant, it is not significant in the biological sense.

According to the point estimates of the parameters of Model 3, no fish move from Mill to Deer creek, but around 9% of the production of Deer Creek returns to Mill Creek. This level of migration is biologically significant, and is near the VSP criteria of 10% migration (McElhany et al., 2000). In order to assess the precision of the estimate of s_{ba}, I computed the profile likelihood of this parameter (shown in Figure 26). According to Model 3, estimates of s_{ba} in the range of 0–0.2 would be expected from repeated observations of the system.

The uncertainty in parameter estimated is most easily conveyed with univariate and bivariate plots of parameter densities (Figure 27). Growth rate and emigration rate are positively correlated within populations, and growth rates and emigration rates are negatively correlated between populations. The probability that $s_{ab} < 0.10$ is 0.52, and the probability that $s_{ba} < 0.10$ is 0.57, i.e., it is slightly more likely than not that migration rates between Mill and Deer creeks are less than 0.10.

Table 4. Summary of parameter estimates and AIC for three models describing dynamics of two salmon populations

parameter	Model 1	Model 2	Model 3
α_a	1.15	1.16	1.04
α_b	1.12	1.12	1.19
c	0.105	0.105	0.071
c_{ab}	NA	9.54×10^{-3}	NA
s_{ab}	NA	NA	0.000
s_{ba}	NA	NA	0.107
δAIC	0	1.91	2.29

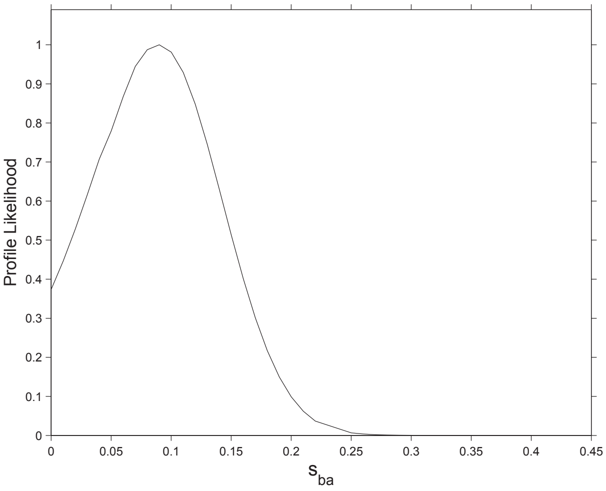

Figure 26. Profile likelihood of the migration parameter describing the fraction of fish moving from Deer to Mill Creek.

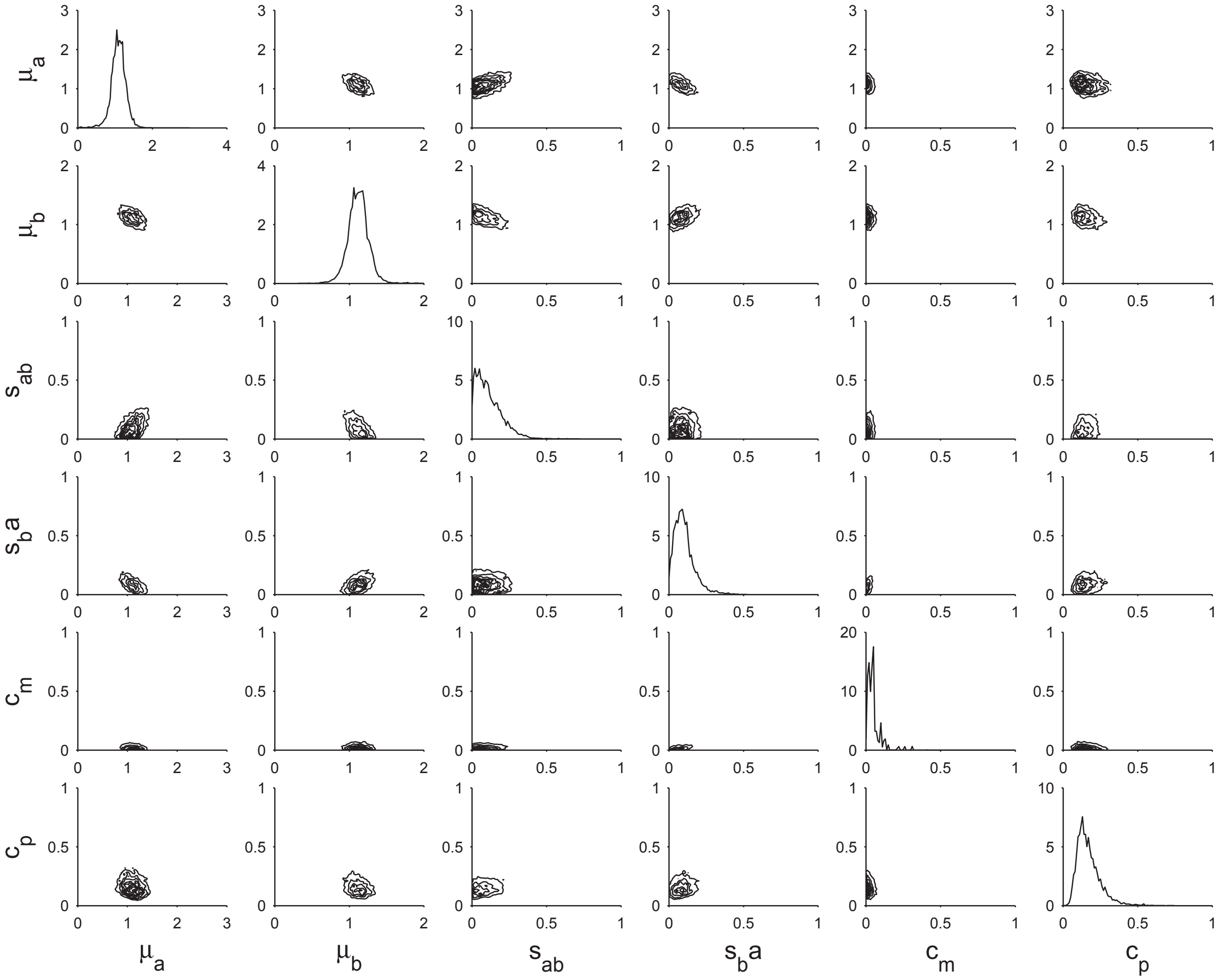

Figure 27. Marginal (on diagonal) and bivariate densities of parameter estimates.

D Multivariate analysis of spring-run Chinook watersheds in the Central Valley

The Central Valley Technical Recovery Team (TRT) is tasked with identifying the structure of historic independent populations. As part of this effort we created an initial classification scheme (see Figure 18) for spring-run chinook salmon watersheds in the Central Valley. This gestalt delineation was based loosely on the following variables: ecoregions, geology, elevation, hydrography, several climatological variables, and timing of peak flow. In order to quantitatively test whether this initial structure was valid and concordant with available environmental data, we ran a series of multivariate analyses on the watershed-level environmental data.

D.1 Methods

D.1.1 Data

We delineated watersheds across the entire Central Valley Basin, and used these polygons as the basis for extracting environmental data and constructing an *m x n* database for ordination. To complete this database we used two different types of joins in ArcInfo GIS (ArcGIS 8.3, Environmental Systems Research Institute, Redlands, CA): a spatial join between two polygon coverages; and a spatial join between one polygon coverage and one raster coverage. ArcInfo splits its data types into two main categories: vector (points, lines & polygons) and raster (a grid-cell based representation of a surface). We use the term coverage to refer to any of the three vector data-types and grid or raster interchangeably to refer to the raster data type.)

Using GIS, we first joined the watershed coverage with the other two polygon coverages: Jepson Ecoregion (Table 5), and Dominant Geology (Table 6). The output of these two joins were summarized by type by watershed. For the second join, we intersected the watershed coverage with several raster layers (Table 7). In addition to these spatial joins, the month of peak flow and the area of each watershed was added to each watershed in the database.

D.2 Data Analysis

We exported the complete database to R (Ihaka and Gentleman, 1996) for statistical analysis. We investigated the use of Non-Metric Multidimensional Scaling (NMMDS) (Shepard, 1962; Kruskal, 1964), but we chose Principal Components Analysis (PCA) (Pearson, 1901; Hotelling, 1933) for the ordination of these data because its easier conceptual underpinnings and because NMMDS lacks an analytical solution. Because PCA makes assumptions about linearity and normality, we scaled and centered the data before analysis.

We ran the PCA on the standard covariance matrix, and explored the output using 2D and 3D plots. Additionally, we produced biplots using the principal component biplot (sensu Gabriel (1971)). This type of biplot shows the descriptors on top of the 2D plots, and allows for visual interpretation of the environmental correlation within the ordination space. For example, if a certain group of watersheds are all high in granitic soil, and are in the Sierra Nevada Ecoregion, then these two vectors will show up along this axis or along this dimension in multivariate space.

While examining the initial biplots we noted several of the environmental descriptors were closely correlated in multivariate space. Because this biplot is a scaled representation of their (the descriptors) relative positions (Legendre and Legendre, 1998), we removed highly correlated ($> 80\%$) descriptors. To do this, we examined the correlation matrix prior to removing one of a correlated pair of descriptors, e.g. remove min January temp from the min annual temp and min January temp pair.

Table 5. Jepson Ecoregion Codes

Item Name	Item Definition
nwca	% (by area) Northwestern California Ecoregion
cwca	% (by area) Central Western California Ecoregion
swca	% (by area) South Western California Ecoregion
gcv	% (by area) Great Central Valley Ecoregion
cscd	% (by area) Cascade Ranges Ecoregion
modc	% (by area) Modoc Plateau Ecoregion
srnv	% (by area) Sierra Nevada Ecoregion

Table 6. Geological Type

Item Name	Item Definition
sedi	% (by area) Sedimentary
gran	% (by area) Granitic
aluv	% (by area) Alluvium
volc	% (by area) Volcanic
watr	% (by area) Water

Table 7. Raster data layers averaged over the whole watershed with units in parentheses

Item Name	Item Definition
Elev Mean	Elevation (meters)
Elev gt 500m	Summed area of elevation greater than 500m (m^2)
Mean Ann Precip	Mean annual precipitation (mm)
Mean Ann Temp	Mean annual temperature (0.1 °C)
Min Ann Temp	Minimum annual temperature (0.1 °C)
Max Ann Temp	Maximum annual temperature (0.1 °C)
Range Ann Temp	Range of annual temperature (0.1 °C)
Min Jan Temp	Minimum average January temperature (0.1 °C)
Max Aug Temp	Maximum average August temperature (0.1 °C)
Jan Aug Temp	Minimum January & maximum August temperature range (0.1 °C)

Table 8. Key to spring run watershed labels in ordination plots

Abbreviation	Stream Name
ANT	Antelope Creek
BAT	Battle Creek
BCH	Big Chico and Mud Creeks
BUT	Butte Creek
CLE	Clear Creek
COT	Cottonwood Creek
DEE	Deer Creek
FAL	Fall River
HAT	Hat Creek
KIN	Kings River
PIT	Lower Pit River
MCC	McCloud River
MER	Merced River
MSJ	Mid San Joaquin River
MAM	Middle Fork American River
MFT	Middle Fork Feather River
MIL	Mill Creek
NAM	North Fork American River
NFT	North Fork Feather River
MOK	Mokelumne River
SAM	South Fork American River
SFT	South Fork Feather River
STA	Stanislaus River
STO	Stony Creek
THO	Thomes Creek
USC	Upper Sacramento River
UTU	Upper Tuolumne River
WFT	West Branch Feather River
YUB	Yuba River

Table 9. Key to color labels in ordination plots

Item Name	Item Definition
LSSJ.NS	Lower Sacramento-San Joaquin/Northern Sierra
LSSJ.SS	Lower Sacramento-San Joaquin/Southern Sierra
US.RD	Upper Sacramento/Rain Driven
US.SF	Upper Sacramento/Spring-Fed

Table 10. Loadings (> ± 0.1) for first three principal components

Variable Name	PCA 1	PCA 2	PCA 3
Peak Flow Month	0.329	0.194	
nwca	-0.106	0.253	
gcv		0.193	-0.361
cwca			0.126
cscd	-0.200	-0.355	
modc		-0.146	-0.108
srnv	0.302	0.113	0.132
sedi	-0.145	0.347	0.159
gran	0.321	0.233	
aluv	-0.217	0.103	-0.476
volc	-0.113	-0.481	0.107
ann.precip			0.609
mean.ann.T	-0.358	0.197	
min.ann.T	-0.330	0.278	
max.ann.T	-0.368	0.103	
range.ann.T		-0.388	
elev	0.377		
area.gt500	0.152		-0.400

Table 11. Percent variance explained by the first three principal components

Component #	% Variance Explained
PCA 1	34
PCA 2	19
PCA 3	9
Cumulative Variance	62

Table 12. Potential non-independent watersheds, as determined by hierarchical clustering.

Pair #	Watershed Pair	
1	Clear Creek	Cottonwood Creek
2	Deer Creek	Mill Creek
3	Pit River	McCloud River
4	Middle Fork Feather River	North Fork Feather River
5	South Fork Feather River	West Fork Feather River
6	Middle Fork American River	North Fork American River
7	Mokulumne River	Stanislaus River
8	South Fork American River	Thomes Creek

References

Adkison, M. D. 1995. Population differentiation in Pacific salmon: Local adaptation, genetic drift, or the environment? Canadian Journal of Fisheries and Aquatic Sciences **52**:2762–2777.

Aeschlimann, P. B., M. A. Haberli, T. B. H. Reusch, T. Boehm, and M. Milinski. 2003. Female sticklebacks *Gasterosteus aculeatus* use self-reference to optimize MHC allele number during mate selection. Behavioral Ecology and Sociobiology **54**:119–126.

Alderice, D. F. and F. P. J. Velsen. 1978. Relation between temperature and incubation time for eggs of chinook salmon (*Oncorhynchus tshawytscha*). Journal of the Fisheries Research Board Canada **35**:69–75.

Banks, M. A., V. K. Rashbrook, M. J. Calavetta, C. A. Dean, and D. Hedgecock. 2000. Analysis of microsatellite DNA resolves genetic structure and diversity of chinook salmon (*Oncorhynchus tshawytscha*) in California's Central Valley. Canadian Journal of Fisheries and Aquatic Sciences **57**:915–927.

Barlow, G. W. 1995. The relevance of behavior and natural history to evolutionarily significant units. In J. L. Nielsen, editor, *Evolution and the aquatic ecosystem: defining unique units in population conservation*, pp. 169–175. American Fisheries Society Symposium 17, Bethesda, MD.

Beer, W. N. and J. J. Anderson. 1997. Modeling the growth of salmonid embryos. Journal of Theoretical Biology **189**:297–306.

Beer, W. N. and J. J. Anderson. 2001. Effects of spawning behavior and temperature profiles on salmon emergence: Interpretations of a growth model for Methow River chinook. Canadian Journal of Fisheries and Aquatic Sciences **58**:943–949.

Berman, C. H. 1990. The effect of elevated holding temperatures on adult spring chinook salmon reproductive success. M.s. thesis, University of Washington.

Billington, N. and P. D. N. Hebert. 1991. Mitochondrial-DNA diversity in fishes and its implications for introductions. Canadian Journal of Fisheries and Aquatic Sciences **48**:80–94.

Brett, J. R. 1979. Environmental factors and growth. In W. S. Hoar, D. J. Randall, and J. R. Brett, editors, *Fish Physiology*. Academic Press, New York.

Burnham, K. P. and D. R. Anderson. 1998. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York.

California Department of Fish and Game. 1998. Report to the Fish and Game Commission: a status review of the spring-run chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento River drainage. California Department of Fish and Game, Sacramento, CA.

California Department of Water Resources (CDWR). 1994. California Central Valley unimpaired flow data. Third edition, California Department of Water Resources, Sacramento, CA.

Candy, J. R. and T. D. Beacham. 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged chinook salmon (*Oncorhynchus tshawytscha*) populations. Fisheries Research **47**:41–56.

Clark, G. H. 1943. Salmon at Friant Dam. California Fish and Game **29**:89–91.

Currens, K., J. Doyle, R. Fuerstenberg, W. Graeber, K. Rawson, M. Ruckelshaus, N. Sands, and J. Scott. 2002. Independent populations of chinook salmon in Puget Sound. Puget Sound TRT final draft. NOAA Fisheries, Seattle, WA.

Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs **61**:115–143.

Gabriel, K. 1971. The Biplot graphic display of matrices with applications to principal component analysis. Biometrika **58**:453–467.

Gall, G. A. E., D. Bartley, B. Bentley, J. Brodziak, R. Gomulkiewicz, and M. Mangel. 1991. Geographic variation in population genetic structure of chinook salmon from California and Oregon. Fishery Bulletin **90**:77–100.

Goodman, D. A. 1987. The demography of chance extinctions. In M. E. Soulé, editor, *Viable populations for conservation*, pp. 11–34. Cambridge University Press.

Hallerman, E. M. 2003. *Population Genetics: Principles and Applications for Fisheries Scientists*. American Fisheries Society, Bethesda, MD.

Hanski, I. and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society **42**:3–16.

Hanson, H. A., O. R. Smith, and P. R. Needham. 1940. An investigation of fish-salvage problems in relation to Shasta Dam. Special Scientific Report No. 10, United States Department of the Interior, Bureau of Fisheries, Washington, DC.

Hard, J. J. and W. R. Heard. 1999. Analysis of straying variation in Alaskan hatchery chinook salmon (*Oncorhynchus tshawytscha*) following transplantation. Canadian Journal of Fisheries and Aquatic Sciences **56**:578–589.

Harvey, A. C. 1989. *Forecasting, structural time series models and the Kalman filter*. Cambridge University Press.

Hastings, W. K. 1970. Monte Carlo sampling methods using Markov chains and their applications. Biometrika **57**:97–109.

Healey, M. C. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). In C. Margolis and L. Groot, editors, *Pacific salmon life histories*, pp. 311–394. University of British Columbia Press, Vancouver.

Healey, M. C. 1994. Variation in the life history characteristics of chinook salmon and its relevance to conservation of the Sacramento winter run of chinook salmon. Conservation Biology **8**:876–877.

Healey, M. C. and A. Prince. 1995. Scales of variation in life history tactics of Pacific salmon and the conservation of phenotype and genotype. In J. L. Nielsen, editor, *Evolution and the aquatic ecosystem: defining unique units in population conservation*, pp. 176–184. American Fisheries Society Symposium 17, Bethesda, MD.

Hedgecock, D. 2002. Microsatellite DNA for the management and protection of California's Central Valley chinook salmon (*Oncorhynchus tshawytscha*). Final report for the amendment to agreement No. B-59638. UC Davis, Bodega Bay, CA.

Hedgecock, D., M. A. Banks, V. K. Rashbrook, C. A. Dean, and S. M. Blankenship. 2001. Applications of population genetics to conservation of chinook salmon diversity in the Central Valley. In: Contributions to the Biology of Central Valley Salmonids. Fish Bulletin (CDFG) **179**:45–70.

Hickman, J. C. 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley, CA.

Hinze, J. A. 1959. Annual report Nimbus salmon and steelhead hatchery fiscal year of 1957-58. California Department of Fish and Game, Sacramento, CA.

Holmes, E. E. 2001. Estimating risks in declining populations with poor data. Proceedings of the National Academy of Sciences **98**:5072–5077.

Hotelling, H. 1933. Analysis of a complex of statistical variables into principal components. Journal of Educational Psychology **24**:417–41, 498–520.

Ihaka, R. and R. Gentleman. 1996. R: A Language for Data Analysis and Graphics. Journal of Computational and Graphical Statistics **5**:299–314.

Interior Columbia Basin Technical Recovery Team. 2003. Independent populations of chinook, steelhead, and sockeye for listed Evolutionary Significant Units within the interior Columbia River domain. Working draft, NOAA Fisheries, Seattle, WA.

Kim, T. J., K. M. Parker, and P. W. Hedrick. 1999. Major histocompatibility complex differentiation in Sacramento River chinook salmon. Genetics **151**:1115–1122.

Kratz, T. K., B. J. Benson, E. R. Blood, G. L. Cunningham, and R. A. Dahlgren. 1991. The influence of landscape position on temporal variability in four North American ecosystems. American Naturalist **138**:355–378.

Kruskal, J. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika **29**:1–27.

Langan, S. J., L. Johnston, M. J. Donaghy, A. F. Youngson, D. W. Hay, and C. Soulsby. 2001. Variation in river water temperatures in an upland stream over a 30-year period. The Science of the Total Environment **265**:195–207.

Legendre, P. and L. Legendre. 1998. *Numerical Ecology*. Elsevier, Amsterdam, 2nd English ed.

Lindley, S. T. 2003. Estimation of population growth and extinction parameters from noisy data. Ecological Applications **13**:806–813.

Mayr, E. 1993. Fifty years of progress in research on species and speciation. Proceedings of the California Academy of Sciences **48**:131–140.

McCullough, D. A. 1999. A review and synthesis of effects of alteration to the water temperature regime on freshwater life stages of salmonids, with special reference to chinook salmon. Document 910-R-99010, United States Environmental Protection Agency, Region 10.

McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonid populations and the conservation of evolutionarily significant units. NOAA Tech. Memo. NMFS-NWFSC-42, U.S. Dept. of Commerce, Seattle, WA. Http://www.nwfsc.noaa.gov/pubs/tm/tm42/tm42.pdf.

Metropolis, N., A. W. Rosenbluth, M. N. Rosenbluth, A. H. Teller, and E. Teller. 1953. Equations of state calculations by fast computing machine. Journal of Chemical Physics **21**:1087–1091.

Mohseni, O., H. G. Stefan, and T. R. Erickson. 1998. A nonlinear regression model for weekly stream temperatures. Water Resources Research **34**:2684–2692.

Montgomery, D. R., J. M. Buffington, N. P. Peterson, D. Schuett-Hames, and T. P. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences **53**:1061–1070.

Moyle, P. B., J. J. Smith, R. A. Daniels, T. L. Taylor, D. G. Price, and D. M. Baltz. 1982. *Distribution and ecology of stream fishes of the Sacramento-San Joaquin drainage system, California*. University of California Press, Berkeley, CA.

Murray, C. B. and T. D. Beacham. 1987. The development of chinook (*Oncorhynchus tshawytscha*) and chum salmon (*Oncorhynchus kisutch*) in British Columbia. Canadian Journal of Zoology **68**:347–358.

Nielsen, J. L., C. Carpanzano, M. C. Fountain, and C. A. Gan. 1997. Mitochondrial DNA and nuclear microsatellite diversity in hatchery and wild *Oncorhynchus mykiss* from freshwater habitats in Southern California. Transactions of the American Fisheries Society **126**:397–417.

Pascual, M. A. and T. P. Quinn. 1995. Factors affecting the homing of fall chinook salmon from Columbia River hatcheries. Transactions of the American Fisheries Society **124**:308–320.

Pearson, K. 1901. On lines and planes of closest fit to a system of points in space. Philosophical Magazine **2**:557–72.

Poff, N. L. and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences **46**:1805–1818.

Poff, N. L. and J. V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. Environmental Management **14**:629–645.

Quinn, T. P. and K. Fresh. 1984. Homing and straying in chinook salmon (*Oncorhynchus tshawytscha*) from Cowlitz River hatchery, Washington. Canadian Journal of Fisheries and Aquatic Sciences **41**:1078–1082.

Quinn, T. P., M. T. Kinnison, and M. J. Unwin. 2001. Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. Genetica **112**:493–513.

Quinn, T. P., R. S. Nemeth, and D. O. McIsaac. 1991. Homing and straying patterns of fall chinook salmon in the lower Columbia River USA. Transactions of the American Fisheries Society **120**:150–156.

Quinn, T. P., M. J. Unwin, and M. T. Kinnison. 2000. Evolution of temporal isolation in the wild: Genetic divergence in timing of migration and breeding by introduced chinook salmon populations. Evolution **54**:1372–1385.

Shepard, R. N. 1962. The analysis of proximities: multidimensional scaling with an unknown distance function. Psychometrika **27**:125–140; 219–246.

Tallman, R. F. and M. C. Healey. 1994. Homing, straying, and gene flow among seasonally separated populations of chum salmon (*Oncorhynchus keta*). Canadian Journal of Fisheries and Aquatic Sciences **51**:577–588.

The Bay Institute. 1998. From the Sierra to the sea: the ecological history of the San Francisco Bay-Delta watershed. The Bay Institute, Novato, CA.

USACOE. 2002. Sacramento and San Joaquin River basins comprehensive study. Appendix B. Synthetic hydrology technical documentation. US Army Corps of Engineers, Sacramento, CA.

Waples, R. S., D. Teel, J. M. Myers, and A. Marshall. 2004. Life history evolution in chinook salmon: historic contingency and parallel evolution. Evolution **58**:386–403.

Williamson, K. and B. May. 2003. Homogenization of fall-run chinook salmon gene pools in the Central Valley of California, USA Completion report for CALFED grant #97-C09 via California Department of Fish and Game Contract Agreement No. P0140015. 150pp.

Yoshiyama, R. M., E. R. Gerstung, F. W. Fisher, and P. B. Moyle. 1996. Historical and present distribution of chinook salmon in the Central Valley drainage of California. Sierra Nevada Ecosystem Project, Final Report to Congress, Volume 3. University of California.

Yoshiyama, R. M., E. R. Gerstung, F. W. Fisher, and P. B. Moyle. 2001. Historic and present distribution of chinook salmon in the Central Valley drainage of California. In R. L. Brown, editor, *Fish Bulletin 179: Contributions to the biology of Central Valley salmonids.*, vol. 1, pp. 71–176. California Department of Fish and Game, Sacramento, CA.

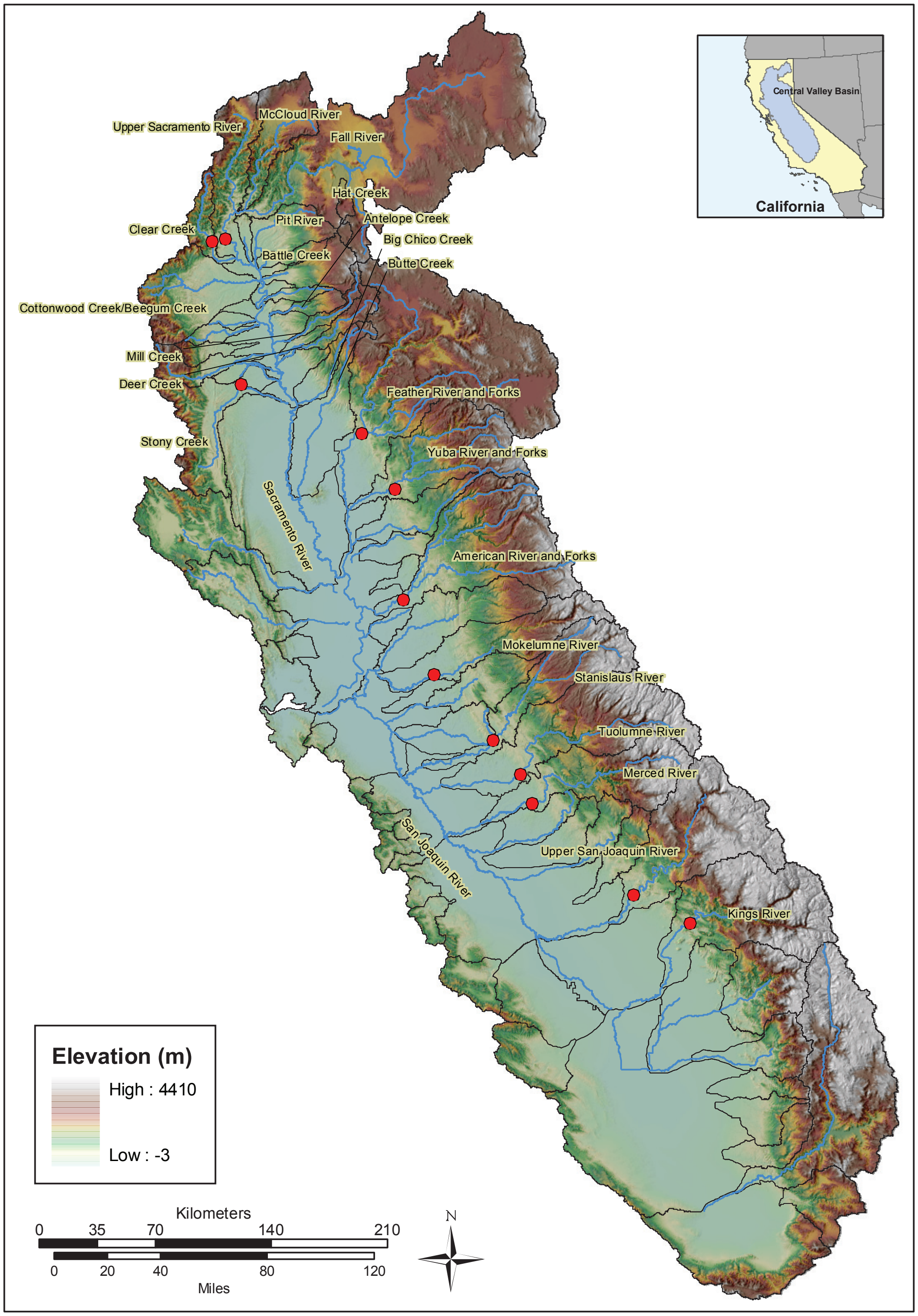

Plate 1. Map of the Central Valley basin, showing elevation, major rivers and streams (blue lines) and their associated watersheds (black lines), and major barriers to fish passage (red dots).

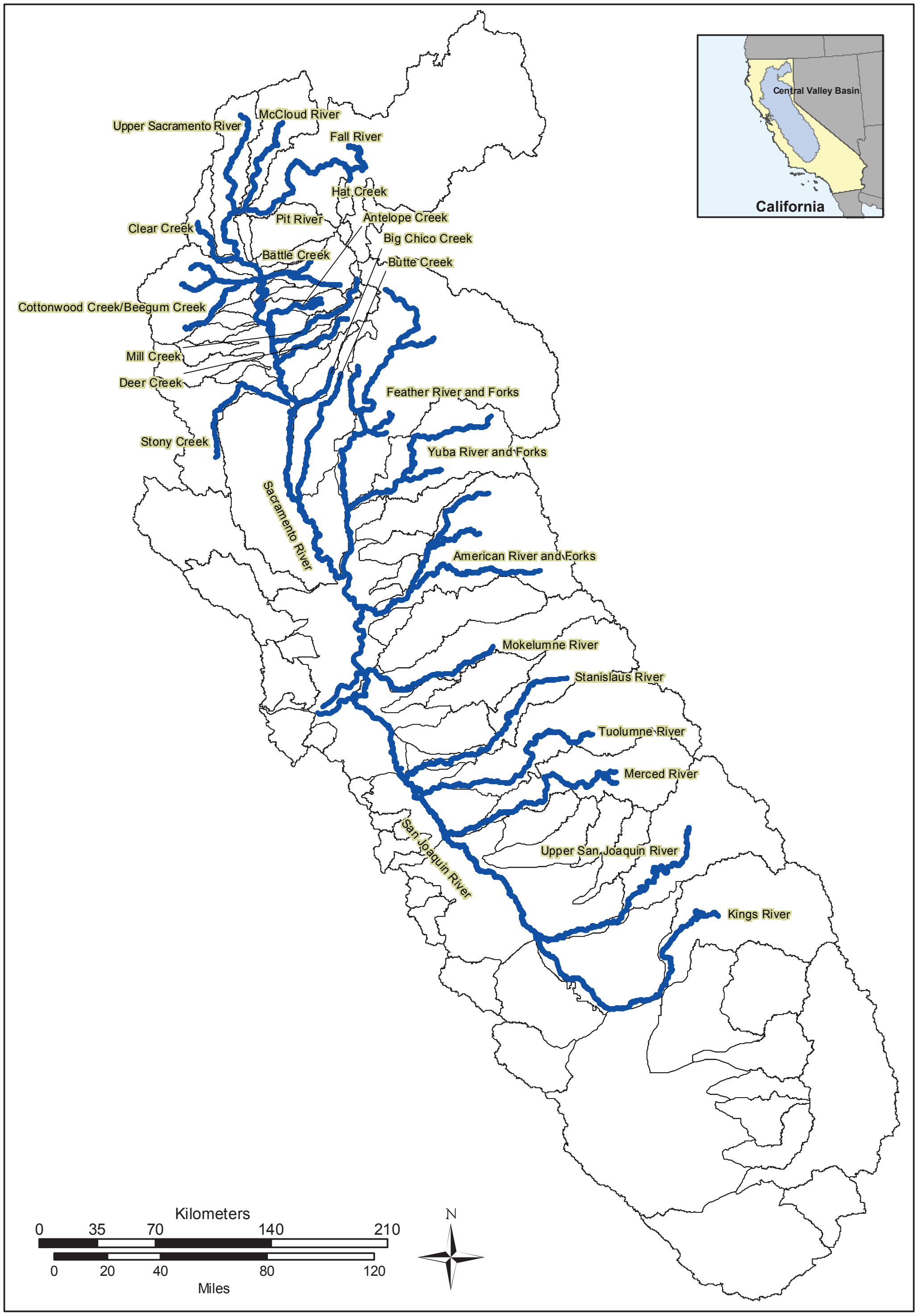

Plate 2. Historic distribution of spring-run chinook salmon in the Central Valley. Distribution information from Yoshiyama et al. (1996).

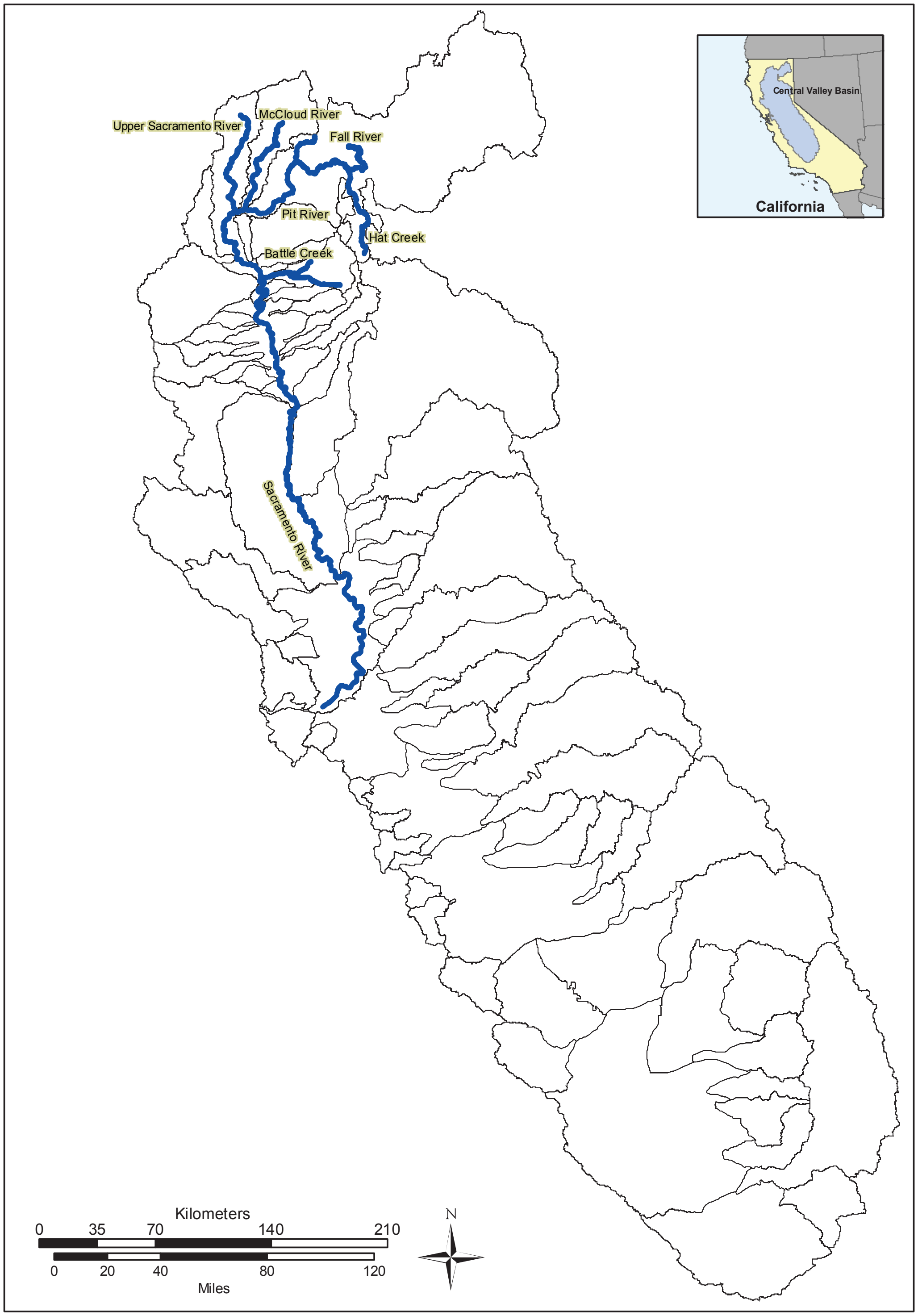

Plate 3. Historic distribution of winter-run chinook salmon in the Central Valley. Distribution information from Yoshiyama et al. (1996).

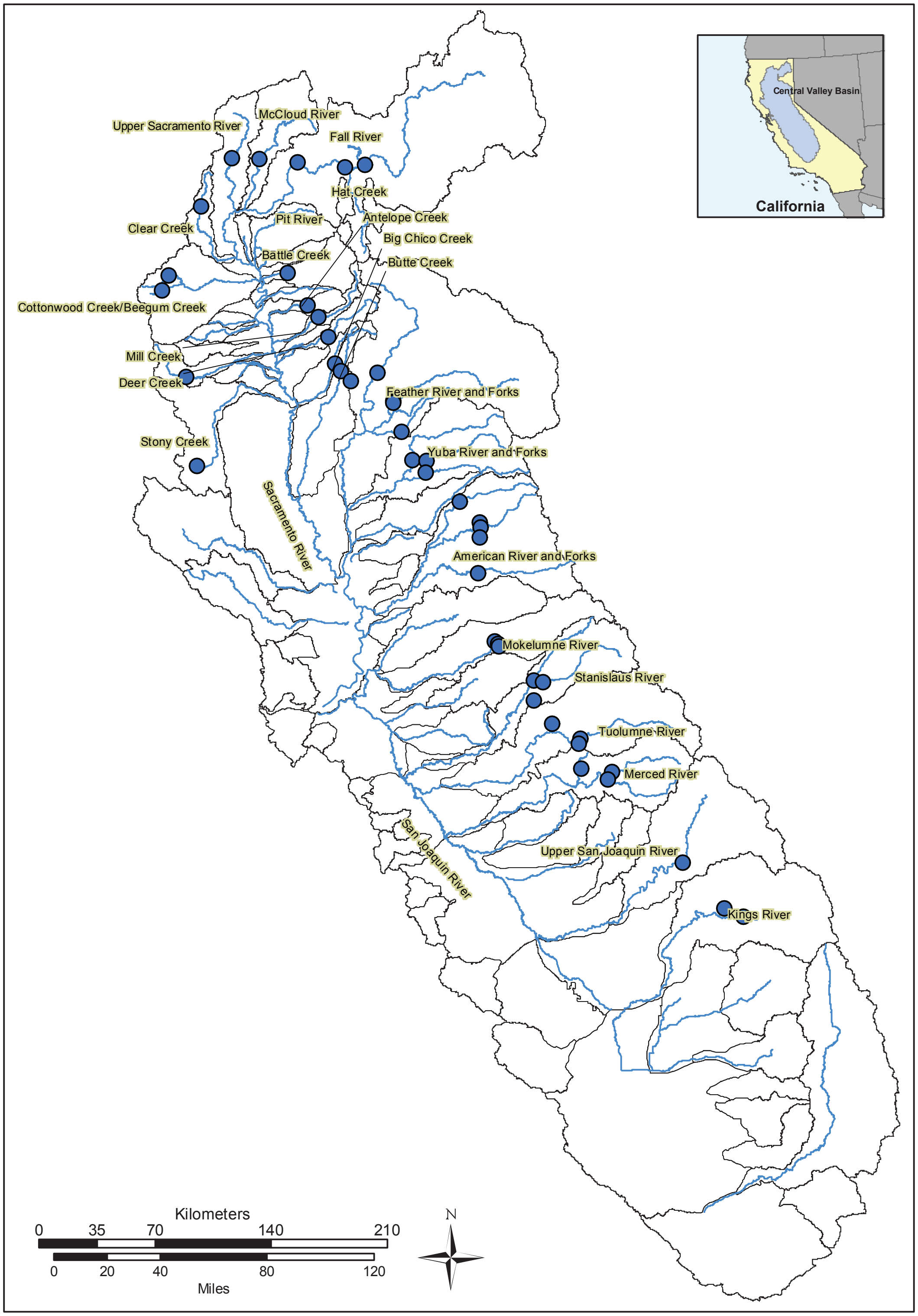

Plate 4. Points used to calculate distances among watersheds.

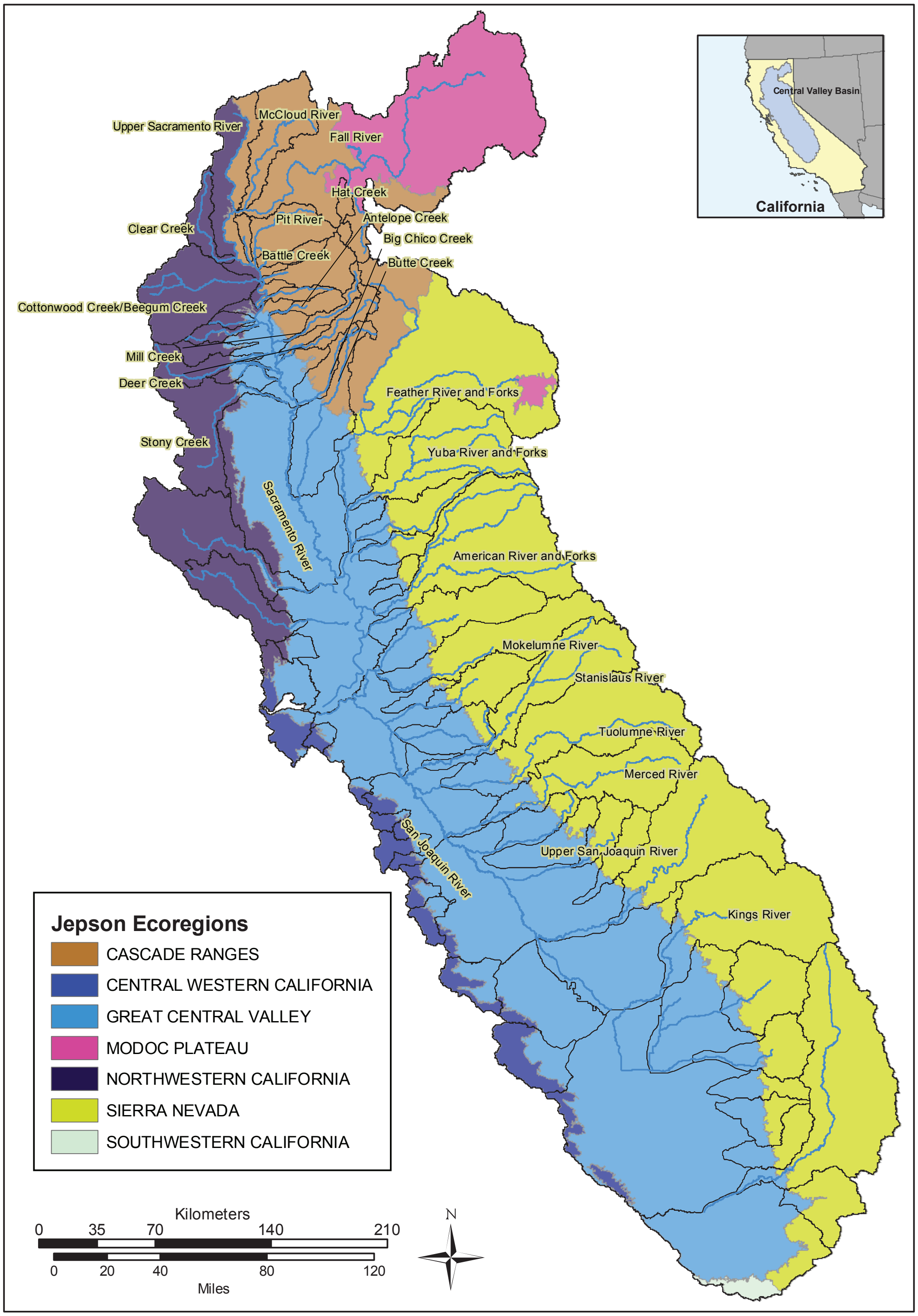

Plate 5. Floristic regions of the Central Valley basin.

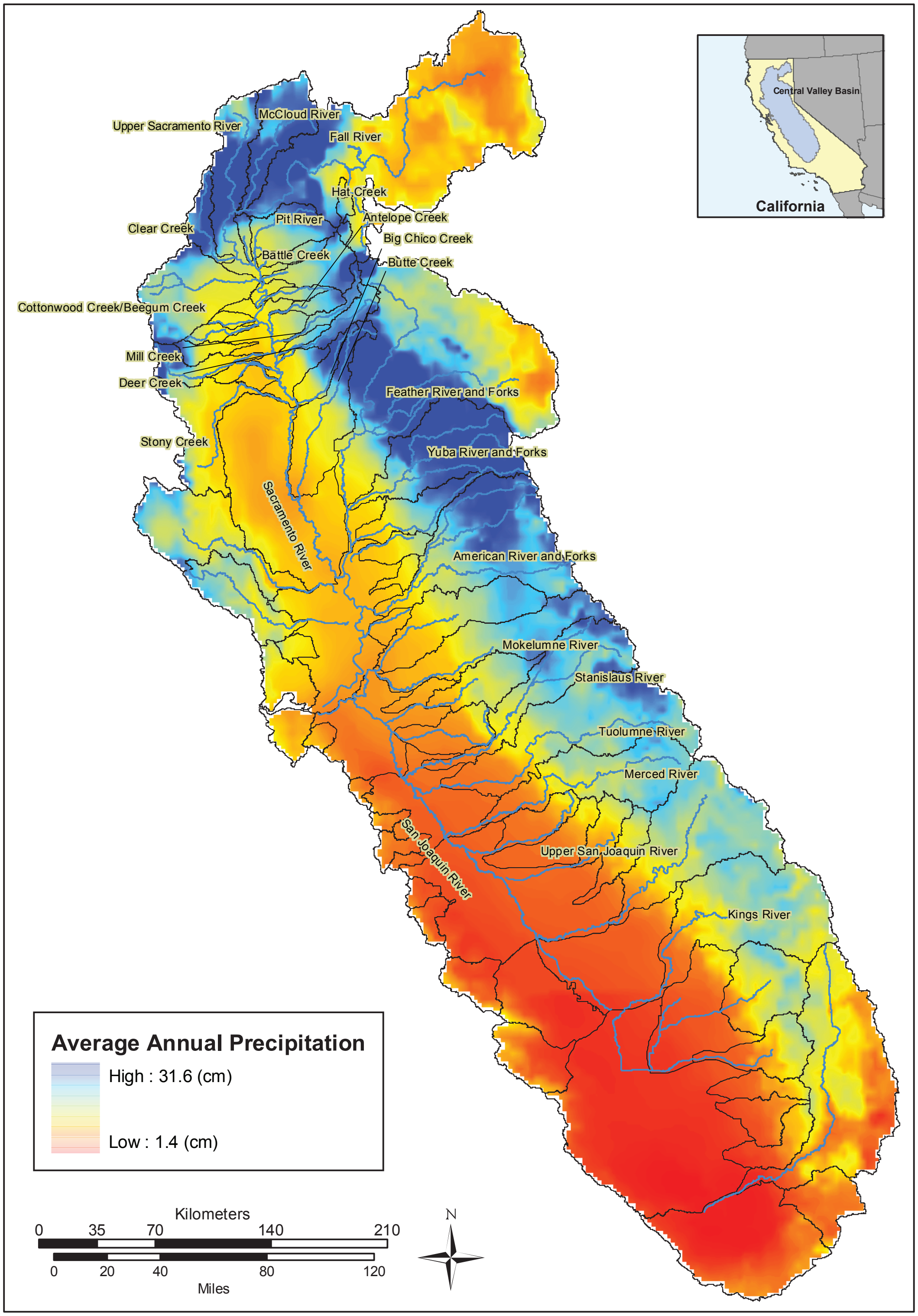

Plate 6. Average annual precipitation.

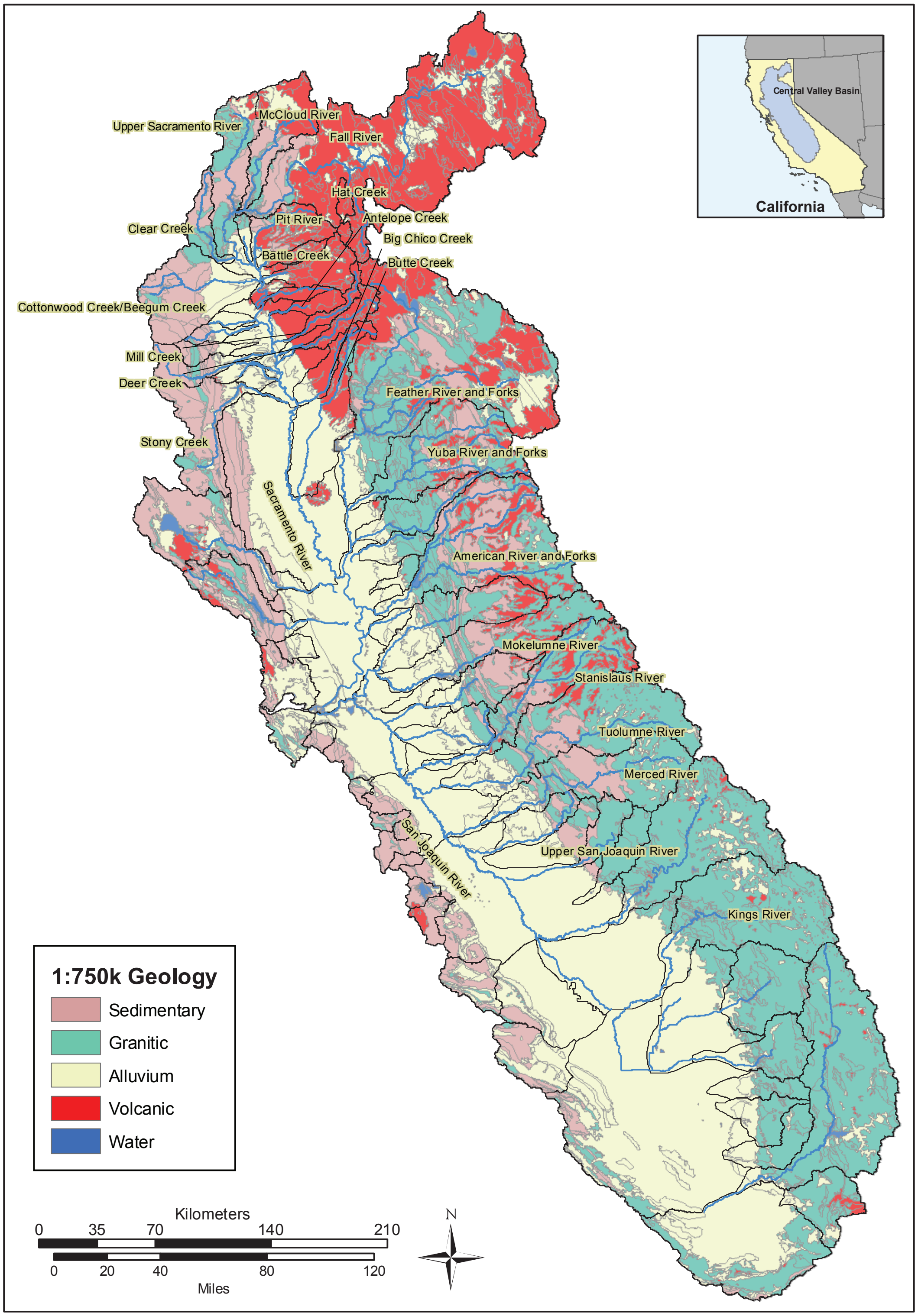

Plate 7. Geology of the Sacramento-San Joaquin basin.

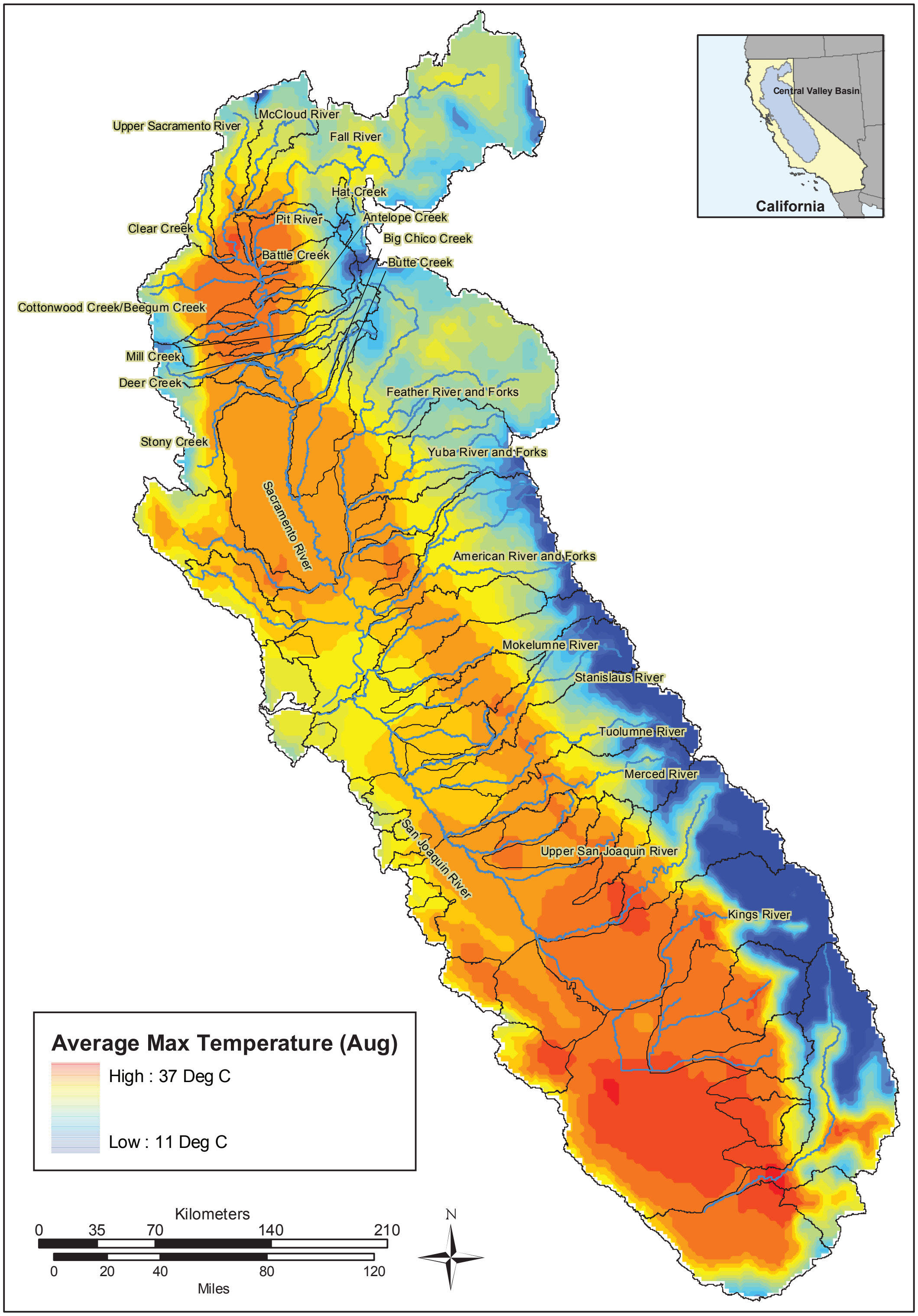

Plate 8. Average maximum August temperature.

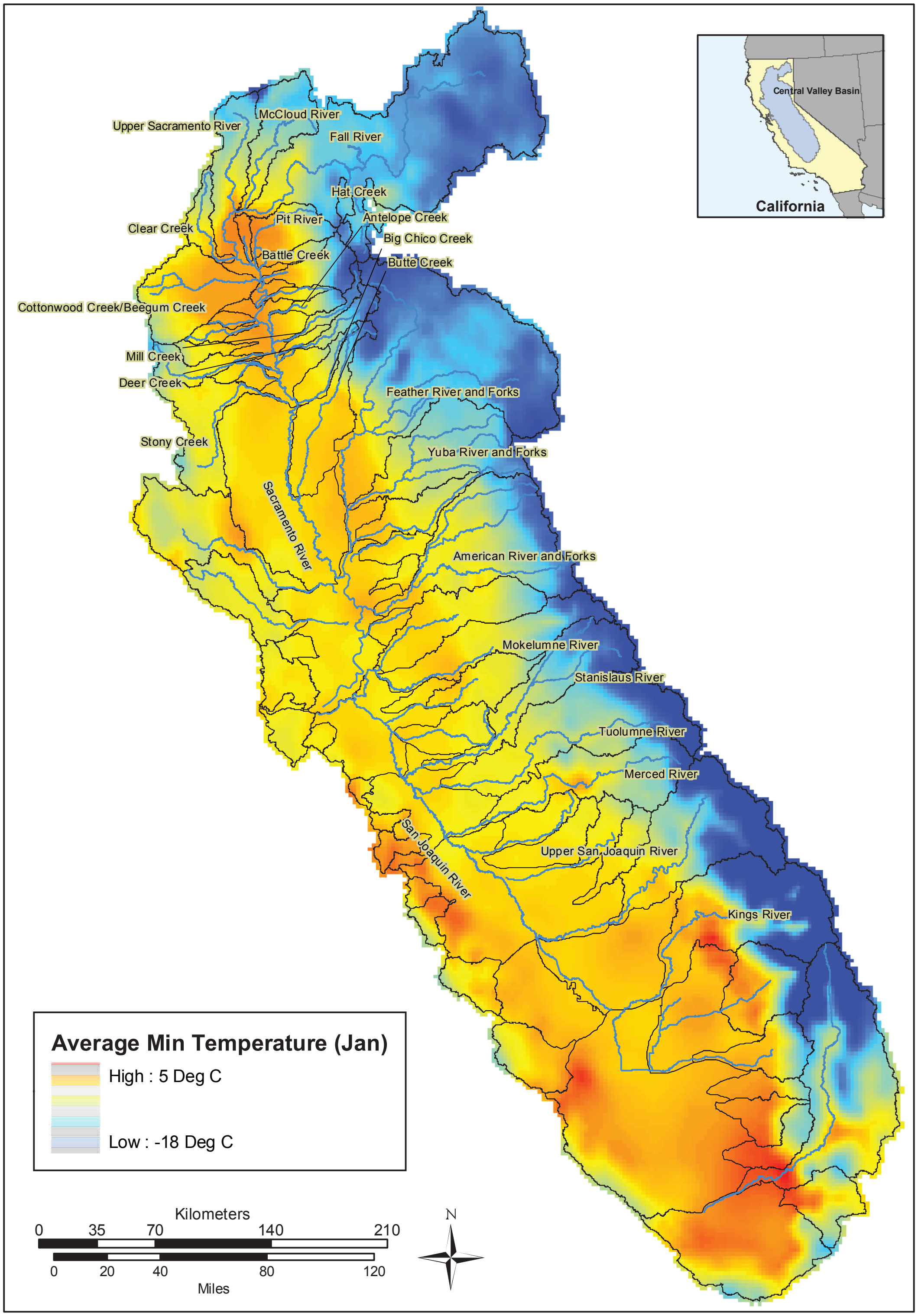

Plate 9. Average minimum January temperature.

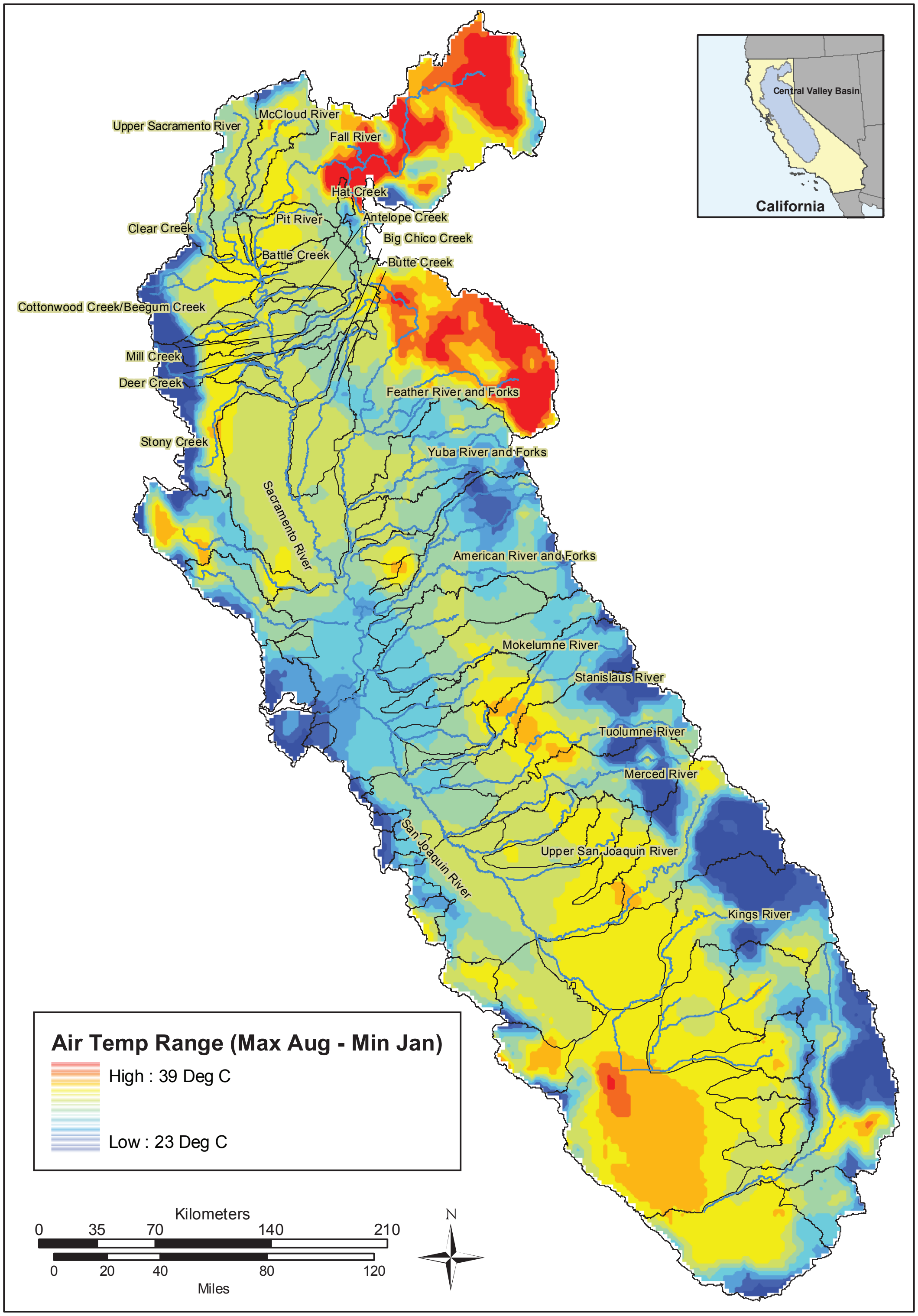

Plate 10. Temperature range (average maximum August temperature - average minimum temperature in January.

SAN FRANCISCO Estuary & Watershed SCIENCE

Historical Population Structure of Central Valley Steelhead and its Alteration by Dams

STEVEN T. LINDLEY[1], ROBERT S. SCHICK[1], ADITYA AGRAWAL[2], MATTHEW GOSLIN[2], THOMAS E. PEARSON[2], ETHAN MORA[2], JAMES J. ANDERSON[3], BERNARD MAY[4], SHEILA GREENE[5], CHARLES HANSON[6], ALICE LOW[7], DENNIS MCEWAN[7], R. BRUCE MACFARLANE[1], CHRISTINA SWANSON[8] AND JOHN G. WILLIAMS[9]

ABSTRACT

Effective conservation and recovery planning for Central Valley steelhead requires an understanding of historical population structure. We describe the historical structure of the Central Valley steelhead evolutionarily significant unit using a multi-phase modeling approach. In the first phase, we identify stream reaches possibly suitable for steelhead spawning and rearing using a habitat model based on environmental envelopes (stream discharge, gradient, and temperature) that takes a digital elevation model and climate data as inputs. We identified 151 patches of potentially suitable habitat with more than 10 km of stream habitat, with a total of 25,500 km of suitable habitat. We then measured the distances among habitat patches, and clustered together patches within 35 km of each other into 81 distinct habitat patches. Groups of fish using these 81 patches are hypothesized to be (or to have been) independent populations for recovery planning purposes. Consideration of climate and elevation differences among the 81 habitat areas suggests that there are at least four major subdivisions within the Central Valley steelhead ESU that correspond to geographic regions defined by the Sacramento River basin, Suisun Bay area tributaries, San Joaquin tributaries draining the Sierra Nevada, and lower-elevation streams draining to the Buena Vista and Tulare basins, upstream of the San Joaquin River. Of these, it appears that the Sacramento River basin was the main source of steelhead production. Presently, impassable dams block access to 80% of historically available habitat, and block access to all historical spawning habitat for about 38% of the historical populations of steelhead.

KEYWORDS

Steelhead, *O. mykiss*, endangered species, population structure, dispersal, habitat model, dams, Central Valley.

---

1. National Oceanic and Atmospheric Administration
2. University of California, Santa Cruz
3. University of Washington
4. University of California, Davis
5. California Department of Water Resources
6. Hanson Environmental, Inc.
7. California Department of Fish and Game
8. The Bay Institute
9. 875 Linden Lane, Davis, CA

INTRODUCTION

Steelhead (*O. mykiss*) in California's Central Valley were identified as an evolutionarily significant unit (ESU) and listed in 1998 as a threatened species under the U.S. Endangered Species Act (1973). Myriad problems afflict steelhead in the Central Valley: impassable dams block access to much of the historically available spawning and rearing habitat (Yoshiyama and others 1996), and water diversions and withdrawals, conversion of riparian zones to agriculture, introduced species, water pollution, disruption of gravel supply, and other factors have degraded much of the habitat below the dams (McEwan 2001). Recovering Central Valley *O. mykiss* presumably will require some mix of improved access to historically available habitat and restoration of degraded habitat. A better understanding of the current and historical distribution and population structure of *O. mykiss* in the Central Valley will be critical for guiding such restoration actions, but currently available information deals with changes in distribution at a fairly coarse level and does not address population structure.

Detailed distribution data at the population level are fundamental to planning effective restoration and protection activities. In the short term, one must know where a species occurs in order to efficiently safeguard its existence. In the longer term, an understanding of historical distribution is important because it gives insight into how the species might have survived catastrophic disturbances. Prior to the era of intensive anthropogenic impacts, the Central Valley steelhead ESU apparently survived prolonged droughts (Ingram and others 1996), catastrophic volcanic eruptions (Kerr 1984), landslides triggered by fires, floods and earthquakes (Keefer 1994), and other devastating events, although individual populations of Central Valley steelhead probably were extirpated from time to time. Following recovery from disturbance, catastrophically disturbed areas likely were recolonized by neighboring populations whose members were adapted to similar environmental conditions. Understanding the historical distribution of populations within an ESU is therefore important to understanding how the ESU persisted in the past and how an altered ESU might or might not persist in the future.

To the extent that environmental conditions vary across the range of an ESU, population structure could influence the ability of the ESU to respond to climate or other sources of ecological change, as well as its resilience to catastrophic disturbances. McEwan (2001) concluded that steelhead were widely distributed in the Central Valley, ranging from the Pit River in the north to perhaps the Kings River in the south, a distribution spanning multiple ecoregions and climate zones. This wide distribution across diverse ecological conditions should have provided Central Valley *O. mykiss* with substantial opportunities for adaptation to local conditions, creating the genetic variation required for adaptation to changing conditions (Darwin 1859). While such variation would be important for ESU persistence, it also limits the ability of some populations to rescue others because the fitness of a locally adapted population would be expected to be lower in other environments (Taylor 1991). Knowing which populations might have members that are ecologically exchangeable would help guide reintroductions, should currently empty and degraded habitats be restored, and help to prioritize populations for conservation.

Habitat modeling is often used to extrapolate from and interpolate between observations of species occurrence to provide the comprehensive picture of the distribution of species that is needed to guide conservation and restoration. Ideally, habitat units are sampled randomly for the presence of the species and various qualities of the habitat are measured, allowing resource selection functions to be estimated (Manly and others 2002). These resource selection functions can then be used to characterize the suitability of habitat units that were not sampled for the occurrence of the species but for which the habitat information is available. A related but simpler approach is to characterize environmental attributes associated with specimen collections in terms of envelopes that characterize habitat as either suitable or unsuitable. The edges of these envelopes are defined by the most extreme conditions under which the organism has been commonly observed. Once defined, the envelopes can be used with appropriate environmental data to predict the distributional limits of the species. Within these distributional limits, the species may or may not be found, depending on the effects of other factors not characterized by the envelopes, but the species is not expected to be found outside of this distribution. Originally developed for predicting the distribution of agricultural pests (Cook 1929), such models are increasingly used in conservation planning for many species (e.g., Johnson and others 2004; Argáez and others 2005; Chefaoui and others 2005), including fish (Burnett and others 2003; Valavanis and others 2004; Wall and others 2004; Quist and others 2005).

In this paper, we use habitat models to describe the historical structure of the Central Valley *O. mykiss* ESU and assess how impassable dams have altered this structure. We start with a model of steelhead habitat to identify stream reaches within the Central Valley that were likely to have supported *O. mykiss* during summer months. We then analyze the spatial distribution of these stream reaches to identify clusters of reaches that are isolated from other clusters. These isolated clusters of stream reaches are presumed to have supported independent populations of *O. mykiss*. We assess the degree to which populations may be exchangeable by quantifying differences in climatic conditions experienced by the populations. Finally, we assess how man-made impassable barriers have reduced the amount of habitat available to steelhead, and how this reduction in habitat has altered the structure of the ESU.

METHODS

Modeling the Distribution of *O. mykiss*

O. mykiss habitat was predicted using two models. The first model predicts the spatial location of stream reaches, along with their mean annual discharge and gradient, using a digital elevation model (DEM) and precipitation (the PRISM data set (Daly and others 2002)) as inputs (Burnett and others 2003). Where available, we used the USGS 10-m DEM; where this was not available, we created a 10-m DEM by interpolating the USGS 30-m DEM to 10 m using a regularized spline procedure (SPLINE function, ArcGIS Ver. 9, ESRI, Redlands, CA). We recalibrated the precipitation-discharge equations in Burnett and others' (2003) model with data from the Central Valley (Appendix A).

The second model is a set of simple rules, or environmental envelopes, that define whether a given stream segment is suitable for steelhead. The envelopes include mean annual discharge (suitable if $>0.028\ m^3s^{-1}$), gradient (suitable if <12%), and mean August air temperature (suitable if <24°C), and whether the area was considered by Knapp (1996) to be fishless prior to anthropogenic introductions. We are aware of no published data suitable for identifying a lower discharge limit for steelhead, but Harvey and others (2002) found that the density of age one-year-old-or-older steelhead was lower in streams with lower discharge in tributaries to the Eel River. A discharge of 0.028 $m^3 s^{-1}$ (or 1 cubic foot per second) was taken as a lower bound, although data of Harvey and others (2002) suggest that steelhead occasionally occur in streams with somewhat lower discharge. Steelhead are commonly found in stream reaches with gradients less than 6% (Burnett 2001; Harvey and others 2002; Hicks and Hall 2003), but in some systems they are not uncommon in reaches with gradients of up to 12% (and occasionally higher) (Engle 2002). Stream temperature is linearly related to air temperature between 0 and 24°C (Mohseni and others 1998). Steelhead in southern California are almost never found in areas where mean August air temperatures exceed 24°C (D. Boughton, NOAA Fisheries Santa Cruz Lab, in preparation). Schmidt and others (1979) reviewed available information on thermal tolerance of *O. mykiss*, and found that 24°C was the highest reported maximum temperature for *O. mykiss* rearing. More recently, Nielsen and others (1994) found that 24°C was the upper lethal temperature for juvenile steelhead in northern California. In the Eel River, steelhead were not found in streams with maximum weekly average summer temperatures greater than 22°C (Harvey and others 2002). Knapp (1996) developed a GIS coverage of historical fish distributions through a survey of published papers and unpublished reports. Most areas of the western Sierra Nevada above 1500-m elevation were historically fishless due to Pleistocene glaciation and numerous migration barriers (Moyle and Randall 1998). The final output of this stage of the analysis was a GIS dataset describing a collection of stream segments suitable for *O. mykiss*, connected by unsuitable stream segments.

Identification of Independent Populations

Following McElhany and others (2000), we define independent populations 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." Within a basin such as the Central Valley, high summer temperatures at lower elevations fragment otherwise acceptable and continuous habitat into enclaves of interconnected habitats isolated from one another by downstream regions of thermally unsuitable habitat (Rahel and others 1996). If these enclaves are far enough apart, we expect that the enclaves will function as independent populations. We therefore intersected the 24°C mean August air temperature isotherm with the stream network to identify downstream boundaries of habitat patches. We assume implicitly that while discharge, gradient, and temperature all affect the suitability of a habitat, only temperature restricts movement between habitat patches. We computed the distance along the stream network among these downstream edges with the NODEDISTANCE function in the Network Module of ArcInfo, creating a matrix of distances among habitat patches. We used hierarchical clustering with a simple distance-based rule to group nearby patches into independent populations using the LINKAGE function (with the single linkage algorithm) in Matlab (Version 6.5.1, The Mathworks, Natick, MA). Following the Interior Columbia Basin Technical Recovery Team (2003), who reviewed available information on straying of Pacific salmonids, we chose 35 km as the critical dispersal distance: patches that link at 35 km were grouped together as independent populations. The sensitivity of the population delineation to the distance criterion was examined by calculating how the number of clusters declines with increasing linkage distance. If the total length of suitable stream habitat was less than 10 km, we ignored these small areas in subsequent analyses, on the assumption that isolated populations with less than 10 km of habitat would be unlikely to persist for long periods without immigration (Bjorkstedt and others 2005).

Quantification of Habitat Similarities

In most basins, spawning by salmonids can be successful only if it occurs at certain times, such that development and migration can occur before temperature or flow conditions become unsuitable (Montgomery and others 1996; Beer and Anderson 2001). Thus, climate, through its effects on stream temperature and flow regime, is thought to be an important selective force leading to local adaptation in salmonids (Burger and others 1985; Konecki and others 1995; Brannon and others 2004; Lytle and Poff 2004). As proxies for water temperature and flow, we characterized mean elevation (from the USGS DEM), mean annual precipitation and the temperature regime (annual mean, maximum monthly mean, minimum monthly mean and range of air temperature (all from PRISM)) over the watersheds containing the spawning and rearing habitats of each of the independent populations identified with the procedure above. Watershed boundaries were based on the CalWater 2.2 watershed map[1] of 1999, but in cases where CalWater boundaries follow political rather than geomorphic boundaries, we delineated boundaries by hand, following the DEM. We characterized the similarity of watersheds by calculating the Mahalanobis (1936) distance among the centroids of watersheds using the PDIST function in Matlab. The Mahalanobis distance reduces the effect of variables that are highly correlated with each other, and is equal to the normalized Euclidean distance between the centroids if variables are uncorrelated. We then used hierarchical clustering based on the average distance to join groups (using the LINKAGE function in Matlab), and plotted the results as a tree (with the DENDROGRAM function in Matlab).

Quantification of Habitat Loss to Dams

Goslin (2005) prepared a nearly comprehensive database of dams for California, using data from the Coastal Conservancy, McEwan (2001), USGS and the U.S. Army Corps of Engineers. We intersected these dams with our stream layer, and computed the amount of suitable habitat within each watershed that was above and below the lower-most dam that was impassable to anadromous fish, using the TRACE function in the network module of ArcInfo.

RESULTS

Distribution of *O. mykiss* Habitat

Our model identifies 25,500 km of stream habitat suitable for *O. mykiss*, broken up into 151 discrete habitat patches, each having at least 10 km of stream habitat (Figure 1). Rivers and streams on the valley floor are largely rated as unsuitable for spawning and rearing because of high summer temperatures. The exception to this are tributaries around Suisun Bay, where summer temperatures are moderated by the marine influence of the nearby San Francisco Bay and Pacific Ocean. Large portions of the upper watersheds draining the central Sierra are ruled out because they were historically fishless according to Moyle and Randall (1998). At intermediate elevations, many small tributaries to the major San Joaquin River tributaries are of too high gradient or too low flow to support *O. mykiss*, and *O. mykiss* are restricted to the mainstems and larger tributaries. Streams in the southern Cascades, coast range and northern Sierra, in contrast, appear to have much more *O. mykiss* habitat due to their lower elevation and more moderate stream gradients.

---

[1] The CalWater data can be obtained from the California Spatial Information Library, 900 N Street, Sacramento, CA 95814.

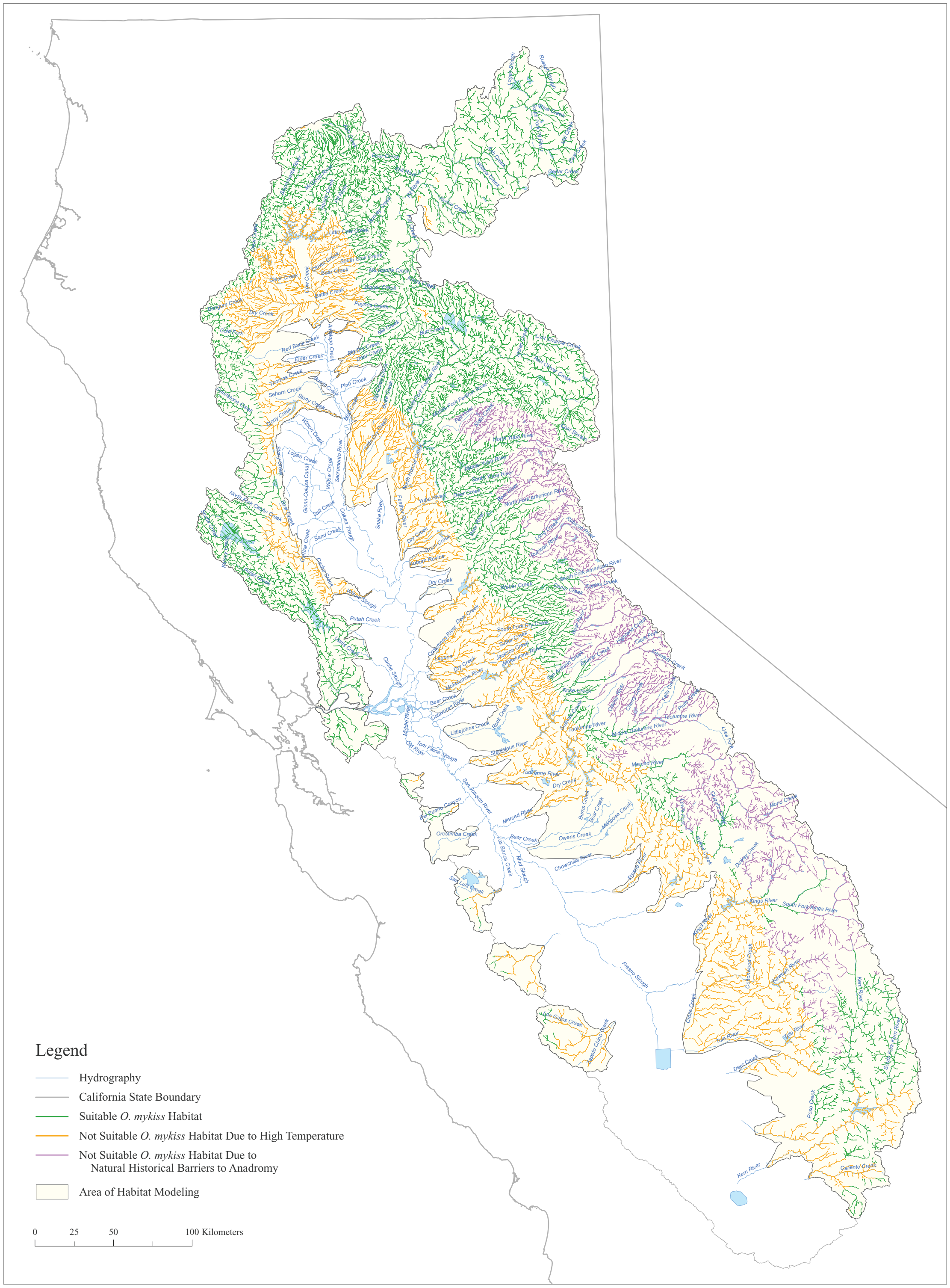

Figure 1. Predicted historical distribution of summer rearing habitat for anadromous *O. mykiss* (green). Stream reaches that would be suitable if not for high summer temperatures are shown in orange, and suitable stream reaches that were historically fishless due to natural migration barriers are shown in magenta. For legibility, streams with unsuitable gradient or discharge are not shown. Hydrography is USGS 1:1,000,000; other data are 1:24,000. (Click here for PDF file of larger image).

Independent Populations

Most subbasins of the Central Valley contain multiple discrete habitat patches, because high temperatures make the lower reaches of tributaries unsuitable in summer months. At a dispersal distance of 35 km, there are 81 clusters of habitat patches, suggesting 81 independent populations of steelhead in the Central Valley (Figure 2, Table 1). The geometry of a watershed and its relationship tothe 24°C August isotherm has a strong effect on the number of clusters within it: Cottonwood Creek, with its highly dendritic form and low elevation, has 6 isolated clusters, while the larger but more pinnate Tuolumne River contains a single cluster, as does the Pit River, which is entirely above the 24°C isotherm. The sizes of clusters are highly variable, with a few large clusters and many small ones (Table 1).

The choice of dispersal distance criterion has a strong effect on the number of independent populations identified by the clustering algorithm. There are only a few obvious breaks in the relationship between the number of clusters and the along-stream distance between them, occurring around 140, 225 and 280 km (Figure 3), corresponding roughly to the distance among the major subbasins of the Central Valley.

Similarity of Habitats

Figure 4 shows the similarity of the habitats occupied by the 81 independent populations of *O. mykiss* as a neighbor-joining tree based on Mahalanobis distance. As expected, nearby streams with similar mean elevations clustered together, although some San Joaquin tributaries clustered with Sacramento tributaries. Well-resolved clusters include the tributaries near Suisun Bay (including Sweany and Marsh creeks), the upper San Joaquin and its major tributaries draining the Sierra Nevada, the small west-side tributaries to the San Joaquin, tributaries to the now-dry Buena Vista and Tulare lakes, and a large group of Sacramento River tributaries. Within the large group of Sacramento tributaries are a few small tributaries that ultimately drain to the San Joaquin, including most notably the Calaveras River, but also smaller tributaries to the Merced, Kings and Mokelumne rivers. Some of the groupings shown in Figure 4 may be artifacts of representing the multidimensional environmental data as a neighbor-joining tree: the cophenetic coefficient (Sokal and Rohlf 1962) relating the tree to the underlying matrix of Mahalanobis distances is only 0.73 (an accurate representation would have a cophenetic coefficient close to 1.0).

Habitat Loss to Dams

About 80% of habitat identified by our model that was historically available to anadromous *O. mykiss* is now behind impassable dams, and 38% of the populations identified by the model have lost all of their habitat (Figure 5). Anadromous *O. mykiss* populations may have been extirpated from their entire historical range in the San Joaquin Valley and most of the larger basins of the Sacramento River. The roughly 52% of watersheds with at least half of their historical area below impassable dams are all small, low elevation systems. Of the eight population clusters that form at a Mahalanobis distance of 2 (Figure 4), for example, only two clusters contain watersheds with habitat that remains accessible to anadromous *O. mykiss*, suggesting that there has been a significant reduction in the diversity of habitats available to Central Valley *O. mykiss*.

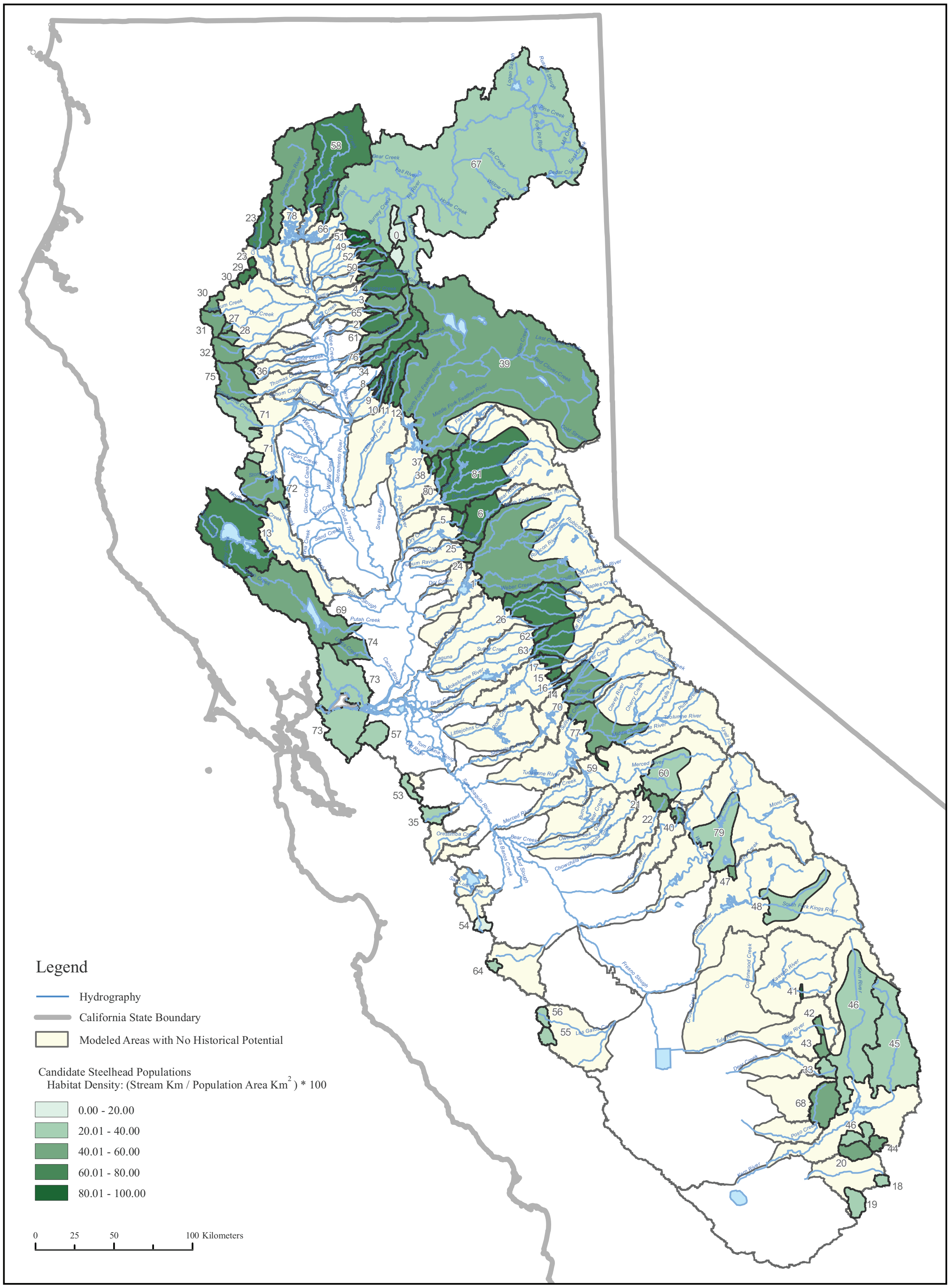

Figure 2. Spawning and rearing habitat areas of independent *O. mykiss* populations. Green polygons indicate habitat boundaries; color intensity indicates the density of habitat (km stream habitat km^{-2} x 100). (Click here for PDF file of larger image).

Table 1. Proposed historical independent populations of steelhead in the Central Valley

Independent Population	*Basin*	*Total Stream (km)*	*Streams*
1	American R.	1357.1	Auburn Ravine, NF
2	Antelope Cr	176.5	Cold Fork
3	Battle Cr	122.8	MF, SF
4	Battle Cr	349.1	Knob Gulch, NF, Rock Cr
5	Bear R (Feather trib)	58.5	NF
6	Bear R (Feather trib)	356.1	Long Valley Cr
7	Bear R (Sac trib)	51.5	Digger Cr, SF Bear Cr
8	Big Chico Cr	30.9	SF
9	Big Chico Cr	46.8	Rock Cr, mainstem
10	Big Chico Cr	114.9	East Branch Mud Cr
11	Butte Cr	29.2	MF
12	Butte Cr	269.4	mainstem
13	Cache Cr	1100.0	Deer Cr, Dry Cr, Wolf Cr, mainstem
14	Calaveras R	14.5	Woods Cr
15	Calaveras R	22.8	mainstem
16	Calaveras R	34.6	San Antonio Cr, San Domingo Cr
17	Calaveras R	71.9	McKinney Cr, O'Neil Cr
18	Caliente Cr	12.4	Indian Cr
19	Caliente Cr	60.5	Tehachapi Cr
20	Caliente Cr	75.8	Walker Basin
21	Chowchilla R	12.9	mainstem
22	Chowchilla R	61.3	Willow Cr, mainstem
23	Clear Cr	255.7	Crystal Cr, mainstem
24	Coon Cr	15.6	mainstem
25	Coon Cr	38.9	mainstem
	Cosumnes R	587.8	Cedar Cr, MF, NF, SF
27	Cottonwood Cr	16.8	mainstem
28	Cottonwood Cr	44.2	SF
29	Cottonwood Cr	55.2	Jerusalem Cr, Moon Fork, NF Bear Cr
30	Cottonwood Cr	62.4	Duncan Cr, Soap Cr, mainstem
31	Cottonwood Cr	96.8	Wells Cr
32	Cottonwood Cr	121.2	mainstem
33	Deer Cr (Kaweah trib)	46.2	Bull Run Cr, Chimney Cr, SF
34	Deer Cr (Sac trib)	299.4	Little Dry Cr
35	Del Puerto Cr	33.8	Whisky Cr
36	Elder Cr	59.3	NF, mainstem
37	Feather R	14.4	Briscoe Cr
38	Feather R	41.7	Rocky Honcut Cr
39	Feather R	5193.5	Canyon Cr, Concow Cr, Little Butte Cr, MF, NF Elk Cr, WB
40	Fresno R	38.6	Big Cr, NF
41	Kaweah R	11.6	SF Tule R

Table 1. Proposed historical independent populations of steelhead in the Central Valley (Continued)

Independent Population	*Basin*	*Total Stream (km)*	*Streams*
42	Kaweah R	20.9	Tyler Cr
43	Kaweah R	42.9	mainstem
44	Kern R	35.1	NF
45	Kern R	532.2	French Gulch, Little Poso Cr, Tillie Cr
46	Kern R	693.0	Fay Cr, Kelso Cr, Marsh Cr,
47	Kings R	20.6	SF
48	Kings R	123.3	Bitterwater Cyn, SF, mainstem
49	Little Cow Cr	33.3	Clover Cr
50	Little Cow Cr	59.4	South Cow Cr
51	Little Cow Cr	83.5	Cedar Cr, mainstem
52	Little Cow Cr	88.5	Gelndenning Cr, Old Cow Cr
53	Lone Tree Cr	28.5	EF
54	Los Banos Cr	10.2	MF Tule R
55	Los Gatos Cr	19.5	mainstem
56	Los Gatos Cr	20.1	Rube Cr
57	Marsh Cr	82.9	SF
58	McCloud R	1201.2	Nosoni Cr, mainstem
59	Merced R	18.1	Snow Cr
60	Merced R	227.9	MF, Miami Cr, mainstem
61	Mill Cr	158.7	NF Willow Cr
62	Mokelumne R	53.3	Sutter Cr, mainstem
63	Mokelumne R	276.8	NF
64	Panoche Cr	11.4	Warthan Cr
65	Paynes Cr	29.9	Beegum Cr
66	Pit R	146.5	Squaw Cr
67	Pit R	3948.0	Potem Cr, mainstem
68	Poso Cr	168.5	Alamo Cr, Indian Cr
69	Putah Cr	982.2	Scott Cr
70	Stanislaus R	218.3	Curtis Cr
71	Stony Cr	184.6	Grindstone Cr, NF, SF, Salt Cr
72	Stony Cr	237.2	Little Stony Cr, Salt Cr, South Honcut Cr
73	Suisun Bay tribs, northern Kelso Cr	573.1	Sullivan Cr, mainstem
74	Sweany Cr	127.6	Jesus Maria Cr
75	Thomes Cr	179.1	Maple Branch Mud Cr
76	Toomes Cr	34.4	Big Dry Cr, mainstem
77	Tuolumne R	323.8	Bear Cr, Corral Hollow Cr, Maxwell Cr, Moccasin Cr, mainstem
78	Upper Sacramento R	766.6	Backbone Cr, Middle Salt Cr, Salt Cr, Squaw Cr, Sugarloaf Cr, mainstem
79	Upper San Joaquin R	205.8	Clear Cr, Erskine Cr, Mill Flat Cr, mainstem
80	Yuba R	138.4	mainstem
81	Yuba R	1077.1	Dry Cr, mainstem

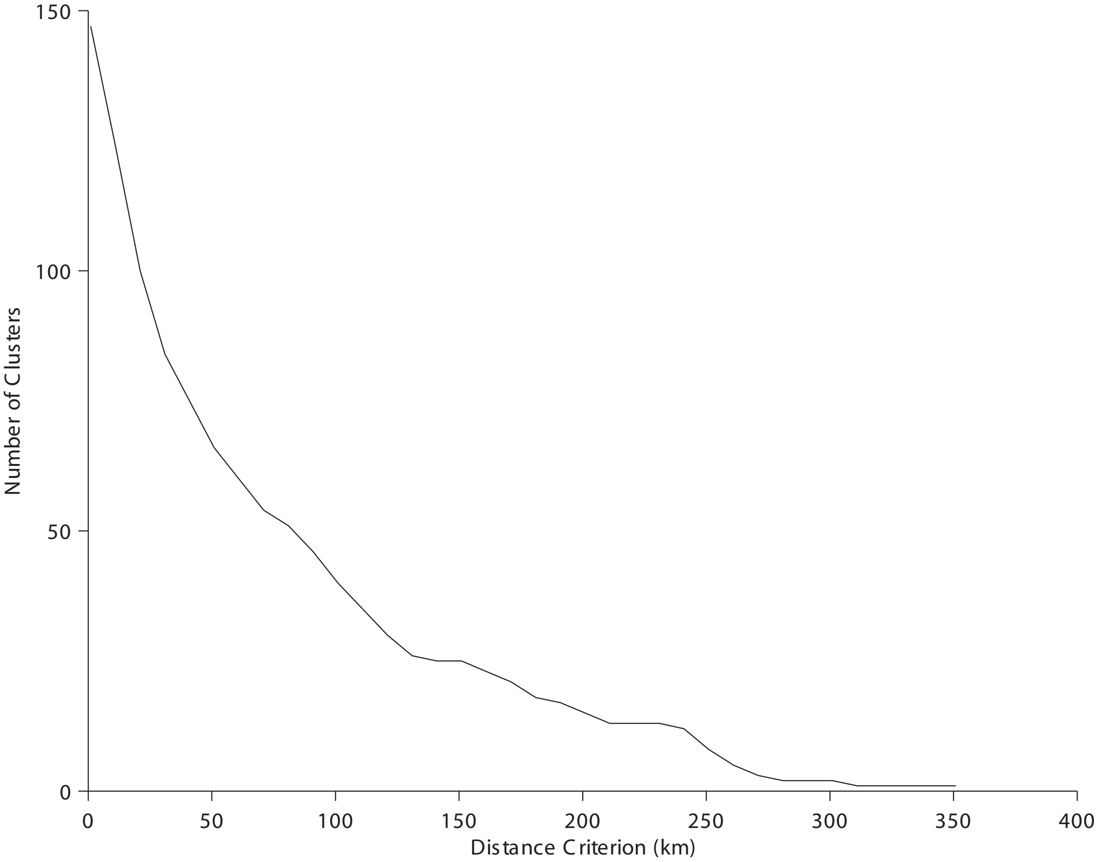

Figure 3. Linkage of habitat patches as a function of distance along the stream network. At a distance of 35 km, there are 81 discrete patches.

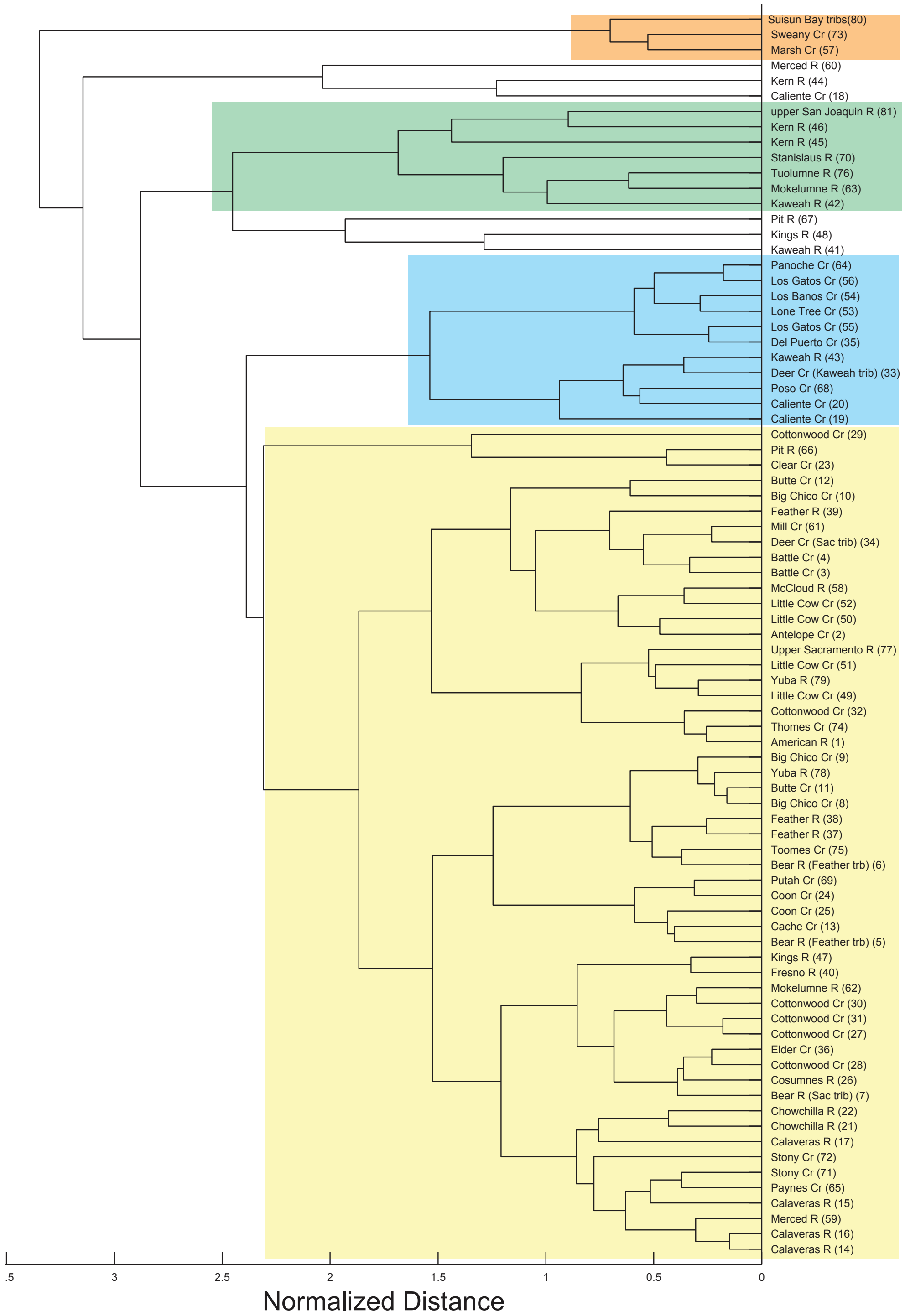

Figure 4. Neighbor-joining tree based on average Mahalanobis distances, calculated from normalized climatic variables and mean elevation. Colored backgrounds envelope clusters of basins that are largely from the same geographic region: orange—tributaries to the Sacramento below the delta; green—the upper San Joaquin and tributaries draining the southern Sierra Nevada; blue—other tributaries to the San Joaquin draining lower elevation areas; yellow—mostly tributaries to the Sacramento River. The numbers in parentheses after the basin name correspond to the population numbers in Table 1. (Click here for PDF file of larger image).

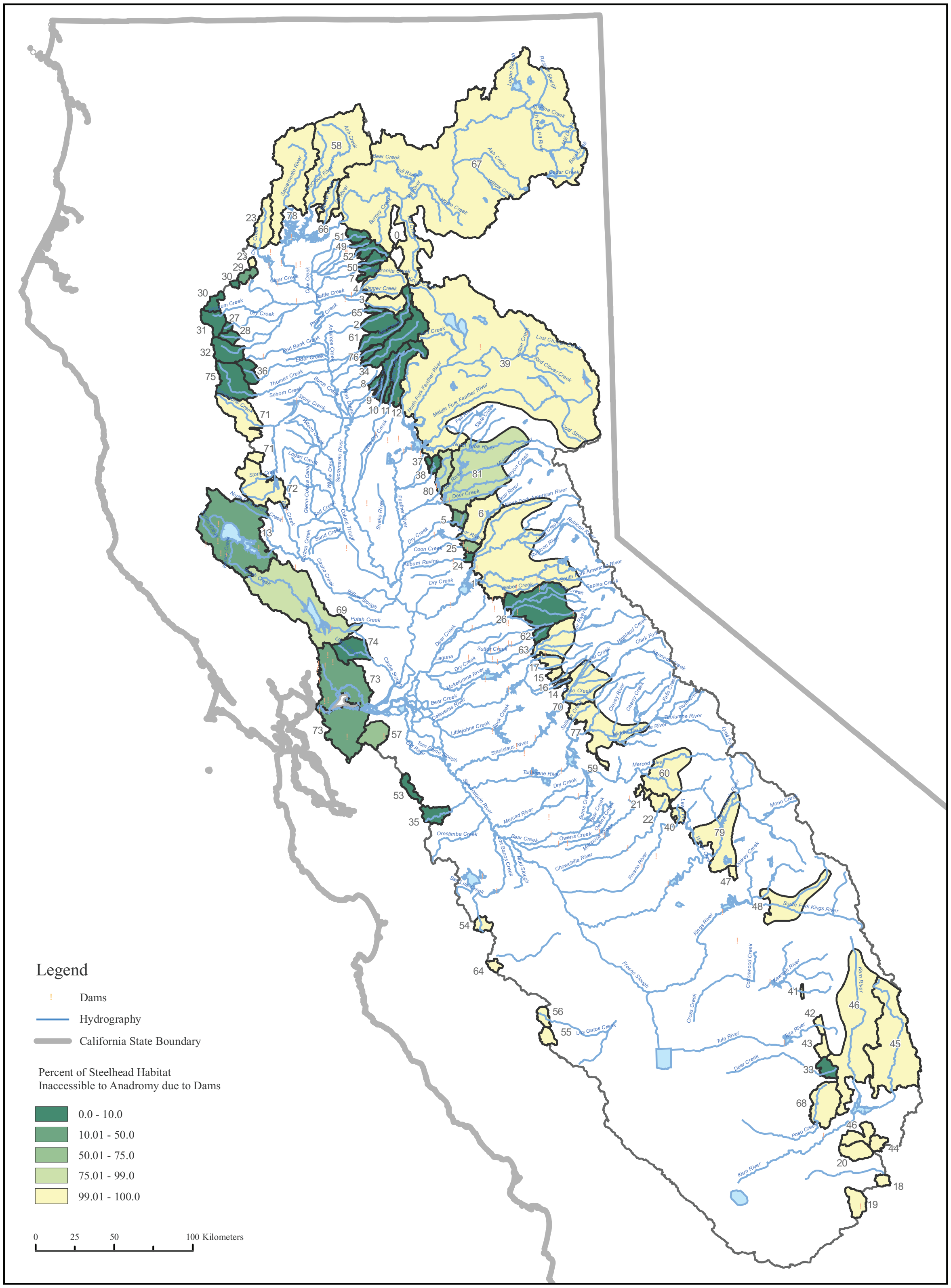

Figure 5. Percentage of historically accessible habitat behind impassable dams. Numbers indicate populations (see Table 1). (Click here for PDF file of larger image).

DISCUSSION

We used a simple habitat model and readily available environmental information to predict the historical distribution of *O. mykiss* spawning and rearing habitat in the Central Valley. In agreement with the suggestions of McEwan (2001) and Yoshiyama and others (1996), our results suggest that *O. mykiss* was widespread throughout the Central Valley, but indicate that *O. mykiss* was relatively less abundant in San Joaquin tributaries than Sacramento River tributaries due to natural migration barriers. Due largely to high summer temperatures on the valley floor, *O. mykiss* habitat is patchily distributed, with 81 discrete patches isolated by >35 km of unsuitable stream habitat. The posited existence of 81 independent populations is likely to be an underestimate because large watersheds that span a variety of hydrological and environmental conditions, such as the Pit River, probably contained multiple populations.

High summer temperature on the valley floor is one important driver of habitat fragmentation, and thus population structure, in our model. At cooler times of the year, *O. mykiss* could potentially move freely among habitat patches. If fish commonly moved from where they were born to distant habitat patches for spawning, then the real population structure could be much simpler than that predicted by our model. It is well known that adult anadromous salmonids are capable of dispersing long distances, but this occurs at a low rate under natural conditions (Quinn 2005). Resident *O. mykiss* in the Kern River basin (Matthews 1996) and other systems (Bartrand and others 1994; Young and others 1997; Meka and others 2003) have small home ranges, on order of a few kilometers or less, suggesting that few juveniles regularly move more than a few kilometers except during their migration to sea. The other main driver of population structure in our model is our choice of 35 km as a threshold for delineating populations. While we believe that 35 km is a reasonable value, 25 or 50 km might also be reasonable, and the number of independent populations identified by our model changes significantly if these alternatives are used (Figure 3). Users of our model results should bear in mind that specific population boundaries are uncertain, and consider how different but still plausible delineations might influence their results.

The distribution of many discrete populations across a wide variety of environmental conditions implies that the Central Valley steelhead ESU contained biologically significant amounts of spatially structured genetic diversity. This hypothesis is bolstered by the presence of distinct subspecies of non-anadromous *O. mykiss* in several regions of the basin (Behnke 2002). According to Behnke's map (his p. 78), coastal rainbow trout (which include Central Valley steelhead) are distributed throughout the Central Valley, with the exception of the Pit and upper Kern rivers. Golden trout were historically found in the mainstem Kern River (*O. mykiss gilberti*), the South Fork Kern and Golden Trout Creek (*O. mykiss aquabonita*), and the Little Kern River (*O. mykiss whitei*). Similarly, redband trout (*O. mykiss stonei*) inhabit the upper Sacramento, including the McCloud, Pit, North and Middle Fork Feather rivers, and Butte Creek. Another implication of these observations is that not all of the *O. mykiss* habitat identified by our model may have been used by Central Valley steelhead, because coastal *O. mykiss* can interbreed with golden and redband trout, yet introgression appears to be a recent phenomenon.

It appears that much of the historical diversity within Central Valley *O. mykiss* has been lost or is threatened by dams. Figure 5 shows that dams have heavily altered the distribution and population structure of steelhead in the Central Valley. Our estimate of steelhead habitat loss is somewhat larger than the 70% habitat loss of Chinook salmon reported by Yoshiyama and others (2001), but quite similar to the 80% loss reported by Clark (1929). The loss is not spread evenly among populations, however. About 38% of the discrete habitat patches are no longer accessible to anadromous *O. mykiss*. For most anadromous fish, such an impact would generally mean extirpation of the affected population, but the life-history flexibility of *O. mykiss* means that formerly anadromous *O. mykiss* populations may persist as resident trout above the dams. Rainbow trout are indeed common in streams above reservoirs in the Central Valley (Knapp 1996; Moyle and others 1996). It is not at all clear, however, whether these populations are the residualized descendants of native anadromous populations, or are the descendants of rainbow trout that have been widely planted throughout California to enhance recreational trout fisheries. Nielsen and others (2005) found that fish from areas above barriers were more similar to other above-barrier populations than to fish from the same river downstream of the barrier. This could indicate a separate phylogenetic origin for these above-barrier populations (in particular, derivation from a common hatchery strain), or may be a case of long-branch attraction (Felsenstein 1978), an artifact of tree construction where widely divergent populations cluster together, away from the more closely-related populations.

The extensive loss of habitat historically available to anadromous *O. mykiss* supports the status of *O. mykiss* as a species threatened with extinction. An important next step is to identify and secure the sources of current natural production of steelhead, limited as they may be. Our model identifies those few streams where historical habitat may still be accessible (e.g., Mill, Deer, Butte and Cottonwood creeks) as likely candidates. Tailwater areas below dams with hypolimnetic releases, while not identified by our model, may also produce steelhead. Natural areas that continue to produce steelhead should be a top priority for conservation. Tailwater and above-barrier populations in the San Joaquin basin could also be important targets for conservation, because any such populations could be the only representatives of a presumably ecologically distinct segment of the ESU, assuming that they are descended from native anadromous populations. The value of these populations for recovering anadromous runs may be reduced due to the selective effects of the dams. Obviously, for populations above dams, reproductive effort devoted to producing anadromous offspring is completely lost to that population. More subtly, water releases from dams like Shasta change the thermal regime and food web structure of the river below (Lieberman and others 2001) in ways that may provide fitness advantages to resident forms. Clearly, the current state of the Central Valley landscape presents a very different selective regime than any faced by *O. mykiss* before, posing thorny issues for conservation of Central Valley steelhead.

ACKNOWLEDGMENTS

STL appreciates useful discussions with B. Spence, T. Williams, E. Bjorkstedt, and D. Boughton. D. Boughton, K. Burnett, M. Mohr, and R. Yoshiyama provided critical reviews of the manuscript. B. Swart assisted with GIS analyses. JJA, BPM and JGW were supported by the CALFED Science Program through Association of Bay Area Governments contract CALFED/DWR 4600001642.

REFERENCES

Agajanian J, Rockwell GL, Anderson SW, Pope GL. 2002. Water resources data California water year 2001. Volume 1. Southern Great Basin from Mexican Border to Mono Lake Basin, and Pacific Slope Basins from Tijuana River to Santa Maria River. Water-Data Report CA-01-1, U.S. Geological Survey.

Argáez JA, Christen JA, Nakamura M, Soberon J. 2005. Prediction of potential areas of species distributions based on presence-only data. Environmental and Ecological Statistics 12:27–44.

Bartrand EL, Pearsons TN, Martin SW. 1994. Movement of rainbow trout in the upper Yakima River basin. Northwest Science 68:114.

Beer WN, Anderson JJ. 2001. Effects of spawning behavior and temperature profiles on salmon emergence: interpretations of a growth model for Methow River chinook. Canadian Journal of Fisheries and Aquatic Sciences 58:943–949.

Behnke RJ. 2002. Trout and salmon of North America. New York: The Free Press.

Bjorkstedt EP, Spence B, Garza JC, Hankin DG, Fuller D, Jones W, Smith J, Macedo R. 2005. An analysis of historical population structure of Evolutionarily Significant Units of Chinook salmon, coho salmon, and steelhead in the North-Central California Coast Recovery Domain. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-SWFSC-382, La Jolla, CA.

Brannon EL, Powell MS, Quinn TP, Talbot A. 2004. Population structure of Columbia River basin chinook salmon and steelhead trout. Reviews in Fisheries Science 12:99–232.

Burger CV, Wilmot RL, Wangaard DB. 1985. Comparison of spawning areas and times for two runs of chinook salmon (*Oncorhynchus tshawytscha*) in the Kenai River, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 42:693–700.

Burnett KM. 2001. Relationships among juvenile anadromous salmonids, their freshwater habitat, and landscape characteristics over multiple years and spatial scales in Elk River, Oregon [PhD dissertation]. Available from: Oregon State University.

Burnett KM, Reeves GH, Miller D, Clark SE, Christiansen KC, Vance-Borland K. 2003. A first step towards broad-scale identification of freshwater protected areas for Pacific salmon and trout. In: Beumer J, editor. Proceedings of the World Congress on Aquatic Protected Areas. Cairns, Australia: Australian Society for Fish Biology.

Chefaoui RM, Hortal J, Lobo JM. 2005. Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: a case study of Iberian *Copris* species. Biological Conservation 122:327–338.

Clark GH. 1929. Sacramento-San Joaquin salmon (*Oncorhynchus tshawytscha*) fishery of California. Fish Bulletin 17:1–73.

Cook WC. 1929. A bioclimatic zonation for studying the economic distribution of injurious insects. Ecology 10:282–293.

Daly C, Neilson RP, Philips DL. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meterology 33:140–158.

Daly C, Taylor G, Kittel T, Schimel D, McNab A. 2002. Development of a 103-year high-resolution climate data set for the conterminous United States. Comprehensive Final Report for 9/1/97 - 5/31/02. NOAA Climate Change Data and Detection Program.

Darwin C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. London: John Murray.

Engle RO. 2002. Distribution and summer survival of juvenile steelhead trout (*Oncorhynchus mykiss*) in two streams within the King Range National Conservation Area, California. [MS thesis]. Available from: Humboldt State University.

Felsenstein J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. Systematic Zoology 27:401–410.

Friebel MF, Freeman LA, Smithson JR, Webster MD, Anderson SW, Pope GL. 2002. Water resources data California water year 2001. Volume 2. Pacific Slope basins from Arroyo Grande to Oregon state line except Central Valley. Water-Data Report CA-01-2, U. S. Geological Survey.

Goslin M. 2005. Creating a comprehensive dam dataset for assessing anadromous fish passage in California. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-SWFSC-376, La Jolla, CA.

Harvey BC, White JL, Nakamoto RJ. 2002. Habitat relationships and larval drift of native and nonindigenous fishes in neighboring tributaries of a coastal California river. Transactions of the American Fisheries Society 131:159–170.

Hicks BJ, Hall JD. 2003. Rock type and channel gradient structure salmonid populations in the Oregon Coast Range. Transactions of the American Fisheries Society 132:468–482.

Ingram BL, Ingle JC, Conrad ME. 1996. A 2000-yr record of Sacramento-San Joaquin River inflow to San Francisco Bay estuary, California. Geology 24:331–334.

Interior Columbia Basin Technical Recovery Team. 2003. Independent populations of chinook, steelhead, and sockeye for listed Evolutionary Significant Units within the interior Columbia River domain. Working draft, NOAA Fisheries, Seattle, WA.

Johnson CJ, Seip DR, Boyce MS. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology 41:238–251.

Keefer DK. 1994. The importance of earthquake-induced landslides to long-term slope erosion and slope-failure hazards in seismically active regions. Geomorphology 10:265–284.

Kerr RA. 1984. Landslides from volcanos seen as common. Science (Washington DC) 224:275–276.

Knapp RA. 1996. Non-native trout in natural lakes of the Sierra Nevada: an analysis of their distribution and impacts on native aquatic biota. Sierra Nevada Ecosystem Project: final report to Congress. Vol. III. Davis (CA): Centers for Water and Wildland Resources, University of California, Davis.

Konecki JT, Woody CA, Quinn TP. 1995. Influence of temperature on incubation rates of coho salmon (*Oncorhynchus kisutch*) from ten Washington populations. Northwest Science 69:126–132.

Lieberman DM, Horn MJ, Duffy S. 2001. Effects of a temperature control device on nutrients, POM and plankton in the tailwaters below Shasta Lake, California. Hydrobiologia 452:191–202.

Lytle DA, Poff NL. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution 19:96–100.

Mahalanobis PC. 1936. On the generalized distance in statistics. Proceedings of the National Institute of Sciences in India 12:49–55.

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002. Resource selection by animals: statistical design and analysis for field studies. 2nd edition. Dordrecht/Boston/London: Kluwer Academic Publishers.

Matthews KR. 1996. Diel movement and habitat use of California golden trout in the Golden Trout Wilderness, California. Transactions of the American Fisheries Society 125:78–86.

McElhany P, Ruckelshaus MH, Ford MJ, Wainwright TC, Bjorkstedt EP. 2000. Viable salmonid populations and the conservation of evolutionarily significant units. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-42, Seattle, WA.

McEwan DR. 2001. Central Valley steelhead. In: Brown RL, editor. Fish Bulletin 179. Contributions to the biology of Central Valley salmonids. Vol. 1. Sacramento (CA): California Department of Fish and Game. p 1–43.

Meka JM, Knudsen EE, Douglas DC, Benter RB. 2003. Variable migratory patterns of different adult rainbow trout life history types in a southwest Alaska watershed. Transactions of the American Fisheries Society 132:717–732.

Mohseni O, Stefan HG, Erickson TR. 1998. A nonlinear regression model for weekly stream temperatures. Water Resources Research 34:2684–2692.

Montgomery DR, Buffington JM, Peterson NP, Schuett-Hames D, Quinn TP. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences 53:1061–1070.

Moyle PB, Randall PJ. 1998. Evaluating the biotic integrity of watersheds in the Sierra Nevada, California. Conservation Biology 12:1318–1326.

Moyle PB, Yoshiyama RM, Knapp RA. 1996. Status of fish and fisheries. Sierra Nevada Ecosystem Project: final report to Congress. Vol II. Davis (CA): Centers for Water and Wildland Resources, University of California, Davis.

Nielsen JL, Lisle TE, Ozaki V. 1994. Thermally stratified pools and their use by steelhead in Northern California streams. Transactions of the American Fisheries Society 123:613–626.

Nielsen JL, Pavey SA, Wiacek T, Williams I. 2005. Genetics of Central Valley *O. mykiss* populations: drainage and watershed scale analyses. San Francisco Estuary and Watershed Science [online]. Vol. 3, Issue 2, Article 3. Available at: http://www.estuaryandwatershedscience.org/vol3/iss2/art3.

Quinn TP. 2005. The behavioral ecology of Pacific salmon and trout. Seattle: University of Washington Press.

Quist MC, Rahel FJ, Hubert WA. 2005. Hierarchical faunal filters: an approach to assessing effects of habitat and nonnative species on native fishes. Ecology of Freshwater Fish 14:24–39.

Rahel FJ, Keleher CJ, Anderson JL. 1996. Potential habitat loss and population fragmentation for cold water fish in the North Platt River drainage of the Rocky Mountains: response to climate warming. Limnology and Oceanography 41:1116–1123.

Rockwell GL, Smithson JR, Friebel MF, Webster MD. 2002. Water resources data California water year 2001. Volume 4. Northern Central Valley basins and the Great Basin from Honey Lake basin to Oregon state line. Water-Data Report CA-01-4, U.S. Geological Survey.

Schmidt AH, Graham CC, McDonald JE. 1979. Summary of literature on four factors associated with salmon and trout fresh water life history. Fisheries and Marine Service Manuscript Report 1487, Vancouver B.C.: Fisheries and Marine Service.

Smithson JR, Freeman LA, Rockwell GL, Anderson SW, Pope GL. 2002. Water resources data California water year 2001. Volume 3. Southern Central Valley basins and the Great Basin from Walker River to Truckee River. Water-Data Report CA-01-3, U.S. Geological Survey.

Sokal RR, Rohlf FJ. 1962. The comparisons of dendrograms by objective methods. Taxon 11:33–40.

Solley WB, Pierce RR, Perlman HA. 1998. Estimated use of water in the United States in 1995. Circular 1200. U.S. Geological Survey.

Taylor EB. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185–207.

Valavanis VD, Georgakarakos S, Kapantagakis A, Palialexis A, Katara I. 2004. A GIS environmental modelling approach to essential fish habitat designation. Ecological Modelling 178:417–427.

Wall SS, Berry CR, Blausey CM, Jenks JA, Kopplin CJ. 2004. Fish-habitat modeling for gap analysis to conserve the endangered Topeka shiner (*Notropis topeka*). Canadian Journal of Fisheries and Aquatic Sciences 61:954–973.

Yoshiyama RM, Gerstung ER, Fisher FW, Moyle PB. 1996. Historical and present distribution of chinook salmon in the Central Valley drainage of California. Sierra Nevada Ecosystem Project, Final Report to Congress, vol III. Centers for Water and Wildland Resources, University of California, Davis.

Yoshiyama RM, Gerstung ER, Fisher FW, Moyle PB. 2001. Historic and present distribution of chinook salmon in the Central Valley drainage of California. In: Brown RL, editor. Fish Bulletin 179. Contributions to the biology of Central Valley salmonids. Vol. 1. Sacramento (CA): California Department of Fish and Game. p 71–176.

Young MK, Wilkison RA, Phelps IJM, Griffith JS. 1997. Contrasting movement and activity of large brown trout and rainbow trout in Silver Creek, Idaho. Great Basin Naturalist 57:238–244.

Monitoring and research needed to manage the recovery of threatened and endangered Chinook and steelhead in the Sacramento-San Joaquin basin

J. G. Williams[1], J. J. Anderson[2], S. Greene[3], C. Hanson[4], S. T. Lindley[5], A. Low[6], B. P. May[7], D. McEwan[6], M. S. Mohr[5], R. B. MacFarlane[5] and C. Swanson [8]

[1]875 Linden Ln., Davis, CA; [2]U. Washington, School of Fisheries; [3]CA Dept. Water Resources; [4]Hanson Environmental; [5]NOAA Fisheries, Southwest Fisheries Science Center; [6]CA Dept. Fish and Game; [7]UC Davis, Department of Animal Science; and [8]The Bay Institute

In this report, we assess whether existing monitoring activities in the Central Valley are sufficient to determine if biological recovery goals are being met, and make recommendations for monitoring and research that could provide critically-needed information for effective management of Chinook salmon and steelhead beyond simple viability assessments. Assessing population status requires, at a minimum, estimates of abundance on the spawning grounds and the fraction of naturally-spawning fish that are of hatchery origin. We find that such data are generally available for independent populations of Chinook salmon, but are almost entirely unavailable for steelhead populations. Effective monitoring of steelhead run sizes at the population scale is needed urgently.

Effective management of listed salmonids requires more information than simply whether populations and ESUs are achieving viability targets. We anticipate that managers will need information on the response of salmonid populations to regional climate change, the use of freshwater habitat, mechanisms and magnitude of mortality in freshwater and the ocean, age- and stock-specific harvest rates, trends in effective population size and genetic diversity within and among populations, the effects of hatchery operations on naturally-spawning populations, how to go about reintroducing fish to reconnected or restored habitats, and the factors controlling and the implications of variable life history tactics of steelhead. We discuss why these information gaps need to be filled, and offer some suggestions on promising approaches to filling them. Finally, we recommend that new and existing data should be made accessible to researchers and managers through a central data portal that can aggregate information from the many existing databases.

1 Background

A key contribution of science to recovery planning is to ensure that recovery plans specify adequate monitoring of species status (Clark et al., 2002). Lindley et al. (in press.) laid out viability criteria for populations and evolutionarily significant units (ESUs) in the Central Valley recovery domain. Populations are assumed to be viable if they satisfy criteria relating to population size, trends in abundance, incidence of catastrophic disturbance, and hatchery impacts. ESUs are assumed to be viable if enough viable are distributed throughout the ESU. Monitoring ESU viability depends on monitoring the viability of populations. The first part of this report discusses the monitoring needed to determine if populations are satisfying viability criteria. Successful recovery of salmonid ESUs, however, will require more detailed information than that needed to merely assess their viability. In the second part of this report, we discuss the kinds of monitoring and research that are needed to guide recovery and management of Central Valley salmonids listed under the Endangered Species Act.

2 Monitoring for viability

Criteria for assessing the viability of threatened and endangered Chinook and steelhead in the Sacramento-San Joaquin basin are presented and discussed in Lindley et al. (in press.), and the populations, population groups, and ESUs to which they are to be applied are described by Lindley et al. (2004) and Lindley et al. (2006). The criteria and associated data requirement are summarized in Tables 1 and 2 (reproduced from Lindley et al. (in press.)). The criteria in Table 1 were modeled after IUCN (1994) as modified for Pacific salmon by Allendorf et al. (1997), and are designed for use with the data that are practical to collect, rather than the data that one might like to have for the purpose. Accordingly, use of the criteria imposes only modest requirements for monitoring: the abundance of returning adults, and the percentage of hatchery fish among the returning adults. High accuracy in these estimates may not be required, if the population clearly is not near the threshold values that separate risk categories. It is also important to note that abundance estimates need to correspond to specific populations. For example, if a simple weir count is to be used, the weir must be below the spawning grounds of a single population.

2.1 Existing monitoring programs

Existing monitoring programs for listed *Oncorhynchus* in the Central Valley are comprehensively described by Pipal (2005), and monitoring programs for all Central Valley *Oncorhynchus* are described by Low (2005); the programs are described only briefly here.

2.1.1 Spring-run Chinook salmon

Estimates of adult returns are routinely made on all Central Valley streams with extant independent populations of listed Chinook salmon, as well as on some streams with historically dependent populations. These data are available from CDFG's Grand Tab database[1], which is produced annually as part of the ocean salmon fishery assessment.

Various methods are used to estimate adult returns, including counts at ladders and weirs, snorkel surveys, and carcass surveys (Pipal, 2005; Low, 2005). Generally, estimates of adult returns in the Central Valley are given without confidence intervals or standard errors, so the accuracy of the estimates is uncertain and the statistical power of trend detection tests is unknown. A joint CDFG-NMFS review (CDFG and NMFS, 2001) noted that "The accuracy and variance of most Central Valley escapement estimates are currently unknown and may not be sufficient to meet management

---

[1] Grand Tab can be obtained from Robert Kano, Wildlife and Habitat Data Analysis Branch, CDFG, Sacramento, CA. or from http://www.delta.dfg.ca.gov/AFRP/

Table 1: Criteria for assessing the level of risk of extinction for populations of Pacific salmonids. Overall risk is determined by the highest risk score for any category. Reproduced from Lindley et al. (in press.) based on Allendorf et al. (1997).

	Risk of Extinction		
Criterion	High	Moderate	Low
Extinction risk from PVA	$> 20\%$ within 20 years	$> 5\%$ within 100 years	$< 5\%$ within 100 years
	– or any ONE of –	– or any ONE of –	– or ALL of –
Population size[a]	$N_e \leq 50$	$50 < N_e \leq 500$	$N_e > 500$
	–or–	–or–	–or–
	$N \leq 250$	$250 < N \leq 2500$	$N > 2500$
Population decline	Precipitous decline[b]	Chronic decline or depression[c]	No decline apparent or probable
Catastrophe, rate and effect[d]	Order of magnitude decline within one generation	Smaller but significant decline[e]	not apparent
Hatchery influence[f]	High	Moderate	Low

[a] Census size N can be used if direct estimates of effective size N_e are not available, assuming $N_e/N = 0.2$.

[b] Decline within last two generations to annual run size ≤ 500 spawners, or run size > 500 but declining at $\geq 10\%$ per year. Historically small but stable population not included.

[c] Run size has declined to ≤ 500, but now stable.

[d] Catastrophes occuring within the last 10 years.

[e] Decline $< 90\%$ but biologically significant.

[f] See Figure 1 of Lindley et al. (in press) for assessing hatchery impacts.

Table 2: Estimation methods and data requirements for population metrics. S_t denotes the number of spawners in year t; g is mean generation time, which we take as 3 years for California salmon.

Metric	Estimator	Data	Criterion
$\hat{S}_t$	$\sum_{i=t-g+1}^{t} S_i/g$	≥ 3 years spawning run estimates	Population decline
N_e	$N \times 0.2$ or other	varies	Population size
N	$\hat{S}_t \times g$	≥ 3 years spawning run estimates	Population size
Population growth rate (% per year)	slope of $\log(S_t)$ v. time $\times 100$	10 years S_t	Population decline
c	$100 \times (1 - \min(N_{t+g}/N_t))$	time series of N	Catastrophe
h	average fraction of natural spawners of hatchery origin	mean of 1-4 generations	Hatchery influence

needs, ...” However, as noted above, use of Table 1 does not necessarily require that abundance estimates be highly accurate (although standard errors for abundance estimates would be extremely useful).

In response to the need to review and improve escapement monitoring programs in the Central Valley, the CALFED Ecosystem Restoration Program approved funding in 2005 to develop a comprehensive Central Valley Chinook Salmon Escapement Monitoring Plan[2]. From January 2007 through June 2008, a project team consisting of a biostatistician, biologist, and database expert, will evaluate existing monitoring programs and make recommendations for new or revised programs, in coordination with the Central Valley Salmonid Escapement Project Work Team. The Plan is intended to improve monitoring programs for winter-run Chinook salmon and spring-run Chinook salmon, and make the data more relevant to recovery planning for these stocks. The Plan will include the design of a consistent, integrated database and data reporting and communication system for Central Valley salmon escapement monitoring data.

Currently, all spring-run Chinook salmon produced at Feather River Hatchery are marked with adipose fin clips and coded-wire tags, so that tracking the percentage of hatchery fish among spawning adults is relatively straightforward in principal. Available information indicates that the spring-run Chinook salmon population in the Feather River is clearly dominated by hatchery-origin fish. One serious complication arises from the fact that early run timing (a defining characteristic of spring Chinook salmon) appears in the progeny of FRH fall-run Chinook salmon. This raises the possibility that unmarked, early-running Chinook salmon from the FRH could stray to natural populations, where they would be difficult to detect. Ideally, all hatchery fish, or at least a constant fraction of every release group, would be marked in some way so that statistically defensible estimates of their straying rates into natural populations could be made.

Although the rugged terrain typically surrounding spring-run Chinook salmon holding and spawning habitat makes estimating the number or returning adults difficult, existing programs seem generally satisfactory for the narrow purpose of assessing population viability using Table 1. Further valuable information comes from monitoring programs for emigrating juveniles. Except for Clear Creek and the Feather River, current spring-run Chinook salmon populations fall either well below or well above the risk criteria for hatchery influence, so for the narrow purpose of applying Table 1 the accuracy of the estimates of hatchery influence for these populations is sufficient.

2.1.2 Winter-run Chinook salmon

Abundance estimates are generated from carcass surveys conducted in the area most heavily used for spawning by winter-run Chinook salmon, and by expanding counts of winter-run Chinook salmon made at Red Bluff Diversion Dam as the last portion of the run ascends seasonally-operated fish ladders. Resource managers use the carcass-based estimates for management purposes. The accuracy and precision of the mark-recapture estimates is uncertain, largely due to uncertainties surrounding how well the survey method meets the assumptions of the Jolly-Seber model used to estimate abundance. However, recent population estimates are much greater than the criterion for low risk in Table 1, and there is no apparent or probable population decline. At current abundance levels, estimates have sufficient accuracy and precision for assessing extinction risk using Table 1. For assessing the effectiveness of restoration actions, however, more accurate estimates may be needed.

In terms of Table 1, the hatchery influence criterion is more critical for winter-run Chinook salmon than the population criteria, since the rising proportion of hatchery fish among returning adults threatens to shift the population from low to moderate risk of extinction (Lindley et al., in press.). If the status of the winter-run Chinook salmon population is downgraded due to hatchery influence, the accuracy of the estimates of hatchery influence may become contentious. Bias may arise if hatchery fish differ from naturally-spawned fish in their distribution within the river, size or sex ratio. This possibility, and its effect on the estimate of hatchery contribution to natural spawning, should be examined.

2.1.3 Steelhead

In contrast to the existing monitoring programs for Central Valley Chinook salmon salmon, steelhead monitoring is insufficient to evaluate populations with respect to the criteria in Table 1, except for streams where hatchery operations likely satisfy the high risk criterion for hatchery effects (Lindley et al., in press.). Unfortunately, such information as does exist indicates sharp declines in abundance over the least half-century (McEwan, 2001). There are reasons for the dearth of data on anadromous steelhead. Steelhead spawn in the winter, when conditions for monitoring are difficult, and although many steelhead die after spawning, their carcasses are not concentrated near the spawning areas. There is also the difficulty of distinguishing resident and anadromous forms, because resident fish in the tail waters of dams that release cool water though the summer can attain the size of typical anadromous fish, and juveniles migrating downstream may not continue to the ocean. Moreover, the effectiveness of screw traps declines for larger fish, and many juvenile steelhead are large enough that they may be able to avoid the traps.

Given that the anadromous component of the ESU is critical for its long-term persistence, as made clear by the discussion of anadromous and resident *O. mykiss* in Travis et al. (2004), monitoring of the anadromous form should be substantially increased. Populations of *O. mykiss* in Central Valley streams with hatcheries are at high risk of extinction because of the high proportion of hatchery fish among naturally spawning fish (Lindley et al., in press.). More accurate estimates of adult returns will not change this assessment. Accordingly, priority should go to monitoring steelhead populations in streams without hatcheries that have the potential to support significant populations. These are likely often the same streams that support spring-run Chinook salmon, which suggests that efficiency could be maximized by employing methods capable of counting both Chinook salmon and steelhead. However, basic distributional data are needed to guide future monitoring efforts.

Traps at dams on some of these streams apparently have been effective for monitoring steelhead in the past (e.g., Figure 1). An automatic counting system such as the Vaki RiverWatcher or DIDSON sonar could be used in place of a trap, to avoid stress associated with trapping, and resistance board weirs might be used

---

[2] The proposal to CALFED is available online at `http://www.delta.dfg.ca.gov/erp/docs/2005grants/Central_Valley_Salmon_Esc_CMP_DA_Proposal.pdf`

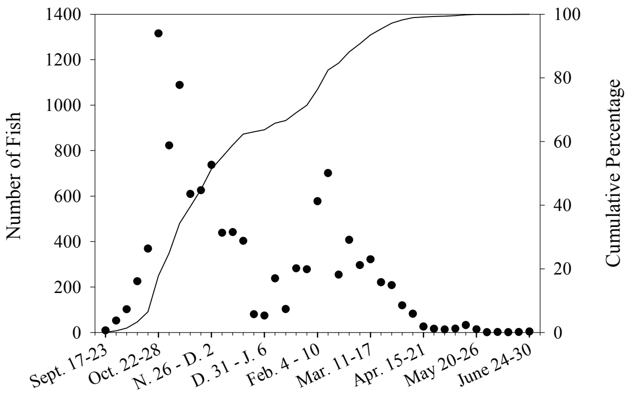

Figure 1: Total number of steelhead observed passing Clough Dam on Mill Creek, 1953-63. Data from Van Woert (1964). On average, 1,160 fish passed the dam each year. Harvey (1995), cited in Pipal (2005), reported that 34 steelhead were observed passing the dam in 1993-94, along with 76 spring Chinook.

instead of dams. Such monitoring will produce partial counts, because some fish will likely bypass the traps during high flows. These partial counts would need to exceed criteria for low extinction risk before the population could be determined to be at low risk. The same facilities could be used to obtain more accurate estimates of returning spring-run Chinook salmon.

In response to the need to develop monitoring programs for Central Valley steelhead, the CALFED Ecosystem Restoration Program approved funding in 2005 to develop a comprehensive Central Valley Steelhead Monitoring Plan[3]. From January 2007 through June 2008, a project team consisting of a biostatistician, biologist, and database expert, will design the comprehensive long-term monitoring program, in coordination with the Central Valley Steelhead Project Work Team. The plan will include the design of a consistent, integrated database and data reporting and communication system. We recommend that serious consideration be given to monitoring returning steelhead adults at weirs or traps on streams that do not have steelhead hatcheries.

3 Research and monitoring to assist management

In this section we provide recommendations regarding research that seems particularly important for improving the scientific basis for management and recovery. At the outset, however, we emphasize the close connection between monitoring and research in the context of adaptive management. The essence of adaptive management is treating management as experimental, so that monitoring provides the experimental results, and is part of science as well as part of management (Peterman et al., 1977; Halbert, 1993; Williams, 1999). Roni (2005) provides a recent review of monitoring and evaluation principles, including adaptive management, as applied to restoration of salmonid-bearing watersheds.

We emphasize that the data required for risk assessment (Table 1) are only a subset of the data required for effective management of the populations and recovery planning. Data on spring-run Chinook salmon in Mill Creek (Figure 2) illustrate this point.

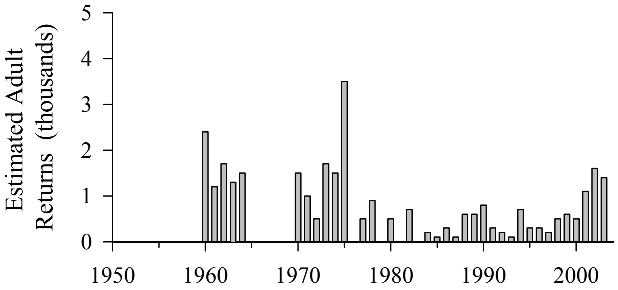

Figure 2: Estimated numbers of adult spring-run Chinook salmon returning to Mill Creek. Data from Van Woert (1964) and the CDFG GrandTab data base. For purposes of the tables, the population is the sum of the returns over a generation, i.e., 3 to 4 years.

Spring-run Chinook salmon in Mill Creek are monitored by redd counts, a not particularly precise method for estimating run sizes. From the data, however, it seems clear that the population has been over 2,500 in recent years, and over the last decade is not decreasing (note that for the genetic considerations underlying the population-size criterion, the population includes the adult returns for each year of a generation, which lasts 3 to 4 years; see the legend for Table 2). Because there is no reason to expect a significant hatchery influence, the population can be assigned to the low risk category, despite the considerable uncertainty in the abundance estimates.

For management, however, better data seem needed, as shown by the following example. Spring-run Chinook salmon in Mill Creek were monitored at a dam below the spawning grounds from 1954-63 (Van Woert, 1964), and the resulting information on the temporal distribution of the migration indicates that diversions for irrigation probably hinder late-arriving fish, especially in dry years (Figure 3). Better monitoring than now occurs would be required to confirm this, and to allow an assessment of the benefit to the population that might result from, say, pumping water from the Sacramento River to replace the water currently diverted from the creek a few miles upstream from the confluence. Put differently, abundance data by themselves say little about what might be done to improve conditions for the population. Similarly, although uncertain abundance estimates may be all that is needed to assess the viability of a population using Table 1, more accurate estimates may be needed to test hypotheses regarding the importance of various factors in regulating populations.

In the following subsections, we outline what we believe to be the major questions that need to be addressed in order to effectively manage salmon and steelhead in the Central Valley.

3.1 Climate change and temperature tolerance

Regional climate change (driven by global warming) is a critical issue for Chinook salmon and steelhead in the Central Valley (Lindley et al., in press.), and better information on future water temperatures and on the temperature tolerance of Chinook salmon and steelhead will be important for developing realistic recovery plans. This will require improved understanding at several levels: how temperature and precipitation will change at regional scales; how

---

[3] The proposal is available online at `http://www.delta.dfg.ca.gov/erp/docs/2005grants/Central_Valley_Steelhead_CMP_DA_Proposal.pdf`

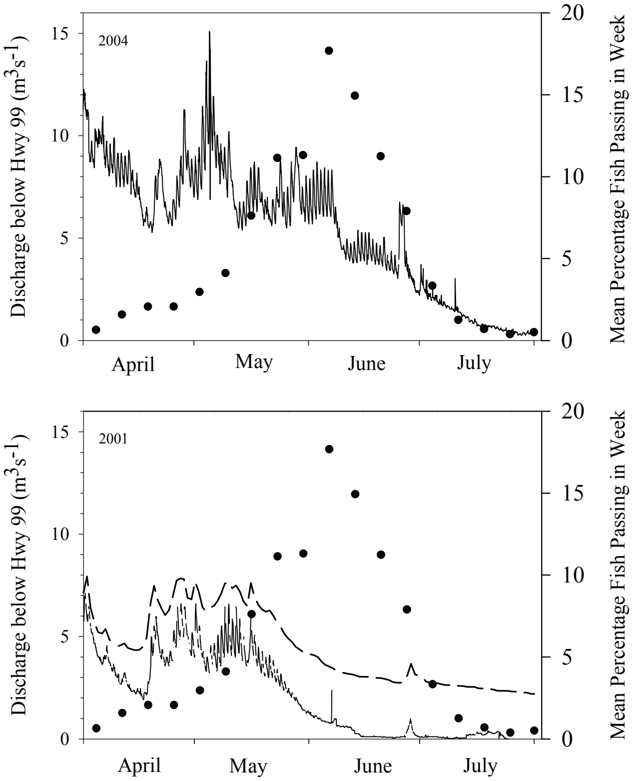

Figure 3: Temporal distribution of adult spring-run Chinook salmon migration for 1954-64 (circles), and discharge in Mill Creek at the DWR gage, downstream from diversions (solid line), and at the USGS gage, upstream from the diversions, 2001 and 2004. Migration data from Van Woert (1964). Copied from Williams (2006).

these regional-scale changes will alter conditions at the scales relevant to individuals and populations; and how individuals and populations will respond to these changes. Recent work has shown that the hierarchical structure linking large-scale climate variation to individual organisms must be understood in order to predict how organisms will respond to climate change (Gilman et al., 2006).

Several climatological studies dealing with warming and subsequent alterations to the hydrologic regime in the Central Valley have been published recently (Wilson, 2003; Dettinger et al., 2004; Hayhoe et al., 2004; Peterson et al., 2005), and we expect that more will be forthcoming. However, more focused efforts will be needed to translate the results of such studies to estimates of actual stream temperatures, which while strongly related to air temperature (Mohseni et al., 1998), are moderated by evapotranspiration, hill shading, groundwater inputs, and hyporheic exchange.

Temperature is a critical determinant of the shifting habitat mosaic (Hauer et al., 2003) that moves in time and space as river temperature isopleths migrate upstream to higher elevations in the spring/summer and downstream to the valley floor in the autumn/winter. For spring-run Chinook salmon the seasonal pattern of temperature is particularly critical. The adults enter in the spring and move to high elevations to avoid the lethal summer temperatures at lower elevations. In the autumn, temperature isopleths move downstream and the adults spread throughout the habitat to spawn. The eggs emerge and the fry move out of the system or seek temperature refugia prior to the next temperature cycle (Lindley et al., 2004).

To understand how climate change and restoration activities will affect this shifting habitat mosaic, salmon ecologist stress a landscape perspective that emphasizes the connectivity of riparian systems to associated terrestrial and aquatic ecosystems (Wissmar and Bisson, 2003). In particular, the hydrological and geological mechanisms controlling stream habitats and the fish responses to the conditions are important. In the Central Valley the seasonal patterns of precipitation and temperature determine snow accumulation and rainfall patterns which are then filtered through the surface and subsurface water exchanges to produce flow and temperature patterns in the salmon habitats. How fish respond to changes in flow and temperature over their critical life stages will determine their ability to respond and adapt to climate change.

While much information is available on the life-stage-specific temperature ranges of Chinook salmon and steelhead (McCullough, 1999) little is known about the specific responses of Central Valley species to temperature. Anecdotal evidence suggests that some species of Central Valley salmonids are heat tolerant: “The high temperature tolerance of San Joaquin River fall run salmon, which survived temperatures of 80° F, inspired interest in introducing those salmon into the warm rivers of the eastern and southern United States” (Ron Yoshiyama, public communication). The full suite of life-stage and species need not be investigated, but rather it may be sufficient to examine those life stages most vulnerable to warming. For winter-run Chinook salmon, which spawn in summer, the embryonic life stage is at greatest risk from warming. Slater (1963) found in laboratory studies that winter-run Chinook salmon eggs and alevins had almost complete mortality by the time water temperatures reached 17.4°C. For spring-run Chinook salmon, the most vulnerable stages are adults holding over the summer in streams, and the gametes that they contain, although spawners, eggs and fry may also be vulnerable into early fall. For steelhead, and for yearling spring-run Chinook salmon, older juveniles are also subject to high summer temperatures. Some juvenile spring-run Chinook salmon and steelhead may encounter stressfully warm water as they migrate through the the lower rivers and Delta in late spring. It may be possible to learn more about the effects of high temperatures under natural conditions by monitoring expression of heat shock proteins (e.g., Viant et al., 2003), viability of gametes, and mortality.

3.2 Use of freshwater habitat

Large numbers of winter-run Chinook salmon fry migrate past the Red Bluff Diversion Dam in late summer and fall (Gaines and Martin, 2002), but little is known about their survival or use of the habitat downstream from the dam. Studying small fish in large rivers is difficult, and it is not obvious how best to proceed, but some combination of exploratory and hypothesis-based research seems in order. A salient question is whether restoring more natural conditions in the Sacramento River upstream from Colusa (the meanderbelt concept) would benefit juvenile winter-run Chinook salmon.

Juvenile spring-run Chinook salmon in Butte Creek have access to a remnant of overbank habitat in the Butte Sinks and the Sutter Bypass, which may help explain the relatively high productivity of this population (Williams, 2006). This hypothesis should be explored, building on earlier Department of Fish and Game studies, because if confirmed it would provide support for the idea of increasing access to the Yolo Bypass for fish moving down the Sacramento River. Microstructural and microchemical analyses of otoliths from returning adults may be a reasonable approach.

The spatial and temporal distribution of fish from various listed ESUs in the Delta is not well known, particularly since the size criteria used to assign juvenile fish to runs are not highly accurate (Hedgecock et al., 2001). How juvenile salmon and steelhead use Delta habitats is also poorly understood, in spite of the long history of sampling in the Delta. This limits the effectiveness of habitat restoration in the Delta. Several management issues of immediate concern involve the effects of water operations on listed runs and whether operations need to be modified to avoid harm to the runs. Better understanding of the spatial and temporal patterns of habitat use by the various runs should allow more effective strategies to balance disruption of water operations and harm to the runs. Such information could be obtained by genetic analysis of tissue samples collected during regular monitoring of juveniles, as well as by more focused studies. To the extent that fish from listed ESUs are sacrificed, it seems appropriate to obtain as much information as is practicable from them; physiologically-based measures of condition, discussed by Williams (2006), should be considered for this purpose.

3.3 Juvenile migration and survival

Low survival of juvenile Chinook salmon during freshwater migration is widely believed to be a serious problem. This belief is based on the propensity of hatchery releases made in San Francisco Bay to yield much higher contribution rates to ocean fisheries than are observed for releases made near the hatchery, at least for the Feather River Hatchery, and on the recognition that river habitats have been highly altered. To date, there has never been a serious attempt to measure the survival of fish migrating down the Sacramento River or to identify locations of unusually high mortality, as has been done for many years on the Columbia River (e.g., Williams et al., 2001; Skalski et al., 2002).

CALFED has funded a collaboration between UC Davis and NOAA to estimate migration and survival patterns of late fall-run Chinook salmon and steelhead smolts as they move from Battle Creek to the ocean in 2007-09. These stocks were selected for logistical reasons, including being large enough to carry the ultrasonic transmitters used by the study, and availability of large numbers of fish. Other agencies will be tagging fish and releasing them in the Delta (USFWS) or Bay (USACOE) in coordinated studies. This study should provide new insights into the magnitude, location and perhaps mechanisms of mortality of salmonids as they migrate through the Sacramento River, Delta and Bay. As tag technology advances and tags become ever smaller, this study design should become feasible for spring-run Chinook salmon and winter-run Chinook salmon.

3.4 Population genetics

Genetic analyses have provided substantial new information about Central Valley Chinook (Banks et al., 2000; Hedgecock et al., 2001; Williamson and May, 2003), and more information will be forthcoming as improved methods for genetic analysis develop. Routine monitoring with population genetics tools can allow detection of population bottlenecks (Garcia and Williamson, 2001), estimation of effective population size (Waples, 2004), and introgression (Aurelle et al., 2002; Cordes et al., 2006). However, the utility of these methods will depend in large part of the availability of tissue samples from which DNA can be extracted. We suggest that fin samples be routinely taken when fish are handled, and sent to the CDFG Salmonid Tissue Archive. Examples of fish that should be routinely sampled would include: fish used for gamete production in hatcheries, migrating juveniles, resident *O. mykiss*, especially where both resident and anadromous forms occur, and fish used in attempts to initiate new runs.

3.5 Harvest

The harvest of listed Central Valley Chinook has generated little controversy in recent years, because populations have been stable or increasing. It seems likely that good ocean conditions have contributed substantially to this state of affairs, however, and harvest may come under greater scrutiny when ocean conditions change (see the current situation regarding Klamath River fall Chinook for a preview of what may happen when fishery management goals in the Central Valley cannot be easily achieved[4]). Harvest affects not only the number of returning adults but also their age structure, and the effects on age structure may be long-lasting (Williams, 2006). It can be anticipated that models will be used to assess the effects of harvest on populations and their viability (Newman and Lindley, 2006), in terms of effects on age structure as well as abundance. To support these assessments, appropriate sampling needs to occur both in the fisheries and on the spawning grounds.

Existing monitoring of ocean harvest provides estimates of total chinook landings and fishing effort stratified by month and catch area. Direct estimates of stock- and age-specific harvest are routinely available only for hatchery coded-wire tagged release groups, and the harvest rates on these CWT groups are used as a proxy measure of the harvest rates on their natural stock counterparts. These hatchery and natural stock counterparts may or may not be different in ways that would effect ocean harvest rates, but in any event the approach is limited to instances in which there is a suitable hatchery/natural counterpart (e.g. Livingston Stone Hatchery/natural born Sacramento River winter Chinook), and is not applicable otherwise (e.g. Central Valley spring Chinook).

Genetic stock identification (GSI) techniques have advanced significantly in recent years. When coupled with the coast-wide microsatellite database for Chinook salmon recently developed by the Pacific Salmon Commission, GSI analysis of fishery harvests should provide a substantial increase in the information available for stock-specific impact assessment and management, particularly for those stocks that do not have a CWT counterpart (although not all listed Central Valley populations are identifiable to river of origin). GSI assessments in themselves, however, do not provide the corresponding age information for the harvests, which is essential for fishery management and population dynamics modeling purposes. Therefore, existing monitoring of the harvest should be expanded to include not only the collection and processing of tissue for the purpose of stock identification, but also the collection and processing of scales or otoliths for the purpose of aging. This data together with stock- and age-specific freshwater harvest and escapement data will enable the estimation of stock-age-specific ocean harvest rates (stratified by month and catch area), maturation rates, and freshwater harvest rates. These estimates in turn provide the foundation for fishery and population viability modeling. We

---

[4] A Google search on “Klamath fishery controversy” on 23 January 2007 yielded 51,300 pages that will give the interested reader a sense of what to expect.

note that CDFG has recently begun routine aging of many Chinook salmon runs in the Central Valley[5]

The temporal distributions of adult freshwater migrations makes it easier to avoid harvest of listed ESUs in the freshwater fishery than in the ocean fishery, but analysis of tissue samples collected at appropriate times would serve as a check, and also provide information on the tails of the temporal distributions of the adult migrations of listed ESUs. Better monitoring of freshwater harvest is needed for effective management of fall-run Chinook salmon, and tissue samples could be collected as an adjunct to such monitoring.

3.6 Ocean climate influence

It is now generally recognized that ocean conditions can have strong effects on salmon populations, and better understanding of these effects is important for assessing the effectiveness of recovery efforts. Ocean conditions for salmon are the subject of a growing literature, but Central Valley salmon enter a unique ocean environment, the Gulf of the Farallones, and seem to respond differently to ocean conditions than do salmon farther north (MacFarlane et al., 2005; Williams, 2006). Moreover, ocean conditions probably affect winter-run Chinook salmon and spring-run differently, since most spring-run Chinook salmon enter the ocean as subyearlings in late spring, but winter-run Chinook salmon enter the ocean at larger size, in the winter or early spring. Accordingly, although studies elsewhere may provide useful information, direct assessment of the effects of ocean conditions on Central Valley ESUs seems necessary.

Studies of juvenile fall-run Chinook salmon in the Gulf of the Farallones, such as (MacFarlane et al., 2005), probably are applicable to spring-run Chinook salmon, and should be continued. Capturing juvenile winter-run Chinook salmon in the ocean does not seem feasible, even if it were desirable, and studying the otolith microstructure and microchemistry of winter-run Chinook salmon sampled during carcass counts or taken at the hatchery may offer the best opportunity for assessing year to year differences in growth during early ocean residency. Less intensive microstructural analyses of spring-run Chinook salmon may be in order, to confirm that most juveniles follow a life history pattern similar to that of fall-run Chinook salmon.

3.7 Hatchery influence

There is a broad range of concern regarding the effects of hatchery culture on salmonids (Utter, 1998; Waples, 1999), and issues at either end of the range are most relevant for Chinook salmon in the Central Valley. Regarding winter-run Chinook salmon, the concern is whether negative effects of culture in conservation hatcheries such as the Livingston Stone Hatchery outweigh the demographic benefits. More generally, work is needed on the dynamics of hatchery impacts and recovery from these impacts: the theoretical studies done to date (Goodman, 2005) examine steady-state solutions. Also, more empirical information is needed on the strength of domestication selection in the hatchery, the fitness consequences of this selection, and the strength of natural selection in counteracting domestication selection, in order to better identify the safe limits of hatchery impacts.

3.8 Estimating spawning run sizes

Despite their widespread use in the Central Valley, models to estimate in-river spawning escapement based on mark-recapture carcass survey data require a number of assumptions which may not be met in the surveys. A principal assumption of mark-recapture surveys is that the marked animals will distribute randomly among the population during the interval before the recapture sampling. This assumption is often violated for carcasses, with differing consequences on the final escapement estimate depending on the size of the run, the area sampled, and the degree to which random resampling designs are used. Another assumption in carcass mark-recapture sampling is that all fish are either available for marking or are available for recapture sampling. This assumption is likely not met in large streams with deep pools. In these areas, some carcasses may be unavailable to sampling by field crews. This may result in under or over-estimation of the actual run size as it represents an unsampled portion of the run. Research is needed to better understand the degree to which these problems may occur in carcass surveys, the effect that these violations of assumptions have on estimates, and analytical and field strategies to reduce bias.

Data should be gathered on the age and size distributions of returning adults, as well as their numbers. Data on size distributions are important for estimating fecundity, which should be taken into account in estimating the reproductive potential of a given year-class of adults, and data on age are important for assessing the effects of harvest, and more generally are needed for the age-structured population models that could be used in improved harvest and viability models. These data could be obtained during carcass surveys by measuring lengths and collecting otoliths from subsamples of fish. Otoliths could also be used for microstructure analysis to elucidate juvenile life histories, as described above. Scales might also be used to collect age information on adults, but would provide much less information on juvenile life histories.

3.9 Estimating juvenile production

Juvenile production estimates, in combination with adult return data, allow for the effects of ocean and freshwater conditions to be teased apart. Such information is extremely valuable for understanding whether habitat restoration is effective and whether ocean climate anomalies are driving abundance trends. Estimating juvenile abundance is challenging, due to problems of operating sampling gear in highly variable flows, estimating the efficiency, or capture probability, of the gear, identifying juveniles to ESU or population, and accounting for the importance of juvenile age. Advances in all of these areas are needed.

3.10 Life history of *O. mykiss*

As a species, *O. mykiss* exhibit great variation in their tendency to migrate, ranging from non-migratory (resident trout) to strongly migratory (anadromous steelhead moving from rivers to the subarctic Pacific). It is now well understood that these two forms represent two distinct life history strategies of the same taxonomic species. In some river systems, it appears that the two forms maintain separate populations; in others there is evidence that they comprise a single interbreeding population where one form can give

---

[5] The proposal for this project can be found online at `http://www.delta.dfg.ca.gov/erp/docs/2005grants/Cohort_Reconstruction_DA_Proposal.pdf`.

rise to the other (Zimmerman and Reeves, 2000). This type of population is said to be "polymorphic" in its life history.

In California, steelhead and resident rainbow trout are often sympatric within stream reaches accessible from the ocean. Resident and anadromous fish could either be two components of a polymorphic and panmictic population, or they might be largely separate breeding populations. In the Central Valley, there is limited evidence that at least some populations are polymorphic (Titus (2000), as cited in McEwan (2001)). How we should think about and manage *O. mykiss* populations depends on the prevalence migratory polymorphism. If it is common, then it is nonsensical to manage one of the morphs without reference to the other, because polymorphic populations should have ecological, demographic and evolutionary properties quite distinct from strictly anadromous or resident populations.

To answer the question of whether steelhead and resident rainbow trout comprise a single interbreeding population, one must determine if the two forms are reproductively isolated from one another. Reproductive isolation may occur through differences in spawning times, differences in spawning habitat, or assortative mating. A particularly attractive approach to this question is based on the ratio of strontium (Sr) to calcium (Ca) within the otolith to identify the migration history of individuals and whether that individual had a resident trout or anadromous steelhead mother. Rainbow trout that have migrated to the ocean retain a Sr/Ca signature in their otoliths. Similarly, a rainbow trout that has a steelhead mother, regardless of its own migratory history, also retains an ocean Sr/Ca signature in the primordia of its otoliths due to the fact that the egg from which it arose was formed while its mother was in the ocean. If anadromous and resident *O. mykiss* interbreed rarely, then this should be detectable as differences in the frequency of neutral genetic markers between the two populations (but such differences will not arise with even limited reproductive exchange).

We suspect that there has been a significant shift in the frequency of resident and anadromous life histories in *O. mykiss* in the Central Valley (Lindley et al., in press.), and this likely has important conservation consequences. A CalFed-funded project[6] at UCSC, NOAA and CDFG is examining the role that river regulation may have in driving these shifts, but further work is needed in documenting the distribution of life history types throughout the range, identifying the factors driving this shift, assessing the degree to which it is reversible, and evaluating the consequences for population and evolutionary dynamics.

3.11 Reintroductions

When previously blocked or degraded habitat is restored and made accessible to anadromous fish, how exactly should salmonids be reintroduced to habitats? A number of critical decisions will need to be made when new habitats are made accessible, including method of reintroduction (natural colonization, transplanting of natural fish, outplanting of hatchery fish), source population of founding stock, and methods to limit access by undesired populations, species or stocks. These decisions in turn hinge upon complex genetic, demographic and ecological processes and principles. The Southwest Fisheries Science Center is undertaking a literature review to develop a decision analysis tool to guide future reintroductions.

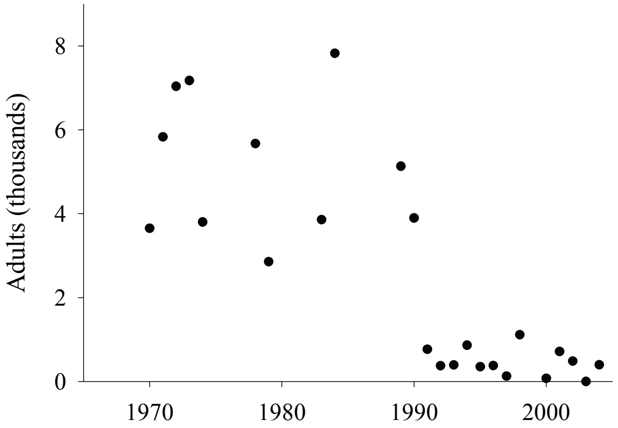

Figure 4: Number of spring Chinook returning to the Sacramento River above the Red Bluff Diversion Dam, as reported in the Grand Tab data base. The decrease after 1990 reflects changes in criteria for assigning fish to runs, not an actual population change.

A related effort is needed to evaluate the prospects for various fish passage technologies that might be employed to allow anadromous fish to move past currently impassable barriers. In concert with this effort, habitat and potential passage opportunities above rim dams in major tributaries of the Central Valley should be assessed.

3.12 Data Management

A good deal of data exist on Central Valley Chinook, steelhead, and their environments, from monitoring programs described by Pipal (2005) and Low (2005), and from other sources. Data are useful to the extent that they are used, however, and by and large the existing data are under used because they are not easily obtained. Worse, some of the data are misleading. Data management is difficult and expensive, but the cost of neglecting data is likely to be greater. Here are some recommendations:

1. Document the the strengths and weaknesses of existing datasets. The quality of existing datasets is highly variable, and sometimes not well documented, although Pipal (2005) provides good preliminary descriptions of many of them. For example, DFG maintains an Excel file, Grand Tab, with historical information on returns of Chinook to Central Valley streams. An apparent decline in returns of spring-run to the upper Sacramento River (above the Red Bluff Diversion Dam) after 1990 reflects a change in the criteria used to allocate fish to runs at the RBDD ladder, rather than an actual change in the population (Williams, 2006). Such problems with existing datasets need to be described before the people who know about them retire, and the descriptions need to be easily available to users of the data. This data about data is called metadata, and using metadata standards is an important step towards making comparisons among datasets feasible.

2. Develop a common portal for basic data on Central Valley salmon and steelhead and related environmental variables, using a common format and data retrieval protocols. A significant number of databases directly connected with ongoing monitoring programs exists for Central Valley fish and habitats. However, the coordination of these databases is weak, in part because the databases

---

[6] Proposal is available online at `https://solicitation.calwater.ca.gov/solicitations/2004.01/reports/public_proposal_compilation?proposal_id=0140`

were developed independently by programs and agencies for specific unrelated purposes. For example, CALFISH (`http://www.calfish.org/DesktopDefault.aspx`) provides information on fish migrations and trends, the IEP Data Vault points to the Bay Delta and Tributaries (BDAT) Project data on `http://bdat.ca.gov/` and the California Data Exchange (CDE; `http://cdec.water.ca.gov`) provides information on flows, storage and snow pack. The CALFISH and BDAT databases share some common variables but neither contains water data available at the CDE database and none of these sites has temperature information. Further, they use different data formats, data retrieval protocols, and have different temporal and spatial coverage.

Coordination of essentially independent databases with unique purposes is a major technical and organizational undertaking. However, the Pacific Northwest faces similar challenges and has developed the Northwest Environmental Data Network (NED) (`http://www.nwcouncil.org/ned/Default.asp`), a cooperative effort to improve collection, management and sharing of environmental data and information. The objective of the NED Portal is to direct scientific and resource management users of data to a consistent source of environmental geospatial and tabular data and metadata. In like fashion, Central Valley and related databases should be coordinated through a common data portal so that data and its metadata can be obtained in a common format using a common retrieval protocol.

3. Develop a portal for graphical data presentation. Analysis and synthesis are necessary to convert data into information. Although researchers and some others need data in numerical form, graphical presentations of data are more useful for most purposes. For example, as part of the Environmental Water Account program, DWR prepares graphics synthesizing data on fish and flow for the weekly conference calls of the Data Assessment Team. Other such graphics, designed to present up-to-date information on particular topics or to meet the needs of particular audiences, should be made available. As an example that might be emulated in the Central Valley, the DART data site (`http://www.cbr.washington.edu`) synthesizes data on fish, climate, and river conditions from various monitoring programs and provides graphical and textual information on historical, current, and forecasted fish migrations and trends. In general, if monitoring data are not worth presenting in graphical formats on a regular basis, probably they are not worth collecting. With modern graphical programs, creating such graphics and keeping them up to date would not be difficult.

4 Acknowledgments

The authors appreciate discussions with D. Windham. D. Boughton and P. Adams provided critical review of this manuscript. The work of JGW, JJA and BPM was supported by the CALFED Science Program through Association of Bay Area Governments contract CALFED/DWR 4600001642.

References

Allendorf, F. W., D. Bayles, D. L. Bottom, K. P. Currens, C. A. Frissell, D. Hankin, J. A. Lichatowich, W. Nehlsen, P. C. Trotter, and T. H. Williams. 1997. Prioritizing Pacific salmon stocks for conservation. Conservation Biology **11**:140–152.

Aurelle, D., G. Cattaneo-Berrebi, and P. Berrebi. 2002. Natural and artificial secondary contact in brown trout (*Salmo trutta*, L.) in the French western Pyrenees assessed by allozymes and microsatellites. Heredity **89**:171–183.

Banks, M. A., V. K. Rashbrook, M. J. Calavetta, C. A. Dean, and D. Hedgecock. 2000. Analysis of microsatellite DNA resolves genetic structure and diversity of chinook salmon (*Oncorhynchus tshawytscha*) in California's Central Valley. Canadian Journal of Fisheries and Aquatic Sciences **57**:915–927.

CDFG and NMFS. 2001. Final report on anadromous salmonid fish hatcheries in California. California Department of Fish and Game and National Marine Fisheries Service Southwest Region. `http://swr.nmfs.noaa.gov/HatcheryReviewPublicDraft2.pdf`.

Clark, J. A., J. M. Hoekstra, P. D. Boersma, and P. Kareiva. 2002. Improving U.S. Endangered Species Act recovery plans: Key findings and recommendations of the SCB recovery plan project. Conservation Biology **16**:1510–1519.

Cordes, J. F., M. R. Stephens, M. A. Blumberg, and B. May. 2006. Identifying introgressive hybridization in native populations of California golden trout based on molecular markers. Transactions of the American Fisheries Society **135**:110–128.

Dettinger, M. D., D. R. Cayan, M. K. Meyer, and A. E. Jeton. 2004. Simulated hydrologic responses to climate variations and change in the Merced, Carson, and American River basins, Sierra Nevada, California, 1900–2099. Climatic Change **62**:283–317.

Gaines, P. D. and C. D. Martin. 2002. Abundance and seasonal, spatial and diel distribution patterns of juvenile salmonids passing the Red Bluff Diversion Dam, Sacramento River. U. S. Fish and Wildlife Serivce. `http://www.fws.gov/redbluff/PDF/Abundance%20Report%20(Final).pdf`.

Garcia, J. C. and E. G. Williamson. 2001. Detection of reduction in population size using data from microsatellite loci. Molecular Ecology **10**:305–318.

Gilman, S. E., D. S. Wethey, and B. Helmuth. 2006. Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales 10.1073/pnas.0510992103. Proceedings of the National Academy of Sciences **103**:9560–9565.

Goodman, D. 2005. Selection equilibrium for hatchery and wild spawning fitness in integrated breeding programs. Canadian Journal of Fisheries and Aquatic Sciences **62**:374–389.

Halbert, C. L. 1993. How adaptive is adaptive management? Implementing adaptive management in Washington State and British Columbia. Reviews in Fisheries Science **1**:261–283.

Harvey, C. D. 1995. Adult steelhead counts in Mill and Deer Creeks, Tehama County, October 1993 - June 1994. Administrative Report No. 95-3 California Department of Fish and Game.

Hauer, F. R., C. N. Dahm, G. A. Lamberti, and J. A. Stanford. 2003. Landscapes and ecological variability of rivers in North America: factors affecting restoration strategies. In R. C. Wissmar and P. A. Bisson, editors, *Strategies for restoring river ecosystems: sources of variability and uncertainty in natural* *and managed systems*, pp. 81–105. American Fisheries Society, Bethesda, MD.

Hayhoe, K., D. Cayan, C. B. Field, P. C. Frumhoff, E. P. Maurer, N. L. Miller, S. C. Moser, S. H. Schneider, K. N. Cahil, E. E. Cleland, L. Dale, R. Drapek, R. M. Hanemann, L. S. Kalkstein, J. Lenihan, C. K. Lunch, R. P. Neilson, S. C. Sheridan, and J. H. Verville. 2004. Emissions pathways, climate change, and impacts on California. Proceedings of the National Academy of Sciences, USA **101**:12442–12427.

Hedgecock, D., M. A. Banks, V. K. Rashbrook, C. A. Dean, and S. M. Blankenship. 2001. Applications of population genetics to conservation of chinook salmon diversity in the Central Valley. In: Contributions to the Biology of Central Valley Salmonids. Fish Bulletin (CDFG) **179**:45–70.

IUCN. 1994. *IUCN Red List Categories*. IUCN Species Survival Commission, Gland, Switzerland.

Lindley, S. T., R. S. Schick, A. Agrawal, M. Goslin, T. Pearson, E. Mora, J. J. Anderson, B. May, S. Greene, C. Hanson, A. Low, D. McEwan, R. B. MacFarlane, C. Swanson, and J. G. Williams. 2006. Historical population structure of Central Valley steelhead and its alteration by dams. San Francisco Estuary and Watershed Science Volume 4, Issue 1, Article 2.

Lindley, S. T., R. S. Schick, B. May, J. J. Anderson, S. Greene, C. Hanson, A. Low, D. McEwan, R. B. MacFarlane, C. Swanson, and J. G. Williams. 2004. Population structure of threatened and endangered chinook salmon ESUs in California's Central Valley basin. U.S. Dept. Commer, NOAA Tech. Memo. NMFS-SWFSC-360.

Lindley, S. T., R. S. Schick, E. Mora, P. B. Adams, J. J. Anderson, S. Greene, C. Hanson, B. P. May, D. McEwan, R. B. MacFarlane, C. Swanson, and J. G. Williams. In press. Framework for assessing viability of threatened and endangered Chinook salmon and steelhead in the Sacramento-San Joaquin basin. San Francisco Estuary and Watershed Science.

Low, A. 2005. Existing program summary: Central Valley salmon and steelhead monitoring programs. California Department of Fish and Game. `http://www.dfg.ca.gov/nafwb/pubs/2005/CV_MonitoringPrograms.pdf`.

MacFarlane, R. B., S. Ralston, C. Royer, and E. C. Norton. 2005. Juvenile chinook salmon (*Oncorhynchus tshawytscha*) growth on the central California coast during the 1998 El Niño and 1999 La Niña. Fisheries Oceanography **14**:321–332.

McCullough, D. A. 1999. A review and synthesis of effects of alteration to the water temperature regime on freshwater life stages of salmonids, with special reference to chinook salmon. Document 910-R-99010, United States Environmental Protection Agency.

McEwan, D. R. 2001. Central Valley steelhead. In R. L. Brown, editor, *Fish Bulletin 179*, pp. 1–43. California Department of Fish and Game, Sacramento, CA.

Mohseni, O., H. G. Stefan, and T. R. Erickson. 1998. A nonlinear regression model for weekly stream temperatures. Water Resources Research **34**:2684–2692.

Newman, K. B. and S. T. Lindley. 2006. Accounting for demographic and environmental stochasticity, observation error and parameter uncertainty in fish population dynamics models. North American Journal of Fisheries Management **26**:685–701.

Peterman, R. M., C. J. Walters, and R. Hilborn. 1977. Systems analysis of Pacific salmon management problems. University of British Columbia, Institute of Resource Ecology.

Peterson, D., R. Smith, I. Stewart, N. Knowles, C. Soulard, and S. Hager. 2005. Snowmelt discharge characteristics Sierra Nevada, California. US Geological Survey. `http://pubs.usgs.gov/sir/2005/5056/`.

Pipal, K. 2005. Summary of monitoring activities for ESA-listed salmonids in California's Central Valley. U.S. Dept. Commer, NOAA Tech. Memo. NMFS-SWFSC-373. `http://swfsc.noaa.gov/publications/TM/SWFSC/NOAA-TM-NMFS-SWFSC-373.PDF`.

Roni, P., editor. 2005. *Monitoring stream and watershed restoration*. American Fisheries Society, Bethesda, MD.

Skalski, J. R., R. Townsend, J. Lady, A. E. Giorgi, J. R. Stevenson, and R. D. McDonald. 2002. Estimating route-specific passage and survival probabilities at a hydroelectric project from smolt radiotelemetry studies. Canadian Journal of Fisheries and Aquatic Sciences **59**:1385–1393.

Slater, D. W. 1963. Winter-run chinook salmon in the Sacramento River, California with notes on water temperature requirements at spawning. United States Department of the Interior, Fish and Wildlife Serivce, Bureau of Sport Fisheries and Wildlife. `http://www.estuaryarchive.org/cgi/viewcontent.cgi?article=1068&context=archive`.

Titus, R. G. 2000. Adult steelhead collected in the Calaveras River below New Hogan Dam in March 2000. Stream Evaluation Program report, California Department of Fish and Game.

Travis, J., R. Lande, M. Mangel, R. A. Myers, C. H. Peterson, M. Power, and D. Simberloff. 2004. Salmon Recovery Science Review Panel: report for the meeting held December 1-3, 2004. National Marine Fisheries Serive. `http://www.nwfsc.noaa.gov/trt/rsrp_docs/rsrpreportdec04finalwbios.pdf`.

Utter, F. 1998. Genetic problems of hatchery-reared progeny released into the wild, and how to deal with them. Bulletin of Marine Science **62**:623–640.

Van Woert, W. 1964. Mill Creek counting station. Office memorandum to Eldon Hughes, May 25, 1964. California Department of Fish and Game, Water Projects Branch, Contract Services Section.

Viant, M. R., I. Werner, E. S. Rosenblum, A. S. Gantner, R. S. Tjeerdema, and M. L. Johnson. 2003. Correlation between heat-shock protein induction and reduced metabolic condition in juvenile steelhead trout (Oncorhynchus mykiss) chronically exposed to elevated temperature. Fish Physiology and Biochemistry **29**:159–171.

Waples, R. S. 1999. Dispelling some myths about hatcheries. Fisheries **24**:12–21.

Waples, R. S. 2004. Salmonid insights into effective population size. In A. P. Hendry and S. C. Stearns, editors, *Evolution illuminated: salmon and their relatives*, pp. 295–314. Oxford University Press, Oxford.

Williams, J. G. 1999. Stock dynamics and adaptive management of habitat: an evaluation based on simulations. North American Journal of Fisheries Management **19**:329–341.

Williams, J. G. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. San Francisco Estuary and Watershed Science Volume 4, Issue 3, Article 2.

Williams, J. G., S. G. Smith, and W. D. Muir. 2001. Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia rivers hydropower system, 1966-1980 and 1993-1999. North American Journal of Fisheries Management **21**:310–317.

Williamson, K. and B. May. 2003. Homogenization of fall-run chinook salmon gene pools in the Central Valley of California, USA Completion report for CALFED grant #97-C09 via California Department of Fish and Game Contract Agreement No. P0140015. 150pp.

Wilson, P. H. 2003. Using population projection matrices to evaluate recovery strategies for Snake River spring and summer chinook salmon. Conservation Biology **17**:782–794.

Wissmar, R. C. and P. A. Bisson. 2003. Strategies for restoring river ecosystems: sources of variability and uncertainty. In R. C. Wissmar and P. A. Bisson, editors, *Strategies for restoring river ecosystems: sources of variability and uncertainty in natural and managed systems*, pp. 1–10. American Fisheries Society, Bethesda, MD.

Zimmerman, C. E. and G. H. Reeves. 2000. Population structure of sympatric anadromous and non-anadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. Canadian Journal of Fisheries and Aquatic Sciences **57**:2152–2162.

FEBRUARY 2007

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

Published by the California Bay-Delta Authority Science Program and the John Muir Institute of the Environment

Framework for Assessing Viability of Threatened and Endangered Chinook Salmon and Steelhead in the Sacramento-San Joaquin Basin

Steven T. Lindley*, National Oceanic and Atmospheric Administration

Robert S. Schick, National Oceanic and Atmospheric Administration

Ethan Mora, University of California, Santa Cruz

Peter B. Adams, National Oceanic and Atmospheric Administration

James J. Anderson, University of Washington

Sheila Greene, California Department of Water Resources

Charles Hanson, Hanson Environmental, Inc.

Bernard P. May, University of California, Davis

Dennis R. McEwan, California Department of Fish and Game

R. Bruce MacFarlane, National Oceanic and Atmospheric Administration

Christina Swanson, The Bay Institute

John G. Williams, independent consultant

***Corresponding author:** steve.lindley@noaa.gov

ABSTRACT

Protected evolutionarily significant units (ESUs) of salmonids require objective and measurable criteria for guiding their recovery. In this report, we develop a method for assessing population viability and two ways to integrate these population-level assessments into an assessment of ESU viability. Population viability is assessed with quantitative extinction models or criteria relating to population size, population growth rate, the occurrence of catastrophic declines, and the degree of hatchery influence. ESU viability is assessed by examining the number and distribution of viable populations across the landscape and their proximity to sources of catastrophic disturbance.

Central Valley spring-run and winter-run Chinook salmon ESUs are not currently viable, according to the criteria-based assessment. In both ESUs, extant populations may be at low risk of extinction, but these populations represent a small portion of the historical ESUs, and are vulnerable to catastrophic disturbance. The winter-run Chinook salmon ESU, in the extreme case, is represented by a single population that spawns outside of its historical spawning range. We are unable to assess the status of the Central Valley steelhead ESU with our framework because almost all of its roughly 80 populations are classified as data deficient. The few exceptions are those populations with a closely associated hatchery, and the naturally-spawning fish in these streams are at high risk of extinction. Population monitoring in this ESU is urgently needed.

Global and regional climate change poses an additional risk to the survival of salmonids in the Central Valley. A literature review suggests that by 2100, mean summer temperatures in the Central Valley region may increase by 2-8°C, precipitation will likely shift to more rain and less snow, with significant declines in total precipitation possible, and hydrographs will likely change, especially in the southern Sierra Nevada mountains. Warming at the lower end of the predicted range may allow spring-run Chinook salmon to persist in some streams, while making some currently utilized habitat inhospitable. At the upper end of the range of predicted warming, very little spring-run Chinook salmon habitat is expected to remain suitable.

In spite of the precarious position of Central Valley salmonid ESUs, there are prospects for greatly improving their viability. Recovering Central Valley ESUs may require re-establishing populations where historical populations have been extirpated (e.g., upstream of major dams). Such major efforts should be focused on those watersheds that offer the best possibility of providing suitable habitat in a warmer future.

KEYWORDS

Central Valley, Chinook salmon, steelhead, *Oncorhynchus tshawytscha, Oncorhynchus mykiss,* population viability, conservation, recovery planning, catastrophes, climate change, endangered species, biocomplexity

SUGGESTED CITATION

Lindley, Steven, T. et al. Framework for Assessing Viability of Threatened and Endangered Chinook Salmon and Steelhead in The Sacramento-San Joaquin Basin.

Vol. 5, Issue 1 [February 2007]. Article 4.

http://repositories.cdlib.org/jmie/sfews/vol5/iss1/art4

INTRODUCTION

Numerous evolutionarily significant units (ESUs) of Pacific salmon and steelhead are listed as threatened or endangered species under the US Endangered Species Act (ESA) of 1973. The ESA, as amended in 1988, requires that recovery plans have quantitative, objective criteria that define when a species can be removed from the list, but does not offer detailed guidance on how to define recovery criteria. Logically, some of the recovery criteria should be biological indicators of low extinction risk. Recovery plans prepared since the 1988 amendment typically have about six recovery criteria, but only about half of these are quantitative or clearly related to biological information (Gerber and Hatch 2002). Gerber and Hatch (2002) found a positive relationship between the number of well-defined biological recovery criteria and the trend in abundance for the species. This empirical finding supports our intuition that well-defined recovery goals are important for recovering species.

Recovery planning seeks to ensure the viability of protected species. Viability of populations and ESUs depends on the demographic properties of the population or ESU, such as population size, growth rate, the variation in growth rate, and carrying capacity (e.g., Tuljapurkar and Orzack 1980). In the short term, the demographic properties of a population depend largely on the quality and quantity of habitat. In the longer term, genetic diversity, and the diversity of habitats that support genetic diversity, become increasingly important (McElhany et al. 2000; Kendall and Fox 2002; Williams and Reeves 2003). Consequently, McElhany et al. (2000) suggested that the viability of Pacific salmon populations should be assessed in terms of abundance, productivity, spatial structure, and genetic and life-history diversity. ESUs can be assessed in these same terms. While providing a useful conceptual framework for thinking about viability of Pacific salmon, McElhany et al. (2000) did not provide quantitative criteria that would allow one to assess whether particular populations or ESUs are viable.

Developing objective, quantitative, and biologically meaningful recovery criteria for Pacific salmonid ESUs is difficult. Ideally, these criteria would be population- and ESU-specific, taking into account the constraints in some factors that influence viability. For example, quantity of suitable habitat will usually set some limit on the size of a population, and populations with less habitat will need to have higher intrinsic growth rates (or less variable growth) than populations with more habitat, if they are to have similar viability. Unfortunately, population-specific information is frequently unavailable. One way out of this problem is to forego population-specific goals and develop biologically relevant criteria that are generic to *Oncorhynchus* species. Conservation biologists have developed a number of such criteria for the related task of identifying and prioritizing species in need of conservation (Mace and Lande 1991; IUCN 1994; Gärdenfors et al. 2001), and these taxonomically general criteria have been modified for application to Pacific salmonids (Allendorf et al. 1997).

If extinction risks of populations were independent, assessing the extinction risk of the ESU would be straightforward—the extinction risk of the ESU would be the product of the extinction risks of all its populations. We expect the extinction risks of populations to be correlated, however, because normal environmental influences affecting the population dynamics of salmonids are spatially correlated. Perhaps even more importantly, the effects of catastrophes (defined as rare environmental perturbations with very strong negative effects on afflicted populations) can be quite widespread. Finally, in cases like the Central Valley, all populations must use certain small areas (e.g., San Pablo Bay) where a single event such as a toxic spill could affect all populations even though they are widely dispersed for most of their life cycle. In some cases, it may be possible to explicitly examine the vulnerability of ESUs to catastrophic risks. We are unlikely to be able to identify all possible sources of risk, however, so we should also think of managing risk by maximizing diversity within ESUs.

In this report, we develop an approach for assessing the viability of Pacific salmonid populations and ESUs, and apply it to listed ESUs in California's Central Valley domain. In the "Assessment Framework" section below, we extend the criteria-based approach of Allendorf et al. (1997) to account for the effects of hatchery fish on the extinction risk of naturally-spawning populations, and explicitly define a "low" extinction risk category. This low-risk definition can serve as a default goal for recovering populations for which too little data exist for more detailed goals to be developed. ESU viability is addressed in two ways. In the first, risk-spreading is assessed by examining how viable populations are spread among geographically-defined regions within the ESU. In the second, we attempt to account explicitly for the spatial structure of the ESU and the spatial structure of various catastrophic risks, including volcanos, wildfires, and droughts. In the "Application to Central Valley Salmonids" section, we apply the analyses to Central Valley spring-run Chinook salmon (*Oncorhynchus tshawytscha)*, Sacramento River winter-run Chinook salmon (*O. tshawytscha)*, and Central Valley steelhead (*Oncorhynchus mykiss)*. As these methods implicitly assume that the future will be like the recent past, we review the likely effects of climate variation and climate change in "Climate Variability and Change." The "Summary and Recommendations" section summarizes our findings and makes some recommendations for recovery planners.

ASSESSMENT FRAMEWORK

Population Viability

Risk Categories

The goal of our population-level viability assessment is to classify populations into one of six categories, including "extinct," "extinct in the wild," "high," "moderate," and "low" extinction risk, or "data deficient," following the general approach of the IUCN (1994) as modified for Pacific salmonids by Allendorf et al. (1997). The goal of recovery activities should be to achieve at least a low risk of extinction for focal populations. We assume that a 5% risk of extinction in 100 years is an acceptably low extinction risk for populations (Thompson, 1991). Many salmonid populations are capable of achieving much lower risk levels and can provide additional benefits to ecosystems (Schindler et al. 2003) and people (e.g., by providing fishing opportunities) at these higher levels of abundance and productivity.

For Chinook salmon, we infer that populations are extinct if all of their historically utilized spawning habitat is blocked by impassable dams. *O. mykiss* pop-

Table 1. Criteria for assessing the level of risk of extinction for populations of Pacific salmonids. Overall risk is determined by the highest risk score for any category. (Modified from Allendorf et al. 1977)

	Risk of Extinction		
Criterion	High	Moderate	Low
Extinction risk from PVA	> 20% within 20 years	> 5% within 100 years	< 5% within 100 years
	– or any ONE of –	– or any ONE of –	– or ALL of –
Population size[a]	$N_e \leq 50$	$50 < N_e \leq 500$	$N_e > 500$
	–or–	–or–	–or–
	$N \leq 250$	$250 < N \leq 2500$	$N > 2500$
Population decline	Precipitous decline[b]	Chronic decline or depression[c]	No decline apparent or probable
Catastrophe, rate and effect[d]	Order of magnitude decline within one generation	Smaller but significant decline[e]	not apparent
Hatchery influence[f]	High	Moderate	Low

[a] Census size N can be used if direct estimates of effective size N_e are not available, assuming $N_e/N = 0.2$.

[b] Decline within last two generations to annual run size ≤ 500 spawners, or run size > 500 but declining at $\geq 10\%$ per year. Historically small but stable population not included.

[c] Run size has declined to ≤ 500, but now stable.

[d] Catastrophes occuring within the last 10 years.

[e] Decline $< 90\%$ but biologically significant.

[f] See Figure 1 for assessing hatchery impacts.

ulations may persist above migration barriers even if spawning habitat is inaccessible to anadromous fish, so migration barriers can not be taken as evidence of extinction for *O. mykiss*. In some cases, dams create suitable habitat in downstream reaches (typically through regulated discharges of cold water), and may support a population. We assess the status of such populations with the criteria described below, but note that the identity of tailwater populations may differ from populations historically found above the barrier.

Populations entirely dependent on artificial production (i.e., found only in a captive broodstock program or hatchery) would be considered extinct in the wild.

Risk categories from "high" to "low" are defined by various quantitative criteria, and correspond to specific risks of extinction within specific time horizons (Table 1). We extend Allendorf et al.'s (1997) criteria categories and risk levels in two ways (Table 1). First, we define criteria for the "low" risk category, which are implicit in Allendorf et al. (1997) Table 1. To simplify analysis, we collapse Allendorf et al. (1997) "very high" and "high" risk categories into a single "high" risk category. We add a set of criteria to deal with fish produced by hatcheries that spawn in the wild. Allendorf et al. (1997) deal with hatchery fish in their assessment of conservation value, but for our purposes of defining recovery criteria, the influence of hatchery fish must be included in the viability criteria.

Populations are classified as "data deficient" when there are not enough data to classify them otherwise. It is possible to classify a population as "high" risk with incomplete data (e.g., if it is known that $N_e < 50$, but trend data and hatchery straying are lacking), but a low risk classification must be met with all criteria.

Risk Criteria

Following Allendorf et al. (1997), the first set of criteria deal with direct estimates of extinction risk from population viability models. If such analyses exist and are deemed reasonable, such assessments may be sufficient for assessing risk; indeed, Allendorf et al. (1997) intended that their other criteria be used when such analyses were not available. The simplest useful population viability assessments are based on the random-walk-with-drift model (Dennis et al. 1991), and can be extended to account for observation error (Lindley 2003); we use this model where possible in this paper. We note that trying to predict absolute extinction risk is subject to many pitfalls and is viewed with skepticism by many conservation biologists and ecologists (Beissinger and Westphal (1998) provides a review of the various issues). We therefore recommend that population viability analysis (PVA) results be compared to the results of applying the simpler criteria, described below.

The effective population size criteria in the second row of Table 1 relate to loss of genetic diversity. The effective population size, N_e, is smaller than the population census size N due to variation in reproductive success among individuals. For Chinook salmon, N_e/N ranges from 0.06 to 0.29 (Waples et al. 2004). N_e can be estimated from detailed demographic or genetic data (e.g., see Ardren and Kapuscinski 2003). Very small populations, for example with $N_e < 50$, suffer severe inbreeding depression (Franklin 1980; Soulé 1980), and normally outbred populations with such low Ne have a high risk of extinction from this inbreeding.

Somewhat larger, but still small, populations can be expected to lose variation in quantitative traits through genetic drift faster than it can be replaced by mutation. Franklin (1980) and Soulé (1980) used population genetics models to show that such drift is significant when $N_e < 500$. The assumptions behind the $N_e > 500$ rule are problematical in two ways. On one hand, the original models used to derive the 500 rule (Franklin 1980; Soulé 1980) assumed that all mutations were mildly deleterious, but later research showed that only 10% of mutations are mildly deleterious (Lande 1995). This means that mutation effectively introduces new genetic variation at only 10% of the rate previously assumed, so N_e should therefore be > 5000 to attenuate the loss of genetic diversity due to drift. On the other hand, the models of Franklin and Sóule also assume that populations are closed to immigration. Very low levels of immigration, on the order of one individual per generation, can prevent the loss of alleles through drift (Wright 1931). We note that salmonid populations within ESUs are expected to have immigration at such low rates. Given the countervailing effects of the violations of the assumptions underlying the $N_e > 500$ rule, we apply the Allendorf et al. (1997) criteria as they stand, but note that with future research, it may be possible to define population size targets that conserve genetic variation and account for migration and genetic structuring within ESUs (e.g., Whitlock and Barton 1997).

The population decline criteria are intended to capture demographic risks. The rationale behind the population decline criteria are fairly straightforward– severe and prolonged declines to small run sizes are strong evidence that a population is at risk of extinction. The criteria have two components– a downward trend in abundance and a critical run size (< 500 spawners). Note that spawning run size is distinct from N_e. Although it is not clear how Allendorf et al. (1997) chose 500 as the threshold spawning run size, we adopt this threshold to maximize consistency with their criteria. We also note that typical salmonid populations near a carrying capacity of 500 spawners require only modest intrinsic growth rates to have low probability of extinction, given typical levels of variation in population growth (D. Boughton, NOAA Fisheries, Santa Cruz, CA; in preparation).

The catastrophe criteria trace back to Mace and Lande (1991), and the underlying theory is further developed by Lande (1993). The overall goal of the catastrophe criteria is to capture a sudden shift from a low risk state to a higher one. Catastrophes are defined as instantaneous declines in population size due to events that occur randomly in time, in contrast to regular environmental variation, which occurs constantly and can have both positive and negative effects on the population. Catastrophes have a qualitatively different effect on the distribution of mean time to extinction than does environmental variation. Because of this, it is sensible to treat catastrophes separately from population declines. We view catastrophes as singular events with an identifiable cause and only negative immediate consequences, as opposed to normal environmental variation which can produce very good as well as very bad conditions. Some examples of catastrophes include disease outbreaks, toxic spills, or vol-

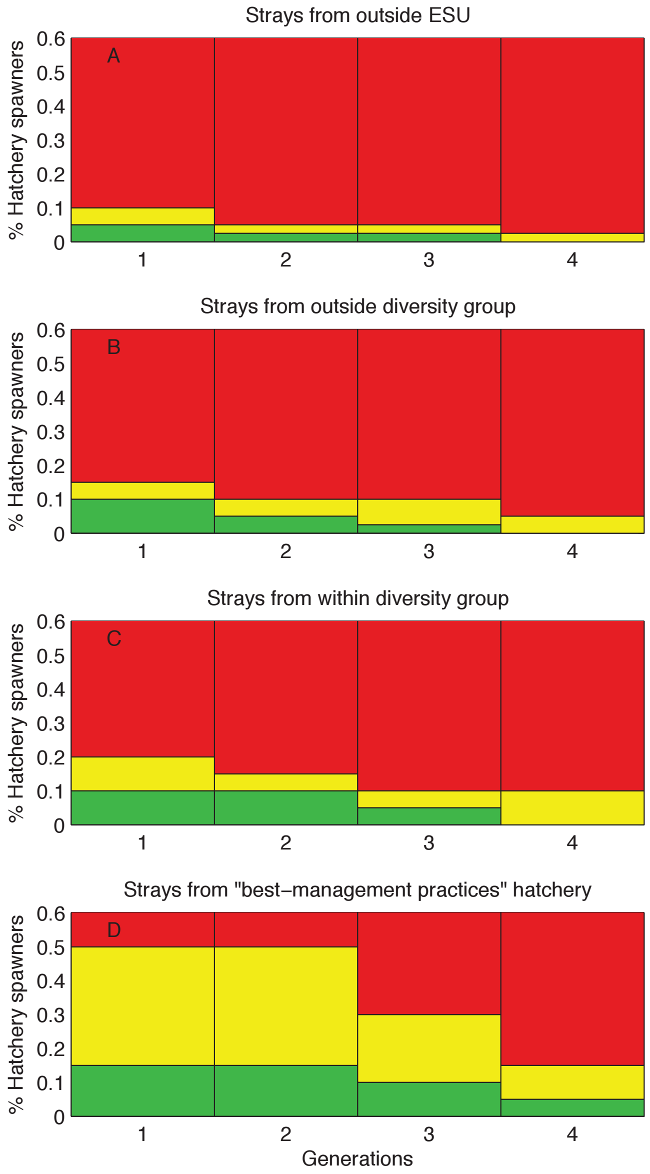

Figure 1. Extinction risk levels corresponding to different amount, duration and source of hatchery strays. Green bars indicate the range of low risk, yellow bars moderate risk, and red areas indicate high risk. Which chart to use depends on the relationship between the source and recipient populations. A: hatchery strays are from a different ESU than the wild population. B: Hatchery strays are from the same ESU but from a different diversity group within the ESU. C: Hatchery strays are from the same ESU and diversity group, but the hatchery does not employ "best management practices." D: Hatchery strays are from the same ESU and diversity group, and the hatchery employs "best management practices." Redrawn from Interior Columbia Basin Technical Recovery Team (2005).

canic eruptions. A high risk situation is created by a 90% decline in population size over one generation. A moderate risk event is one that is smaller but biologically significant, such as a year-class failure.

We view the spawning of hatchery fish in the wild as a potentially serious threat to the viability of natural populations. Population genetics theory predicts that fish hatcheries can negatively impact wild populations when hatchery fish spawn in the wild (e.g., Emlen 1991; Lynch and O'Hely 2001; Ford 2002; Goodman 2005). These predictions are supported by mounting empirical evidence (e.g., Reisenbichler and McIntyre 1977; Chilcote et al. 1986; Reisenbichler and Rubin 1999; McLean et al. 2003; Kostow 2004). In assessing the genetic impact of immigration on a population, one must consider the source of the immigrants, how long the impact goes on, the number of immigrants relative to the size of the recipient population, and how divergent the immigrants are from the recipient population. We adopt the approach of the Interior Columbia Basin Technical Recovery Team (TRT) (2005) to define how different scenarios relate to extinction risk for natural populations, summarized in Figure 1. We made one significant change to the Interior Columbia Basin Technical Recovery Team (2005) hatchery introgression criteria, allowing up to 5% of naturally spawning fish to be of hatchery origin while maintaining a low risk, if the hatchery fish are from a hatchery using "best management practices" (see Flagg et al. 2004; Olson et al. 2004; Mobrand et al. 2005, for a description of these practices) using broodstock derived from the wild population. This is consistent with the ICBTRT scheme, which can result in a low-risk classification even with moderate amounts of straying from best-practices hatcheries, so long as other risk measures are acceptable. We note that the risk levels depicted in Figure 1 are based on expert opinion, and that the empirical basis for relating hatchery impacts to extinction risk is currently limited (Bilby et al. 2003).

Allendorf et al. (1997) did not specify how to calculate estimates for the various viability criteria. Table 2 provides estimators that we have used in this paper. The average run size is computed as the mean of up to the three most recent generations, if that much data are available. Mean population size is estimated as the

Table 2. Estimation methods and data requirements for population metrics. St denotes the number of spawners in year t; g is mean generation time, which we take as three years for California salmon.

Metric	Estimator	Data	Criterion
$\hat{S}_t$	$\sum_{i=t-g+1}^{t} S_i/g$	≥ 3 years spawning run estimates	Population decline
N_e	$N \times 0.2$ or other	varies	Population size
N	$\hat{S}_t \times g$	≥ 3 years spawning run estimates	Population size
Population growth rate (% per year)	slope of $\log(S_t)$ v. time $\times 100$	10 years S_t	Population decline
c	$100 \times (1 - \min(N_{t+g}/N_t))$	time series of N	Catastrophe
h	average fraction of natural spawners of hatchery origin	mean of 1-4 generations	Hatchery influence

product of the mean run size and the average generation time. Population growth (or decline) rate is estimated from the slope of the natural logarithm of spawners versus time for the most recent 10 years of spawner count data. The fraction of naturally spawning fish of hatchery origin is the mean fraction over one to four generations.

ESU Viability

ESU viability depends on the number of populations within the ESU, their individual status, their spatial arrangement with respect to each other and sources of catastrophic disturbance, and diversity of the populations and their habitats. In the most general terms, ESU viability increases with the number of populations, the viability of these populations, the diversity of the populations, and the diversity of habitats that they occupy. Under natural conditions, most salmonid ESUs have persisted for at least many centuries, and perhaps much longer, given the observed level of genetic differentiation within and among them. How much can an ESU be altered before it is considered at risk of extinction? While we will not assess ESU viability in absolute terms, we assume that recovery planners will want ESUs to be likely to persist in the face of environmental variation of the sort we know has occurred over the last 500-1000 years. Such variation has included natural catastrophes such as prolonged drought, volcanic eruptions, large wildfires, and anthropogenic impacts such as the 1991 Cantara metam sodium spill. Such catastrophes could occur at any time in the foreseeable future. Therefore, for ESUs to be considered viable, they should at a minimum be able to persist if challenged by any one of these types of catastrophes.

Viability by Representation

We assess ESU viability with two different approaches. The goal of both approaches is to spread risk and maximize future potential for adaptation. The Puget Sound, Willamette/Lower Columbia and Interior Columbia TRTs have used variations on the idea of dividing ESUs into subunits (Myers et al. 2003; Ruckelshaus et al. 2002; Interior Columbia Basin Technical Recovery Team 2003), and requiring representation of all subunits and redundancy within the subunits (which we call the “representation and redundancy” rule). The ESU subunits are intended to capture important components of habitat, life history or genetic diversity that contribute to the viability of salmonid ESUs (Hilborn et al. 2003; Bottom et al. 2005). If extinction risks are not strongly correlated between populations, two populations, each with low risk of extinction, would be extremely unlikely to go extinct simultaneously (McElhany et al. 2003). Should one go extinct, the other could serve as a source of colonists to re-establish the extirpated population. Therefore, at

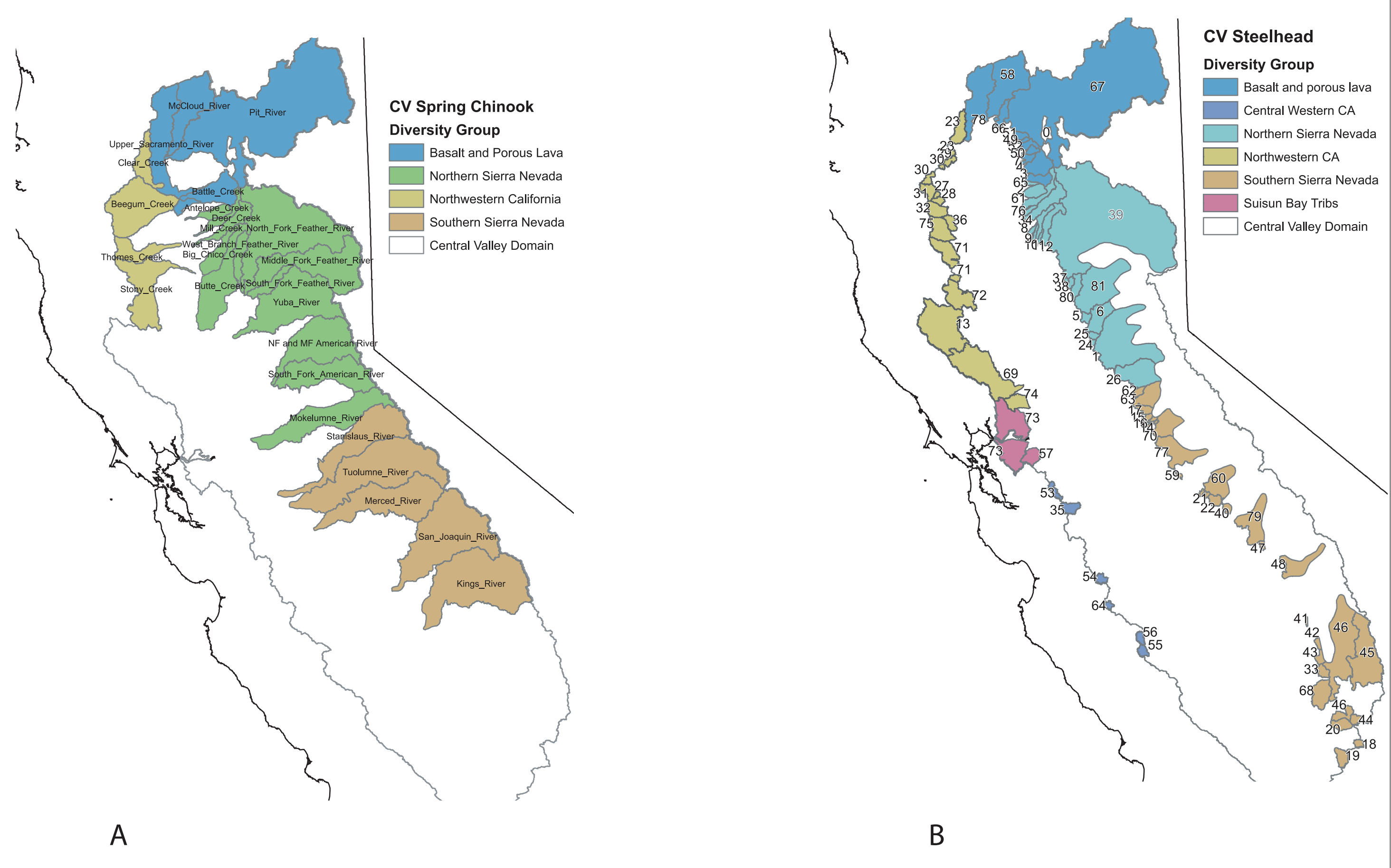

Figure 2. Salmonid ecoregions within the Central Valley. Map A: Central Valley spring-run Chinook salmon. Map B: Central Valley steelhead. Sacramento River Winter-run Chinook salmon not shown because this ESU has only one region (Basalt and porous lava). The numbers identifying steelhead populations correspond to Table 1 in Lindley et al. (2006).

least two viable populations within each ESU subunit are required to ensure viability of the subunit, and hence the ESU. In the cases of large subunits, more than two viable populations may be required to maintain connectivity among populations.

As discussed in Lindley et al. (2004), drainages in the Central Valley basin are characterized by a wide variety of climatological, hydrological, and geological conditions. To a first approximation, floristic ecoregions, such as the Jepson ecoregions defined by Hickman (1993), provide an integrative view of these differences. We use the Jepson ecoregions as a starting point for salmonid ecoregions, but modify them to account for the effect of springs, which are very influential on salmonids, but less influential to upland plants (Figure 2). Instead of the Cascade Ranges region, we define a "basalt and porous lava" region that comprises the streams that historically supported winter-run Chinook salmon. All of these streams receive large inflows of cold water from springs through the summer, upon which winter-run Chinook salmon depended. This region excludes streams south of Battle Creek, but would include the part of the Upper Sacramento drainage used by winter-run, and part of the Modoc Plateau region. The southern part of the Cascades region (i.e., the drainages of Mill, Deer, and Butte creeks) is added to the Sierra Nevada region, but the Sierra Nevada region is divided into northern and southern parts (split somewhat arbitrarily south of the Mokelumne River). This split reflects the greater importance of snowmelt runoff in the southern part, and distinguishes tributaries to the Sacramento and

San Joaquin rivers. The Central Valley steelhead ESU has two additional salmonid ecoregions: the Suisun Bay region which consists of tributaries to or near Suisun Bay, where summer temperatures are moderated by the marine influence of nearby San Francisco Bay and the Pacific Ocean, and the Central Western California ecoregion, which contains west-side San Joaquin Valley tributaries.

Viability by Assessment of Specific Threats

An alternative to the representation and redundancy rule is to assess the relationship between ESU structure and specific sources of catastrophic risk. For example, one can assess whether a spill of toxic material at a certain point could extirpate all populations of an ESU. The advantage of this approach is that it is explicit: benefits or shortcomings of a particular ESU structure can be seen. The disadvantage is that we are unlikely to foresee all possible catastrophes, and more generally, this approach does not fully consider the value that biocomplexity has for ESUs. With this caution in mind, we assess the present structure of ESUs in relation to volcanic eruptions, wildfire, and drought[1].

Volcanos may seem like an unlikely threat, but the Mt. St. Helens eruptions of 1980 extirpated salmon in the Toutle River (Jones and Salo, 1986). The Cascades Range, of which Mt. St. Helens is a member, forms the northeastern boundary of the Sacramento River basin and is volcanically active. To assess the risk from volcanic eruptions, we obtained data on impact for lava flow, volcanic blast, pyroclastic flows, and debris-lahar flows from Hoblitt et al. (1987). For each volcano and impact type, we computed the percentage of habitat that would be impacted for each population.

While probably less devastating than a major volcanic eruption, fires can cause large injections of fine particles into streams, and fires have been implicated in the extinction of trout populations (e.g., Rinne 1996; Brown et al. 2001). In addition, fire-fighting chemicals are toxic to juvenile salmon (Buhl and Hamilton 1998). Assessing whether two populations might be vulnerable to a single large fire is in part a question of how frequently fires of such size arise. Moritz (1997) provides a way of estimating the relationship between fire size and return frequency from fire size data. We acquired data on fire sizes within the Central Valley domain from the California Department of Forestry, and created a time series of the largest fire in each year for the period 1908–2003. We then found the maximum diameter of the polygon describing each fire. The probability of the largest fire in a year having a maximum diameter less than than some specific size x, P(Xmax ≤ x), was estimated empirically following Moritz (1997).

Prolonged droughts have been implicated in the extinction of riverine fish species in the southwestern US (Douglas et al. 2003; Matthews and Marsh-Matthews, 2003), and a short drought had severe impacts on Sacramento River winter-run Chinook salmon broods in 1976 and 1977 (National Marine Fisheries Service, 1997). We estimated the correlation scale for drought by computing the correlation among the Palmer drought severity index scores among the grid points within CA presented by Cook et al. (2004) using a spline correlogram, which estimates a non-parametric covariance function (Bjornstad et al. 1999). Of particular interest is whether this characteristic scale is larger or smaller than the scale of ESUs—if it is larger, then drought risk can not be mitigated by maintaining widely-separated populations (although it would reduce the risk of simultaneous drought).

APPLICATION TO CENTRAL VALLEY SALMONIDS

Central Valley Spring-run Chinook Salmon

Perhaps 15 of the 18 or 19 historical populations of Central Valley spring-run Chinook salmon are extinct, with their entire historical spawning habitats behind various impassable dams (Figure 3 and Table 3). Butte Creek and Deer Creek spring-run Chinook salmon are at low risk of extinction, satisfying both the PVA (Figure 4) and other viability criteria (Table 3). Mill Creek is at moderate extinction risk according to the PVA, but appear to satisfy the other viability criteria for low-risk status. Lindley et al. (2004) were uncertain whether Mill and Deer creek populations were each independent or two parts of a single larger population. If viewed as a single population, Mill and Deer Creek spring-run Chinook salmon are at low extinction risk. Early-returning Chinook salmon persist within the

Feather River Hatchery population and spawn in the Feather River below Oroville Dam and the Yuba River below Englebright Dam. The current status of these fish is impossible to assess due to insufficient data.

With demonstrably viable populations in only one of at least three diversity groups that historically con-

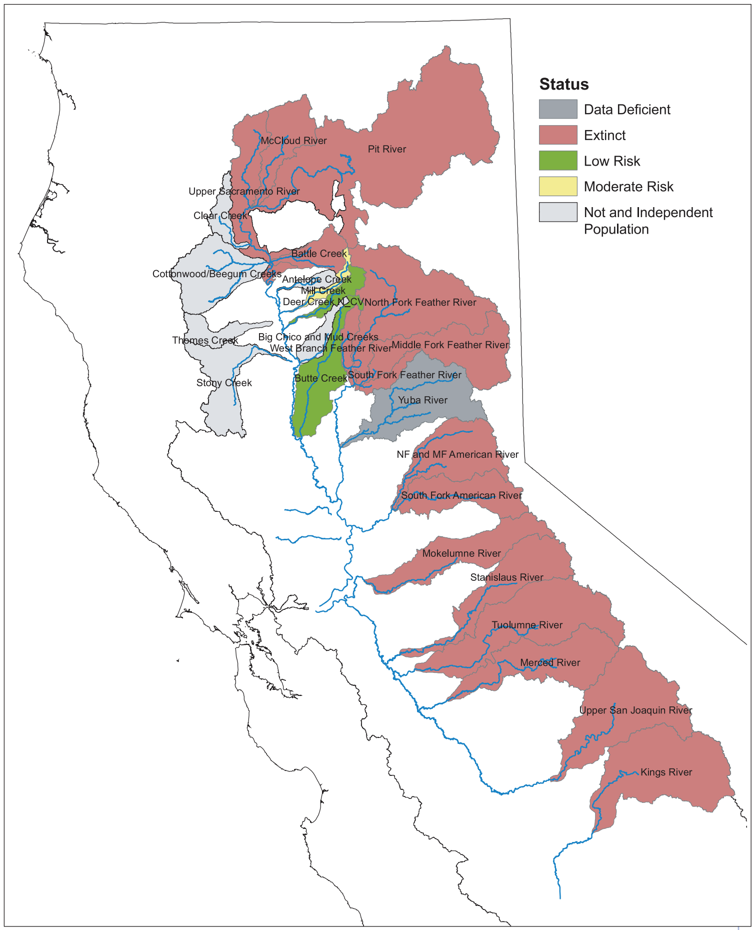

Figure 3. Status of historical Central Valley spring-run Chinook salmon populations.

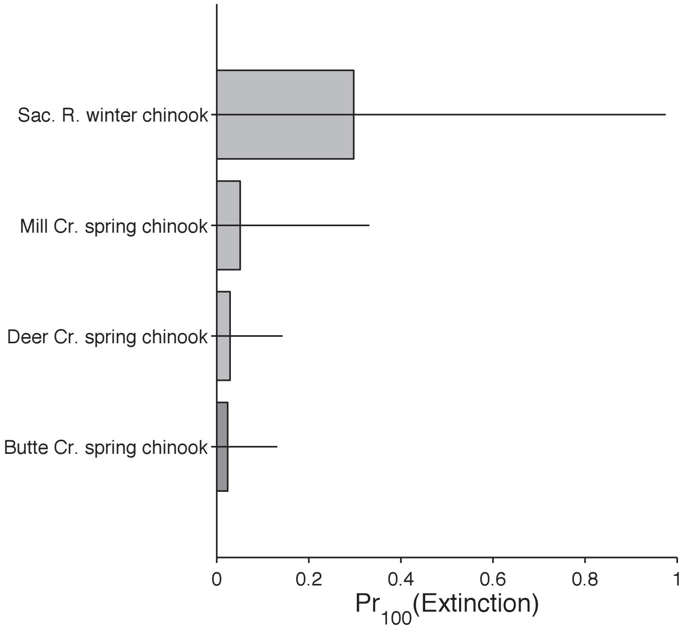

Figure 4. Probability of population extinction as estimated by the random-walk-with-drift model. Bars indicate the expected probability of extinction; lines indicate the 90% central interval for the estimate of the mean.

Table 3. Viability of populations. Steelhead populations that are not listed are data deficient. Chinook populations that are not listed are presumed extinct, due to impassable dams blocking access to spawning habitat. WRC = winter-run Chinook salmon; SRC = spring-run Chinook salmon. Catastrophes not included in this table because none were observed in the last decade. See Table 2 for definition of metrics. Spawning escapement data was obtained from California Department of Fish and Game's 2005 GrandTab database, available from the Native Anadromous Fish & Watershed Branch, 830 S Street, Sacramento, CA 95814. Steelhead data for American River from McCracken et al. (2005).

ESU	Population Name	PVA result	N	std	Pop. growth (% per year)	std	$\hat{S}$	std	h	Risk Category
Sac. R. WRC	mainstem	Moderate	26,870	2280	27.7	6.3	8140	691	Low	Low
C. V. SRC	Butte Cr	Low	22,630	7400	11.4	12.6	6860	2240	Very Low	Low
C. V. SRC	Mill Cr	Moderate	3360	1300	17.9	5.95	1020	394	Very Low	Low
C. V. SRC	Deer Cr	Low	6320	1920	7.63	7.58	1920	1010	Very Low	Low
C. V. SRC	Yuba									Data Deficient
C. V. SRC	Feather									Data Deficient
C. V. Steelhead	Feather								High	High
C. V. Steelhead	Battle Cr								High	High
C. V. Steelhead	American						< 500		High	High
C. V. Steelhead	Mokelumne								High	High

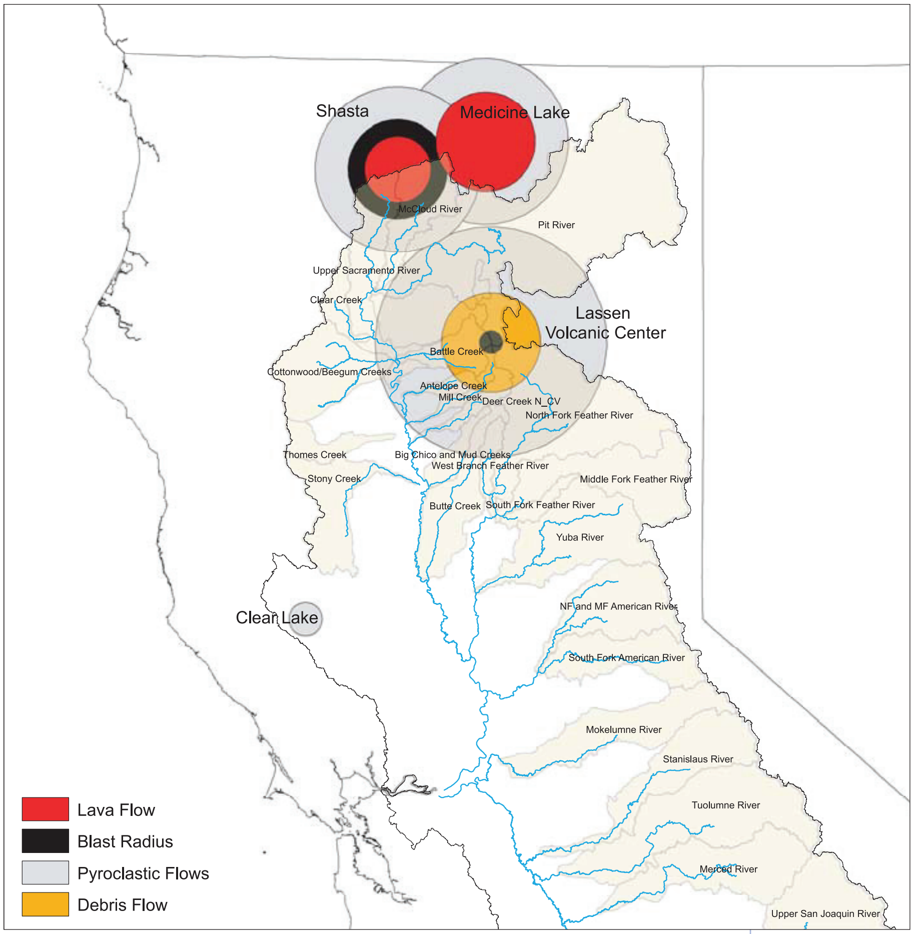

Figure 5. Volcanic hazards affecting the Central Valley recovery domain. Circles indicate the possible spatial extent of various kinds of volcanic effects that could devastate salmonid stream habitat, including lava flow, blast, pyroclastic flow, and debris. Data from Hobblitt et al. (1987)

tained them, Central Valley spring-run Chinook salmon fail the representation and redundancy rule for ESU viability. Historically, the Central Valley spring-run Chinook salmon ESU spanned four ecoregions: the region used by winter-run Chinook salmon plus the northern and southern Sierra Nevada and the northwestern California region. There are two or three viable populations in the northern Sierra Nevada (Mill, Deer and Butte creeks), although these populations were once probably relatively small compared to populations such as the Feather River. A few ephemeral or dependent populations are found in the Northwestern California region (e.g., Beegum and perhaps Clear creeks). Spring-run Chinook salmon have been entirely extirpated from both the basalt and porous lava region and the southern Sierra Nevada region.

The current distribution of viable populations makes the Central Valley spring-run Chinook salmon ESU vulnerable to catastrophic disturbance. All three extant independent populations are in basins whose headwaters lie within the debris and pyroclastic flow radii of Mt. Lassen (Figure 5), an active volcano that the USGS views as highly dangerous[2] (Hoblitt et al. 1987). The historical ESU was of such a large scale that neither Mt. Lassen, Mt. Shasta, or Medicine Lake could have extirpated even an entire diversity group, let alone the entire ESU. The current ESU structure is, not surprisingly, vulnerable to drought, which has a correlation scale of approximately 640 km (Figure 6), on order of the length of the historical ESU. Even wildfires, which are of much smaller scale than droughts or large volcanic eruptions, pose a significant threat to the ESU in its current configuration. A fire with a maximum diameter of 30 km, big enough to burn the headwaters of Mill, Deer and Butte creeks simultaneously, has roughly a 10% chance of occurring somewhere in the Central Valley each year (Figure 7).

We note that the historical Central Valley spring-run Chinook salmon ESU was widespread enough to be invulnerable to all of these catastrophes, except perhaps prolonged drought. The correlation scale of drought is roughly 640 km, and the Central Valley spring-run Chinook salmon ESU is about 500 km from the Pit River to the Kings River. It is possible that Central Valley spring-run Chinook salmon were less vulnerable to drought than might be expected because they once occupied diverse types of watersheds, including those with very high influence from springs. In fact, annual mean stream flow in Southern Cascade streams is less well correlated with annual mean precipitation than in other regions (see Appendix A in Lindley et al. (2006)).

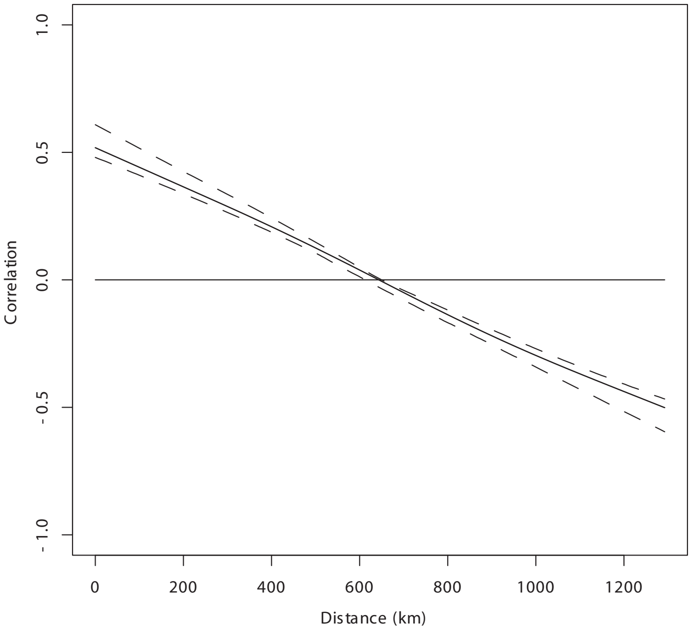

Figure 6. Spline correlogram fit to the gridded Palmer drought severity index data for California of Cook et al. (2004). Solid line indicates the estimated correlation function; dashed lines are the 95% confidence interval. Note that the correlation of drought indices declines with distance between locations, with no correlation evident at a distance 640 km.

Sacramento River Winter-run Chinook Salmon

All four historical populations of Sacramento River winter-run Chinook salmon are extinct in their historical spawning range (Table 3). The upper Sacramento, McCloud and Pit River populations had spawning and rearing habitat far upstream of impassable Keswick and Shasta dams, although these populations were apparently in poor condition even before the construction of Shasta dam in the 1940s (Moffett 1949). Winter-run Chinook salmon no longer inhabit Battle Creek as a self-sustaining population, probably because hydropower operations make conditions for eggs and fry unsuitable (National Marine Fisheries Service 1997). Also, until recently access to much of the basin was blocked by the Coleman National Fish Hatchery barrier weir.

The population of Sacramento River winter-run Chinook salmon that now spawns below Keswick dam is at moderate extinction risk according to the PVA (Figure 4), and at low risk according to the other criteria. Since roughly the mid-1990s, this population has been growing, although its previous precipitous decline to a few hundred spawners per year would have qualified it as high risk at that time, and prior to that, the 1976-77 drought would have qualified as a high-risk catastrophe. At present, the population easily satisfies the low-risk criteria for population size, population decline, and catastrophe, but hatchery influence is a looming concern. Since 2001, hatchery-origin winter-run Chinook salmon from Livingston Stone National Fish Hatchery (LSNFH, perhaps one of the best examples of a “best-management practices” Chinook salmon hatchery) have made up more than 5% of the natural spawning run, and in 2005 it exceeded >18% (K. Niemela, USFWS, Red Bluff CA, unpublished data). If the contribution of LSNFH to natural spawning exceeds 15% in 2006-07, the winter-run Chinook salmon population would be reclassified as moderate risk, and even the lower observed rates will become problematic if they continue for the next decade.

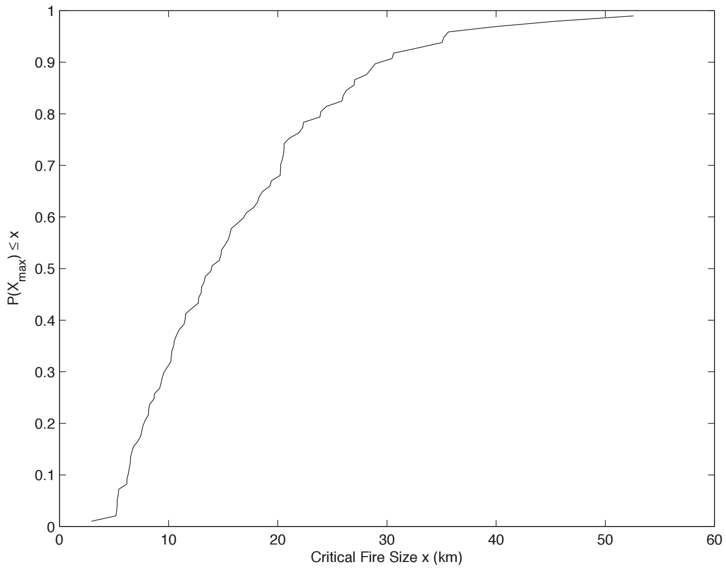

Figure 7. The probability that the largest fire in a year (Xmax) will be smaller than the critical size x. Based on observed fire sizes for the Central Valley recovery domain during the 1908–2003 period.

The Sacramento River winter-run Chinook salmon ESU does not currently satisfy the representation and redundancy rule because it has only one population, and that population spawns outside of the ecoregion where it evolved. For the Sacramento River winter-run Chinook salmon ESU to satisfy the representation and redundancy rule, at least two populations would need to be re-established in the basalt-and-porous-lava region. This may require passage past Shasta and Keswick dams.

Obviously, an ESU represented by a single population at moderate risk of extinction is at high risk of extinction over the long run. A single catastrophe could extirpate the entire Sacramento River winter-run Chinook salmon ESU, if its effects persisted for four or more years. The entire stretch of the Sacramento River used by winter-run Chinook salmon is within the zone of influence of Mt. Lassen. Some other possible catastrophes include a prolonged drought that depletes the cold water storage of Lake Shasta or some related failure to manage cold water storage, a spill of toxic materials with effects that persist for four years, or a disease outbreak.

Central Valley Steelhead

There are almost no data with which to assess the status of any of the 81 Central Valley steelhead populations described by Lindley et al. (2006). With few exceptions, therefore, Central Valley steelhead populations are classified as data deficient. The exceptions are restricted to streams with long-running hatchery programs: Battle Creek and the Feather, American and Mokelumne rivers. In all cases, hatchery-origin fish likely comprise the majority of the natural spawning run, placing the natural populations at high risk of extinction. In the American River, the natural spawning run appears to be comprised mostly of hatchery-origin spawners (McCracken et al. 2005). The broodstock used by Feather River Hatchery is derived from native fish from the Feather River, but hatchery-origin fish probably play a large role in maintaining the Feather River population (Kindopp et al. 2003). The Coleman National Fish Hatchery steelhead program uses many "best management practices," but hatchery fish make up substantially more than 15% of the natural spawners in Battle Creek (Campton et al. 2004).

There is no evidence to suggest that the Central Valley steelhead ESU is at low risk of extinction, or that there are viable populations of steelhead anywhere in the ESU. Conversely, there is evidence to suggest that the Central Valley steelhead ESU is at moderate or high risk of extinction (McEwan 2001; Good et al. 2005). Clearly, most of the historical habitat once available to steelhead has been lost (Yoshiyama et al. 1996; McEwan 2001; Lindley et al. 2006). Furthermore, the observation that anadromous *O. mykiss* are becoming rare in areas where they were probably once abundant (California Department of Fish and Game, unpublished data; McEwan (2001)) indicates that an important component of life history diversity is being suppressed or lost. It should be noted, however, that habitat fragmentation, degradation, and loss are likely having a strong negative impact on many resident as well as anadromous *O. mykiss* populations (Hopelain 2003).

Discussion

Population Viability

In this section, we applied viability criteria, and PVA where possible, to assess the status of Sacramento River winter-run Chinook salmon, Central Valley spring-run Chinook salmon, and Central Valley steelhead populations identified by Lindley et al. (2004) and Lindley et al. (2006). For Central Valley steelhead, we were only able to assess the status of populations with a strong hatchery influence, even though the criteria-based approach that we employed has low data requirements compared to some PVA approaches. For extant, independent Chinook salmon populations, we were able to apply a PVA model as well as the simpler criteria (because relatively long time series of spawning run size are available for these populations). In two cases, the PVA gave the same result (Butte Creek and Deer Creek both classified as low risk), and in the other two cases, risk assignments differed by one category (winter-run Chinook salmon and Mill Creek spring-run Chinook salmon classified by the PVA as moderate risk, while the criteria indicate low risk). That populations can satisfy the criteria for low risk while just failing a PVA suggests that the criteria for low risk really are criteria for minimal viability. Recovery planners may want to aim somewhat higher for at least some populations as a precautionary measure.

There have been three population-level risk assessments for winter-run Chinook salmon, by Botsford and Brittnacher (1998), Lindley and Mohr (2003), and Good et al. (2005). The analysis of Botsford and Brittnacher (1998) was conducted at a time when it was much less clear that winter-run Chinook salmon were on an upward trend, and not surprisingly, Botsford and Brittnacher (1998) found that winter-run Chinook salmon were certain to go extinct if the trends seen up to the time of their analysis were to continue. Lindley and Mohr (2003) used a model that allowed for a change in population growth rate following initiation of conservation measures in 1989 and density-dependent reproduction. Allowing for the possibility that winter-run Chinook salmon population growth rate increased after 1989 led to a much more optimistic prediction for extinction risk of 24% in 100 years. The analysis in Good et al. (2005), like Lindley and Mohr (2003), allowed for a change in population growth in 1989, but included more recent data and ignored density dependence. Good et al. (2005) found that if the 1989-present growth rate holds into the future, the winter-run Chinook salmon population has essentially no risk of extinction. The varying conclusions of these studies illustrates the sensitivity of PVA results to both data and model assumptions, especially those about future conditions and the effect of density on population growth rate.

ESU Viability

Our assessment of the viability of Central Valley Chinook salmon ESUs is broadly consistent with other recent assessments. Good et al. (2005), based on the combined opinion of an expert panel, considered the Sacramento River winter-run Chinook salmon ESU to be in danger of extinction, and the Central Valley spring-run Chinook salmon ESU to be likely to become endangered in the foreseeable future. These findings were essentially unchanged from the earlier review of Myers et al. (1998). United States Fish and Wildlife Service (1994) suggested that Central Valley spring-run Chinook salmon could be considered “restored” when Mill and Deer creeks both have >500 spawners, and the average total number of spawners in Sacramento tributaries exceeds 8,000, with a minimum of 5,000 spawners, over a 15 year period that includes at least three critically dry years. Central Valley spring-run Chinook salmon have achieved these abundance levels since about 1998, but are not yet “restored” as defined by United States Fish and Wildlife Service (1994). The restoration goals of United States Fish and Wildlife Service (1994) are based on estimates of what could be attained in Sacramento River tributaries that are still accessible to spring-run Chinook salmon, and do not address issues of viability.

National Marine Fisheries Service (1997) proposed that for Sacramento River winter-run Chinook salmon to be recovered, there would need to be on average 10,000 females spawning naturally in the mainstem Sacramento River, and recommended creation of a second winter-run Chinook salmon population in Battle Creek. Should Sacramento River winter-run Chinook salmon achieve these draft goals, their status would be much improved, but they would still be excluded from much of the apparently unique areas in the upper Sacramento, McCloud, and Pit River tributaries that gave rise to their unique life-history strategy.

Good et al. (2005) found Central Valley steelhead to be in danger of extinction in the foreseeable future, in agreement with an earlier assessment (Busby et al. 1996). We were unable to assess the status of the Central Valley steelhead ESU with the more quantitative approach developed in this paper, because of data limitations. This should not be viewed as a contradictory finding—what little information is available for Central Valley steelhead is not positive (Busby et al. 1996; McEwan, 2001; Good et al. 2005).

Even if there were adequate data on the distribution and abundance of steelhead in the Central Valley, our approaches for assessing population and ESU viability might be problematical because the effect of resident *O. mykiss* on the viability of populations and ESUs is unknown. From one perspective, resident fish may reduce the extinction risk of the ESU through the production of anadromous individuals that can bolster or rescue weak steelhead populations. Such life history diversity also confers risk spreading, in that members of the ESU are spread among habitats that are subject to independent sources of disturbance. For instance, fish in the ocean are unaffected by flooding, while fish in rivers are immune to poor feeding conditions in the ocean. At the margins of a species' range, where conditions may be more frequently unfavorable, such life history diversity could be an adaptation to the unpredictable environment (Jonsson and Jonsson 1993.)

On the other hand, the apparent dominance of the resident form is a recent and unnatural phenomenon. It is likely that the apparent shift towards the resident life history strategy is partly a response to hypolimnetic releases from reservoirs, which alter trophic, temperature and flow conditions for some distance below the dam (McEwan, 2001). *O. mykiss* may take up residency in these altered areas due to their phenotypic plasticity, or the fitness of *O. mykiss* using these areas may exceed the fitness of anadromous fish, which would drive an evolutionary (i.e., genetic) change if life history strategy is heritable. Another component of the shift is likely the decline of steelhead due to loss of suitable steelhead habitat. Even if the shift in life history strategy is a plastic response, the fitness of steelhead may decline due to relaxed selection pressure. At longer time scales, this is likely to be a problem, because storage reservoirs have finite lifetimes, and when they are filled with sediments, the rivers downstream will be much less suitable for year-round residency.

Both the United States Fish and Wildlife Service (1994) goals for Central Valley spring-run Chinook salmon and the National Marine Fisheries Service (1997) goals for Sacramento River winter-run Chinook salmon are primarily focused on abundance and productivity, a traditional fisheries and natural resource perspective. In light of the mounting failures of that traditional perspective, ecologists are increasingly recognizing the importance of diversity in sustaining ecological processes (e.g., Daily 1999; Pauly et al. 2002; Elmqvist et al. 2003; Fischer et al. 2006). Recent thinking on salmonids (e.g., McElhany et al. 2000; Hilborn et al. 2003; Bottom et al. 2005) highlights the importance of habitat, life history, and genetic diversity as the foundation for productivity (and hence abundance). Our approach to assessing and specifying ESU viability broaden the focus from abundance and trends to include the numbers, diversity, and spatial distribution of populations across the landscape. Restoring and sustaining diverse populations of salmonids will require restoring and sustaining the habitats and ecological processes upon which they depend.

Summary

In this paper, we have developed a framework for evaluating the viability of salmonid populations and ESUs, based on simple criteria and rules that have modest data requirements. When applied to Chinook salmon ESUs, the framework makes clear that the risk facing these ESUs is not so much the low viability of extant populations, but rather that much of the diversity historically present in these ESUs has been lost. While the criteria and rules that comprise our framework are based in no small part on expert judgment and are subject to considerable uncertainty, our conclusions are not particularly sensitive to the exact values of the criteria.

The utility of our framework can be judged in several ways. It provides quantitative criteria that allow that status of salmonid ESUs to be assessed in an objective way, and it points out areas where things need to improve for ESUs to be removed from the endangered species list. The framework is, however, rather simplistic, and significant improvements, especially at the ESU level, could be made as our understanding of salmonid population biology improves. Perhaps the most significant shortcoming of our framework is the implicit assumption that future will be like the past. In the next section, we evaluate this critical assumption.

CLIMATE VARIABILITY AND CHANGE

Introduction

Viability assessments, including ours, typically attempt to answer the question of whether the population will persist into the future if it continues to experience conditions like it has in the recent past. Future conditions, however, are not likely to be like the recent past. In this section, we briefly review descriptions of natural climate variability, and regional-scale predictions of how climate might change over the next century in response to rising atmospheric greenhouse gas concentrations. Natural climate variation will make it difficult to properly assess whether ESUs are recovering in response to management actions. Anthropogenic climate change may preclude some otherwise attractive recovery strategies, depending on future greenhouse gas emissions and the response of regional climate.

Natural Climate Variability

Fisheries scientists have shown that ocean climate varies strongly at decadal scales (e.g., Beamish 1993; Beamish and Bouillon 1993; Graham, 1994; Miller et al. 1994; Hare and Francis 1995; Mantua et al. 1997; Mueter et al. 2002). In particular, the identification of the Pacific Decadal Oscillation (Mantua et al. 1997) seems to have led to the belief that decadal-scale variation may be cyclical, and thus predictable. As pointed out by Rudnick and Davis (2003) and Hsieh et al. (2005), apparent regime shifts need not be cyclical or predictable, but rather may be the expression of a stochastic process with red noise. If this interpretation is correct, then we should expect future ocean climate conditions to be different than those we have observed in the past few decades.

Terrestrial climate, like ocean climate, appears more variable the longer that it is observed. For example, Ingram et al. (1996) showed that freshwater inputs to San Francisco Bay varied with a period of 200 years, and several extreme and prolonged wet and dry periods occurred over the last 2,000 years. A 7,000-year river-flow reconstruction by Goman and Wells (2000) for the same area shows even longer-lasting periods of extreme conditions. Analysis of tree-ring data show that prolonged and intense droughts were more common during the period 750-1100 before present than in more recent centuries (Cook et al. 2004).

Natural climate variability poses several potential challenges for recovery planners. First, the population viability criteria that we have proposed may not offer sufficient protection in the case of a prolonged period of unfavorable climatic conditions. Second, a prolonged period of unusually favorable climatic conditions could cause populations to grow enough that they satisfy our biological viability criteria even though serious problems with habitat quality remain. In other words, the ESU may temporarily appear to be recovered, but its status would decline as soon as conditions become more typical. Conversely, the effects of substantial improvements to habitat quality could be masked by poor climatic conditions, possibly eroding society's enthusiasm for doing the hard work of salmon recovery. The key to overcoming these challenges is to consider climate variation in future assessments, hopefully with the benefit of improved understanding of the links between specific populations and regional climate conditions. Research is needed in this area.

Presumably, Central Valley salmonid ESUs are capable of surviving the kinds of climate extremes observed over the past few thousand years if they have functional habitats, because these lineages are on order of a thousand years old or older[3]. There is rising concern, however, that the future climate will be unlike that seen since perhaps the Pliocene, due to global warming in response to anthropogenic greenhouse gas emissions.

Climate Warming

The consensus of climate scientists is that the Earth's climate is warming, and that the warming is caused in part by the accumulation of greenhouse gases in the atmosphere (McCarthy et al. 2001; Oreskes, 2004). While there is a scientific consensus about global climate change, the effects of global warming at regional scales are generally less certain. Here, we briefly review available regional-scale forecasts relevant to the Central Valley domain, and then speculate on possible impacts on Central Valley salmonids.

Climate forecasts for the Central Valley

Making regional-scale climate forecasts involves choosing an "emissions pathway" and running one of a number of global climate models with an embedded regional-scale model that can capture features, such as mountain ranges, that can significantly modify the global pattern. As in any modeling exercise, there are a number of sources of uncertainty, but particularly important ones in this case are the assumption about future emissions and the choice of climate model. The uncertainties are addressed by examining a number of emissions pathways and by using several models.

The recent paper by Hayhoe et al. (2004) examines multiple emissions pathways using two global models to make regional forecasts for California. Their results are alarming. The more sensitive Hadley Center Climate Model (HadCM3) predicts that under the high emissions scenario (where CO_2 rises to 970 ppm by 2100, also known as the "business as usual" scenario), average summer temperature would rise 8.3°C and snowpack would be reduced by 89%. The HadCM3 also predicts that the climate will get drier, with possibly a 43% reduction of inflows to southern Sierra reservoirs. At the other extreme, the low-sensitivity Parallel Climate Model (PCM) predicts that average summer temperature would rise slightly more than 2°C if emissions were curtailed such that CO_2 rises to 550 ppm by 2100. The PCM predicts that total precipitation could rise slightly, but snowpack would still be reduced by 28% in this scenario.

Dettinger (2005) analyzed six different climate models under three emissions scenarios to produce distributions of future temperature and precipitation. This analysis showed that uncertainty due to the models was about equal to that due to emission scenario. There was general agreement among the models that temperatures will rise significantly (between 2 and 7 °C by 2100), while total precipitation is expected to decline slightly. Temperature and precipitation predictions were negatively correlated (i.e., warming is associated with drying).

Dettinger et al. (2004) and VanRheenen et al. (2004) used the PCM to investigate in detail how climate change may influence the hydrology of Central Valley rivers. These analyses find that average precipitation will decline over time, while the variation in precipitation is expected to increase substantially. Extreme discharge events are predicted to become more common, as are critically dry water years. Peak monthly mean flows will generally occur earlier in the season due to a decline in the proportion of precipitation falling as snow, and earlier melting of the (reduced) snowpack. By the end of the century, it may be difficult to achieve current operations targets for fish conservation even with substantial decreases in other demands for water. Knowles and Cayan (2002) show that in summer, saline water will intrude farther into the Bay and Delta than it does now. Within some limits, water storage reservoirs might be operated to mitigate changes to the hydrograph caused by climate change, although water project operations are likely to become even more contentious as temperature rises, snowmelt falls, and population rises.

Possible Effects on Salmon and Steelhead

Regional-scale climate models for California are in broad agreement that temperatures in the future will warm significantly, total precipitation may decline, and snowfall will decline significantly. What are the likely consequences for salmon and steelhead in the Central Valley? Melack et al. (1997) states that predicting the response of salmon to climate warming "requires examination of the responses of all life history stages to the cumulative effects of likely environmental changes in the lakes, rivers and oceans inhabited by the fish." Such an endeavor is beyond the scope of this paper, and the question of climate change effects on Pacific salmonids has received surprisingly little attention to date. In this subsection, we briefly review the literature and conduct a simple assessment of the effects of warmer summer temperature on the availability of freshwater habitat.

Focusing on freshwater life history phases, Neitzel (1991) reviewed the likely responses of salmonids in the Columbia River basin to climate warming, which he anticipated would affect salmonids through alterations to the timing of discharge and changes in sedimentation rate, temperature, and flow. Effects are predicted to depend on the river and on the species or run. As in the case of many salmonid populations in the Columbia River basin, spring-run Chinook salmon are likely to be negatively impacted by the shift in peak discharge (needed for smolt migration), and juvenile steelhead are likely to be negatively impacted by reduced summer flows. All Central Valley salmonids are likely to be negatively affected by warmer temperatures, especially those that are in freshwater during the summer.

Recent summer mortality of adult spring-run Chinook salmon in Butte Creek offers a case in point. Mean July water temperature in the middle of the spawning reach of Butte Creek is often around 18-20°C in July. In 2002 and 2003, mean water temperature in Butte Creek exceeded 21°C for 10 or more days in July, and 20-30% of adults in 2002 and 65% of adults in 2003 died (reviewed by Williams 2006), primarily from columnaris.

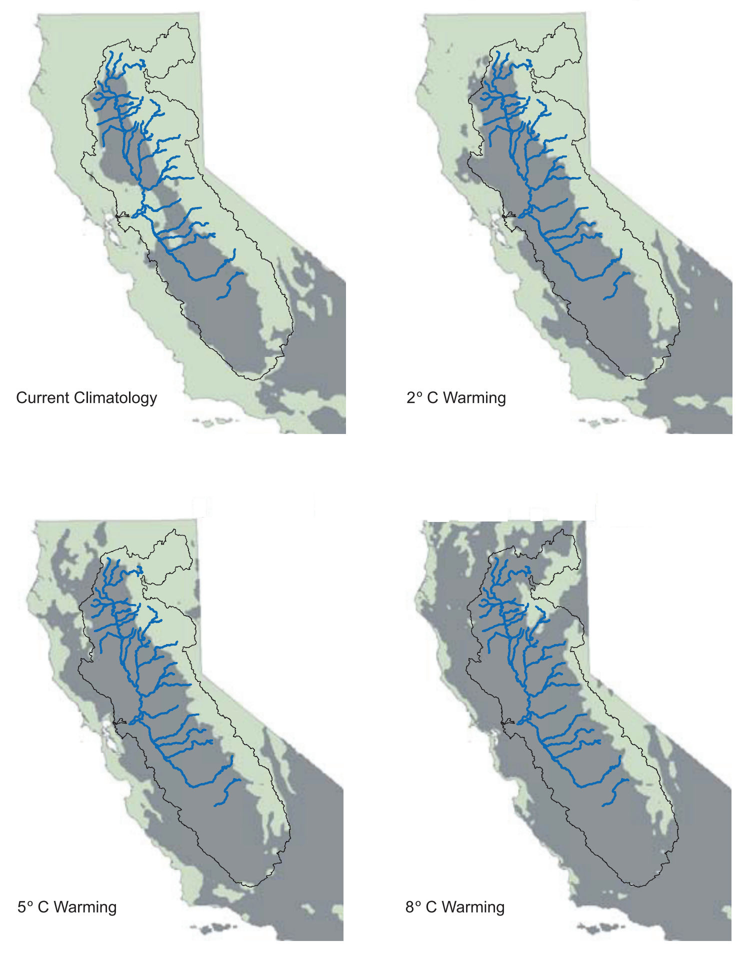

Figure 8. Effects of climate warming on availability of over-summer habitat. Mean August air temperatures exceeding 25°C are shown in gray; blue lines indicate the historical distribution of spring-run Chinook salmon.

Less obvious effects, such as reduced viability of gametes, may also have occurred. These data suggest that existing conditions in Butte Creek are close to the thermal tolerance limit for Chinook salmon.

Myrick and Cech (2004) state that juvenile Chinook salmon are unlikely to be capable of rearing for extended periods in temperatures exceeding 24°C, and juvenile steelhead may be able to withstand slightly higher temperatures. Maximum in-stream temperatures of many streams frequently exceed 24°C at lower elevations, which may determine the lower distributional limit of salmonids (Yoshiyama et al. 1996; Lindley et al. 2006). Distributions at higher elevations were once largely restricted by natural barriers to movement, but are now limited by dams in many streams (Lindley et al. 2006). If these artificial migration barriers are not removed, climate warming is expected to reduce the amount of habitat available to Central Valley salmonids that reside in freshwater during summer months, as the lower distributional limit rises, and the upper limit remains constrained by physical barriers.

A rough view of the consequences for Central Valley spring-run Chinook salmon and Central Valley steelhead can be obtained by adding the regional warming forecasts of Dettinger (2005) to PRISM temperature fields, and overlaying this with the distributional data presented in Lindley et al. (2004). Figure 8 shows how the area with high summer temperatures (mean August air temperature > 25°C) may expand under three warming scenarios. Under current conditions, streams that had major independent populations of spring-run Chinook salmon all have significant amounts of habitat above the 25°C isotherm, although dependent populations generally had little or no habitat above the 25°C isotherm (Figure 8, upper left). By 2100, mean summer air temperatures are expected to rise by at least 2°C. Under this scenario, the amount of habitat above the 25°C isotherm is reduced, but in general, most streams that historically contained habitat above this isotherm would not lose all such habitat. The exceptions are the Tuolumne, Merced, and upper San Joaquin rivers, and Butte Creek, where the 25°C isotherm might just rise to the upper limit of the historical distribution of spring-run Chinook salmon (Figure 8, upper right). Under the expected warming of around 5°C, substantial habitat would be lost, with significant amounts of habitat remaining primarily in the Feather and Yuba rivers, and remnants of habitat in the upper Sacramento, McCloud, and Pit rivers, Battle and Mill creeks, and the Stanislaus River (Figure 8, lower left). Under the less likely but still possible scenario of an 8°C warming, spring-run Chinook salmon habitat would be found only in the upper-most reaches of the north fork Feather River, Battle Creek, and Mill Creek. This simple analysis suggests that Central

Valley salmonids are vulnerable to warming, but more research is needed to evaluate the details of how warming would influence individual populations and subbasins.

The hydrologic effects of climate change are harder to evaluate. Increased frequency of scouring floods might be expected to reduce the productivity of populations, as egg scour becomes a more common occurrence. The timing of various life history events is presumably an adaption to past climate conditions (temperature and discharge timing), and populations may not be well-adapted to future hydrographs. One concern is that warmer summers will delay spawning, and earlier and more frequent floods will impact eggs and alevins before they emerge from the gravel, a phenomenon thought to limit the productivity of some Chinook salmon stocks (Beer and Anderson 2001), and one that might be impossible for salmonids to adapt to, given fundamental constraints on development.

The flip side of frequent flooding is the possibility of more frequent and severe droughts. Long-term climate records show that warm periods have been associated with droughts in California (Davis 1999; Cook et al. 2004), and the regional climate change models reviewed above hint at the possibility of increasing frequency of droughts. In the Central Valley, low flows during juvenile rearing and outmigration are associated with poor survival (Kjelson and Brandes 1989; Baker and Morhardt 2001; Newman and Rice 2002) and poor returns in subsequent years (Speed 1993).

Climate change may also impact Central Valley salmonids through community effects. For example, warming may increase the activity and metabolic demand of predators, reducing the survival of juvenile salmonids (Vigg and Burley, 1991). Peterson and Kitchell (2001) showed that on the Columbia River, pikeminnow predation on juvenile salmon during the warmest year was 96% higher than during the coldest.

To summarize, climate change may pose new threats to Central Valley salmonids by reducing the quantity and quality of freshwater habitat. Under the worst-case scenario, spring-run Chinook salmon may be driven extinct by warming in this century, while the best-case scenario may allow them to persist in some streams. Uncertainties abound at all levels, however. First, the composition of Earth's atmosphere is partly under human control, and we cannot predict how it might be managed in the future. Even if the emissions pathway was known, different climate models offer significantly different climate forecasts (although we note that the differences are quantitative, and the models are in qualitative agreement). Finally, we have only the crudest understanding of how salmonid habitats will change and how salmonid populations will respond to those changes, given a certain climate scenario. This is another area where research is needed.

SUMMARY AND RECOMMENDATIONS

For Central Valley steelhead, there are insufficient data to assess the risk of any but a few populations, and therefore, we cannot assess the viability of this ESU using the quantitative approach described in this paper. However, qualitative information does suggest that the Central Valley steelhead ESU is at a moderate or high risk of extinction. Most of the historical habitat once available to steelhead is largely inaccessible and the observation that the anadromous forms of *O. mykiss* are becoming less abundant or rare in areas where they were probably once abundant indicates that an important component of life history diversity is being suppressed or lost. Even in populations that exhibit life-history polymorphism, steelhead are important to viability and long-term persistence and are critical to the conservation of the population (Travis et al. 2004; Bilby et al. 2005).

For the Chinook salmon ESUs, we found that extant populations are now at low or moderate risk of extinction, but the extensive extirpation of historical populations has placed these ESUs in jeopardy of extinction. The proximate problem afflicting these ESUs and the Central Valley steelhead ESU is that their historical spawning and rearing areas are largely inaccessible, due to the direct or indirect effects of dams.

Recovering even a few populations may therefore be a challenging and slow process, although we stress that there appear to be some opportunities that, if successful, would greatly increase the viability of all three ESUs. Some possibilities that are being considered include restoring flows and habitat in the San Joaquin River below Friant Dam and in Battle Creek, and restoring access to the Yuba River above Englebright Dam. All of these actions, in our view, have the potential to significantly improve the status of affected ESUs, but achieving recovery may require access to additional historically-utilized spawning areas that are currently blocked by dams.

As we pursue the more ambitious and long-term habitat restoration solutions, there are some easier but very important things that should be done as soon as possible. These include the following, in no particular order:

1. Secure all extant populations. All three ESUs are far short of being viable, and extant populations, even if not presently viable, may be needed for recovery. An important lesson to draw from Hilborn et al. (2003) is that tomorrow's most important populations might come from populations that are relatively unimpressive today. We recommend that every extant population be viewed as necessary for the recovery of the ESU. Wherever possible, the status of extant populations should be improved.

2. Begin collecting distribution and abundance data for *O. mykiss* in habitats accessible to anadromous fish. This is fundamental to designing effective recovery actions and eventual delisting. Of equal importance is assessing the relationship of resident and anadromous forms of *O. mykiss*. Any quantitative assessment of population or ESU viability could be inadequate unless we know the role resident fish play in population maintenance and persistence. It has been well-documented that Chinook salmon has been the major focus of anadromous fish monitoring, assessment, and research in the Central Valley (McEwan 2001) and there needs to be a more equitable partitioning of research funds and effort.

3. Minimize straying from hatcheries to natural spawning areas. Even low levels of straying from hatchery populations to wild ones works against the goal of maximizing diversity within ESUs and populations. Current mark and recovery regimes do not generally allow reliable estimation of contributions of hatchery fish to natural spawning, so we recommend that all hatchery fish be marked in some way. A number of actions could reduce straying from hatcheries to natural areas, including replacing off-site releases with volitional releases from the hatchery, allowing all fish that attempt to return to the hatchery to do so, and reducing the amount of fish released (see CDFG and NMFS 2001, for a review of hatchery issues).

4. Begin conducting critical research on fish passage, reintroductions, and climate change[4]. To recover Central Valley salmon and steelhead ESUs, some populations will need to be established in areas now blocked by dams or insufficient flows. Assuming that most of these dams will remain in place for the foreseeable future, it will be necessary to move fish around the dams. We are unaware of such projects involving dams of the scale typical in the Central Valley. Assuming that a feasible solution to that problem is found, it is necessary to reintroduce fish to the newly available habitat. Should this be allowed to occur naturally, or should a more active approach be taken? If so, which fish should be used as the donors? Finally, in a warmer future, some basins might cease to be suitable for salmon or steelhead. It would be a costly mistake to invest heavily in restoring habitat that will become too warm to support salmonids.

5. Accept the notion that listed salmonid ESUs are likely to be conservation-reliant (Scott et al. 2005). It seems highly unlikely that enough habitat can be restored in the foreseeable future such that Central Valley salmonid ESUs could be expected to persist without continued conservation management. Rather, it may be possible to restore enough habitat such that ESUs can persist with appropriate management, which should focus on maintaining ecological processes at the landscape level. NOAA regulators should begin considering how to implement conservation agreements among agencies and stakeholders that will be acceptable to all parties and ensure the persistence of populations and ESUs.

ACKNOWLEDGMENTS

Steven T. Lindley appreciates discussions with B. Spence, T. Williams, D. Boughton, E. Bjorkstedt, M. Mohr, D. Windham, T. Cooney, A. Low, and the Recovery Science Review Panel. D. Boughton, M.

Banks and an anonymous reviewer provided critical review of an earlier version of the manuscript. James J. Anderson, Bernard P. May, and John G. Williams were supported by the CALFED Science Program through Association of Bay Area Governments contract CALFED/DWR 4600001642.

ENDNOTES

[1] We also examined the potential of toxic spills, earthquakes, and landslides to extirpate ESUs, but concluded that these risk sources were generally not a threat to ESUs with more than one population.

[2] We note that any particular debris flow would cover only a portion of the circle depicted in Figure 5, and that a single flow might not necessarily devastate all three spring-run Chinook salmon streams.

[3] Using data in Lindley et al. (2004) and relationships in Waples et al. (2004), the Fst observed between Sacramento River winter-run Chinook salmon and fall-run Chinook salmon (based on neutral markers) could have arisen in around 780 years if these ESUs were completely isolated from one another.

[4] The CVTRT is preparing a comprehensive list of research recommendations.

REFERENCES

Allendorf FW, Bayles D, Bottom DL, Currens KP, Frissell CA, Hankin D, Lichatowich JA, Nehlsen W, Trotter PC, Williams TH. 1997. Prioritizing Pacific salmon stocks for conservation. Conservation Biology 11:140–152.

Ardren WR, Kapuscinski AR. 2003. Demographic and genetic estimates of effective population size (*Ne*) reveals genetic compensation in steelhead trout. Molecular Ecology 12:35–49.

Baker PF, Morhardt JE. 2001. Survival of chinook salmon smolts in the Sacramento-San Joaquin delta and Pacific Ocean. In: Brown RL, editor, Fish Bulletin 179, volume 2, pp. 163–182. Sacramento, CA: California Department of Fish and Game.

Beamish RJ. 1993. Climate and exceptional fish production off the west coast of North America. Canadian Journal of Fisheries and Aquatic Sciences. 50:2270–2291.

Beamish RJ, Bouillon DR. 1993. Pacific salmon production trends in relation to climate. Canadian Journal of Fisheries and Aquatic Sciences. 50:1002–1016.

Beer WN, Anderson JJ. 2001. Effects of spawning behavior and temperature profiles on salmon emergence: Interpretations of a growth model for Methow River chinook. Canadian Journal of Fisheries and Aquatic Sciences 58:943–949.

Beissinger SR, Westphal MI. 1998. On the use of demographic models of population viability analysis in endangered species management. Journal of Wildlife Management 62:821–841.

Bilby RE, Bisson PA, Coutant CC, Goodman D, Gramling RB, Hanna S, Loudenslager EJ, McDonald L, Philipp DP, Riddell B. 2003. Review of Salmon and Steelhead Supplementation. Independent Scientific Advisory Board. ISAB 2003-3. 851 SW 6th Avenue, Suite 1100, Portland, Oregon 97204.

Bilby RE, Bisson PA, Coutant CC, Goodman D, Hanna A, Huntly N, Loudenslager EJ, McDonald L, Philipp DP, Riddell B, Olsen J, Williams R. 2005. Viability of ESUs containing multiple types of populations. Independent Scientific Advisory Board. ISAB 2005-2. Portland, OR.

Bjornstad ON, Ims RA, Lambin X. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends in Ecology and Evolution 14:427–432.

Botsford LW, Brittnacher JG. 1998. Viability of Sacramento River winter-run chinook salmon. Conservation Biology 12:65–79.

Bottom DL, Simenstad CA, Burke J, Baptista AM, Jay DA, Jones KK, Casillas E, Schiewe MH. 2005. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. U.S. Dept. Commer. NOAA Tech. Memo. NMFS-NWFSC-68. Seattle, WA.

Brown DK, Echelle AA, Propst DL, Brooks JE, Fisher WL. 2001. Catastrophic wildfire and number of populations as factors influencing risk of extinction for Gila trout (*Oncorhynchus gilae*). Western North American Naturalist 61:139–148.

Buhl KJ, Hamilton SJ. 1998. Acute toxicity of fire-retardant and foam-suppressant chemicals to early life stages of chinook salmon (*Oncorhynchus tshawytscha*). Environmental Toxicology and Chemistry 17:1589–1599.

Busby PJ, Wainwright TC, Bryant GJ, Lierheimer LJ, Waples RS, Waknitz FW, Neely K, Lagomarsino IV. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon, and California. U. S. Dept. Commer. NOAA Tech. Memo. NMFS-NWFSC-27. Seattle WA.

Campton D, Ardren B, Hamelberg S, Niemela K, Null B. 2004. Supplementation of steelhead in Battle Creek, California: history, strategy, objectives, biological uncertainties, and a proposed genetic monitoring and evaluation plan. U.S. Fish and Wildlife Service, Abernathy Fish Technology Center. Longview, WA.

CDFG and NMFS. 2001. Final report on anadromous salmonid fish hatcheries in California. California Department of Fish and Game and National Marine Fisheries Service Southwest Region. NMFS Southwest Regional Office, Long Beach, CA.

Chilcote MW, Leider SA, Loch JJ. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. Transactions of the American Fisheries Society 115:726–735.

Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW. 2004. Long-term aridity changes in the western United States. Science 306:1015–1018.

Daily GC. 1999. Developing a scientific basis for managing Earth's life support systems. Conservation Ecology 3, Issue 2, Article 14. [online] URL: http://www.consecol.org/vol3/iss2/art14/.

Davis OK. 1999. Pollen analysis of Tulare Lake, California: Great Basin-like vegetation in Central California during the full-glacial and early Holocene. Review of Palaeobotany and Palynology 107:249–257.

Dennis B, Munholland PL, Scott JM. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs 61:115–143.

Dettinger MD. 2005. From climate-change spaghetti to climate-change distributions for 21st Century California. San Francisco Estuary and Watershed Science 3, Issue 1, Article 4.

Dettinger MD, Cayan DR, Meyer MK, Jeton AE. 2004. Simulated hydrologic responses to climate variations and change in the Merced, Carson, and American River basins, Sierra Nevada, California, 1900–2099. Climatic Change 62:283–317.

Douglas MR, Brunner PC, Douglas ME. 2003. Drought in an evolutionary context: molecular variability in Flannelmouth Sucker (*Catostomus latipinnis*) from the Colorado River Basin of western North America. Freshwater Biology 48:1254–1273.

Elmqvist T, Folke C, Nyström M, Peterson G, Bengston J, Walker B, Norberg J. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1:488–494.

Emlen JM. 1991. Heterosis and outbreeding depression: a multi-locus model and application to salmon production. Fisheries Research 12:187–212.

Fischer J, Lindenmayer DB, Manning AD. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment 4:80–86.

Flagg TA, Mahnken CVW, Iwamoto RN. 2004. Conservation hatchery protocols for Pacific salmon. American Fisheries Society Symposium 44:603–619.

Ford MJ. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. Conservation Biology 16:815–825.

Franklin IR. 1980. Evolutionary changes in small populations. In: Soulé ME, Wilcox BA, editors, Conservation biology: an evolutionary-ecological perspective, pp. 135–149. Sunderland, MA: Sinauer Associates.

Gärdenfors U, Hilton-Taylor C, Mace GM, Rodriguez JP. 2001. The application of IUCN Red List criteria at regional levels. Conservation Biology 15:1206–1212.

Gerber LR, Hatch LT. 2002. Are we recovering? An evaluation of recovery criteria under the U.S. Endangered Species Act. Ecological Applications 12:668–673.

Goman M, Wells L. 2000. Trends in river flow affecting the Northeastern reach of the San Francisco Bay estuary over the past 7000 years. Quaternary Research 54:206–217.

Good TP, Waples RS, Adams P. 2005. Updated status of federally listed ESUs of west coast salmon and steelhead. U.S. Dept. Commer. NOAA Tech. Memo. NMFS-NWFSC-66. Seattle, WA.

Goodman D. 2005. Selection equilibrium for hatchery and wild spawning fitness in integrated breeding programs. Canadian Journal of Fisheries and Aquatic Sciences 62:374–389.

Graham NE. 1994. Decadal-scale climate variability in the tropical and North Pacific during the 1970s and 1980s: Observations and model results. Climate Dynamics 10:123–162.

Hare SR, Francis RC. 1995. Climate change and salmon production in the Northeast Pacific Ocean. In: Beamish RJ, editor, Climate Change and Northern Fish Populations. Canadian Special Publications in Fisheries and Aquatic Sciences 121, pp. 357–372.

Hayhoe K, Cayan D, Field CB, Frumhoff PC, Maurer EP, Miller NL, Moser SC, Schneider SH, Cahil KN, Cleland EE, Dale L, Drapek R, Hanemann RM, Kalkstein LS, Lenihan J, Lunch CK, Neilson RP, Sheridan SC, Verville JH. 2004. Emissions pathways, climate change, and impacts on California. Proceedings of the National Academy of Sciences, USA 101:12442–12427.

Hickman JC. 1993. The Jepson manual: higher plants of California. Berkeley, CA: University of California Press.

Hilborn R, Quinn TP, Schindler DE, Rogers DE. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences, USA 100:6564–6568.

Hoblitt RP, Miller CD, Scott WE. 1987. Volcanic hazards with regard to siting nuclear-power plants in the Pacific Northwest. USGS Open-File Report 87-297. Vancouver, WA.

Hopelain JS. 2003. Strategic Plan for Trout Management. A Plan for 2004 and Beyond. Sacramento California Department of Fish and Game.

Hsieh CH, Glaser SM, Lucas AJ, Sugihara G. 2005. Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. Nature 435:336–340.

Ingram BL, Ingle JC, Conrad ME. 1996. A 2000 yr record of Sacramento-San Joaquin River inflow to San Francisco Bay estuary, California. Geology 24:331–334.

Interior Columbia Basin Technical Recovery Team. 2003. Independent populations of chinook, steelhead, and sockeye for listed Evolutionary Significant Units within the interior Columbia River domain. NOAA Fisheries. Working draft. Seattle, WA.

Interior Columbia Basin Technical Recovery Team. 2005. Viability criteria for application to Interior Columbia Basin salmonid ESUs. NOAA Fisheries. Draft report. Seattle, WA.

IUCN. 1994. IUCN Red List Categories. Gland, Switzerland: IUCN Species Survival Commission.

Jones RP, Salo EO. 1986. Status of anadromous fish habitat in the north and south fork Toutle River Watersheds, Mount St. Helens, Washington, 1984. Fisheries Research Institute, University of Washington. Report FRI-UW-8601. Seattle, WA.

Jonsson B, Jonsson N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3:348-365.

Kendall BE, Fox GA. 2002. Variation among individuals and reduced demographic stochasticity. Conservation Biology 16:109–116.

Kindopp J, Kurth R, Gonzales D. 2003. Lower Feather River steelhead (*Oncorhynchus mykiss*) redd survey. California Department of Water Resources SP F-10 task 2b report, Oroville Facilities Relicensing FERC Project No. 2100.

Kjelson MA, Brandes PL. 1989. The use of smolt survival estimates to quantify the effects of habitat changes on salmonid stocks in the Sacramento-San Joaquin rivers, California. In: Levings CD, Holtby LB, Henderson MA, editors, Proceedings of the National Workshop on the effects of habitat alteration on salmonid stocks, volume 105 of Canadian Special

Publications in Fisheries and Aquatic Sciences, pp. 100–115.

Knowles N, Cayan D. 2002. Potential effects of global warming on the Sacramento/San Joaquin watershed and the San Francisco estuary. Geophysical Research Letters 29(18), 1891, doi:10.1029/2001GL014339.

Kostow KE. 2004. Differences in juvenile phenotypes and survival between hatchery stocks and a natural population provide evidence for modified selection due to captive breeding. Canadian Journal of Fisheries and Aquatic Sciences 61:577–589.

Lande R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

Lande R. 1995. Mutation and conservation. Conservation Biology 9:782–791.

Lindley ST. 2003. Estimation of population growth and extinction parameters from noisy data. Ecological Applications 13:806–813.

Lindley ST, Mohr MH. 2003. Predicting the impact of striped bass (*Morone saxatilis*) population manipulations on the persistence of winter-run chinook salmon (*Oncorhynchus tshawytscha*). Fishery Bulletin 101:321–331.

Lindley ST, Schick RS, Agrawal A, Goslin M, Pearson T, Mora E, Anderson JJ, May B, Greene S, Hanson C, Low A, McEwan D, MacFarlane RB, Swanson C, Williams JG. 2006. Historical population structure of Central Valley steelhead and its alteration by dams. San Francisco Estuary and Watershed Science 4, Issue 1, Article 2.

Lindley ST, Schick RS, May B, Anderson JJ, Greene S, Hanson C, Low A, McEwan D, MacFarlane RB, Swanson C, Williams JG. 2004. Population structure of threatened and endangered chinook salmon ESUs in California's Central Valley basin. U.S. Dept. Commer. NOAA Tech. Memo. NMFS-SWFSC-360. La Jolla, CA.

Lynch M, O'Hely M. 2001. Captive breeding and the genetic fitness of natural populations. Conservation Genetics 2:363–378.

Mace GM, Lande R. 1991. Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. Conservation Biology 5:148–157.

Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069–1079.

Matthews WJ, Marsh-Matthews E. 2003. Effects of drought on fish across axes of space, time and ecological complexity. Freshwater Biology 48:1232–1253.

McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS, editors. 2001. Climate Change 2001: Impacts, Adaptation and Vulnerability. Cambridge: Cambridge University Press.

McCracken C, Winternitz L, Foley S. 2005. Lower American River: state of the river report. Water Forum. 660 J Street, Suite 260, Sacramento, CA 95814.

McElhany P, Backman T, Busack C, Heppell S, Kiolmes S, Maule A, Myers J, Rawding D, Shively D, Steel A, Steward C, Whitesel T. 2003. Interim report on viability criteria for Willamette and Lower Columbia basin Pacific salmonids. National Marine Fisheries Service. Seattle, WA.

McElhany P, Ruckelshaus MH, Ford MJ, Wainwright TC, Bjorkstedt EP. 2000. Viable salmonid populations and the conservation of evolutionarily sigificant units. U.S. Dept. Commer. NOAA Tech. Memo. NMFS-NWFSC-42. Seattle, WA.

McEwan DR. 2001. Central Valley steelhead. In: Brown RL, editor, Fish Bulletin 179, pp. 1–43. Sacramento, CA: California Department of Fish and Game.

McLean JE, Bentzen P, Quinn TP. 2003. Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead trout (*Oncorhynchus mykiss*) through the adult stage. Canadian Journal of Fisheries and Aquatic Sciences 60:433–440.

Melack JM, Dozier J, Goldman CR, Greenland D, Milner AM, Naiman RJ. 1997. Effects of climate change on inland waters of the Pacific coastal mountains and western Great Basin of North America. Hydrological Processes 11:971–992.

Miller AJ, Cayan DR, Barnett TP, Graham NE, Oberhuber JM. 1994. The 1976-77 climate shift of the Pacific Ocean. Oceanography 7:21–26.

Mobrand LE, Barr J, Blankenship L, Campton DE, Evelyn T, Flagg TA, Mahnken CVW, Seeb LW, Seidel PR, Smoker WW. 2005. Hatchery reform in Washington state: principles and emerging issues. Fisheries 30:11–23.

Moffett JW. 1949. The first four years of king salmon maintenance below Shasta Dam, Sacramento River, California. California Fish and Game 35:77–102.

Moritz MA. 1997. Analyzing extreme disturbance events: fire in the Los Padres National Forest. Ecological Applications 7:1252–1262.

Mueter FJ, Peterman RM, Pyper BJ. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus spp.*) in northern and southern areas. Canadian Journal of Fisheries and Aquatic Sciences 59:456–463.

Myers J, Busack C, Rawding D, Marshall A. 2003. Historical population structure of Willamette and Lower Columbia River Basin Pacific salmonids. WLC-TRT Report. NOAA Fisheries Northwest Fisheries Science Center. Seattle, WA.

Myers JM, Kope RG, Bryant GJ, Teel D, Lierheimer LJ, Wainwright TC, Grant WS, Waknitz FW, Neely K, Lindley ST, Waples RS. 1998. Status review of chinook salmon from Washington, Idaho, Oregon, and California. U.S. Dept. Commer. NOAA Tech. Memo. NMFS-NWFSC-35. Seattle, WA.

Myrick CA, Cech JJ. 2004. Temperature effects on juvenile anadromous salmonids in California's central valley: what don't we know? Reviews in Fish Biology and Fisheries 14:113–123.

National Marine Fisheries Service. 1997. NMFS proposed recovery plan for the Sacramento River winter-run chinook. NOAA/NMFS Southwest Regional Office. Long Beach, CA.

Neitzel DA. 1991. The effect of climate change on stream environments: the salmonid resource of the Columbia River basin. The Northwest Environmental Journal 7:271–293.

Newman KB, Rice J. 2002. Modeling the survival of chinook salmon smolts outmigrating through the lower Sacramento River system. Journal of the American Statistical Association 97:983–993.

Olson DE, Spateholts B, Paiya M, Campton DE. 2004. Salmon hatcheries for the 21st century: a model at Warm Springs National Fish Hatchery. American Fisheries Society Symposium 44:581–598.

Oreskes N. 2004. Beyond the ivory tower: The scientific consensus on climate change. Science 306:1686.

Pauly D, Christensen V, Guénette S, Pitcher TJ, Sumaila UR, Walters CJ, Watson R, Zeller D. 2002. Towards sustainability in world fisheries. Nature 418:689–695.

Peterson JH, Kitchell JF. 2001. Climate regimes and water temperature changes in the Columbia River: bioenergetic implications for predators of juvenile salmon. Canadian Journal of Fisheries and Aquatic Sciences 58:1831–1841.

Reisenbichler RR, McIntyre JD. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 34:123–128.

Reisenbichler RR, Rubin SP. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. ICES Journal of Marine Science 56:459–466.

Rinne JN. 1996. Short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. North American Journal of Fisheries Management 16:653–658.

Ruckelshaus MH, Currens K, Furstenberg R, Graeber W, Rawson K, Sands N, Scott J. 2002. Planning ranges and preliminary guidelines for the delisting and recovery of the Puget Sound Chinook salmon Evolutionarily Significant Unit. NOAA Northwest Fisheries Science Center. Seattle, WA.

Rudnick DL, Davis RE. 2003. Red noise and regime shifts. Deep Sea Research Part I: Oceanographic Research Papers 50:691–699.

Schindler DE, Scheuerell MD, Moore JW, Gende SM, Francis TB, Palen WJ. 2003. Pacific salmon and the ecology of coastal ecosystems. Frontiers in Ecology and the Environment 1:31–37.

Scott JM, Goble DD, Wiens JA, Wilcove DS, Bean M, Male T. 2005. Recovery of imperiled species under the Endangered Species Act: the need for a new approach. Frontiers in Ecology and the Environment 7:383–389.

Soulé ME. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. In: Soulé ME, Wilcox BA, editors, Conservation biology: an evolutionary-ecological perspective, pp. 151–170. Sunderland, MA: Sinauer Associates.

Speed T. 1993. Modelling and managing a salmon population. In: Turkman V, Barnett KF, editors, Statistics for the environment, pp. 267–292. New York: J. Wiley and Sons.

Thompson GG. 1991. Determining minimum viable populations under the Endangered Species Act. U.S. Dept. Commer. NOAA Tech. Memo. F/NWC-198. Seattle, WA.

Travis J, Lande R, Mangel M, Myers RA, Peterson CH, Power M, Simberloff D. 2004. Salmon Recovery Science Review Panel: report for the meeting held December 1-3, 2004. National Marine Fisheries Service. Santa Cruz, CA 95060.

Tuljapurkar SD, Orzack SH. 1980. Population dynamics in variable environments I. Long-run growth rates and extinction. Theoretical Population Biology 18:314–342.

United States Fish and Wildlife Service. 1994. Technical/agency draft recovery plan for the Sacramento-San Joaquin delta native fishes. United States Fish and Wildlife Service. Portland, OR.

VanRheenen NT, Wood AW, Palmer RN, Lettenmaier DP. 2004. Potential implications of PCM climate change scenarios for Sacramento-San Joaquin river basin hydrology and water resources. Climatic Change 62:257–281.

Vigg S, Burley CC. 1991. Temperature-dependent maximum daily consumption of juvenile salmonids by northern squawfish (*Ptychocheilus oregonensis*) from the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 48:2491–2498.

Waples RS, Teel D, Myers JM, Marshall A. 2004. Life history divergence in chinook salmon: historic contingency and parallel evolution. Evolution 58:386–403.

Whitlock MC, Barton NH. 1997. The effective size of a subdivided population. Genetics 146:427–441.

Williams JG. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. San Francisco Estuary and Watershed Science 4:Article 2.

Williams TH, Reeves GH. 2003. Ecosystem diversity and the extinction risk of Pacific salmon and trout. In: MacCall AD, Wainwright TC, editors, Assessing extinction risk for west coast salmon: proceedings of the workshop, NOAA Tech. Memo. NMFS-NWFSC-56, pp. 107–115. Seattle, WA: U.S. Dept. Commer.

Wright S. 1931. Evolution in Mendelian populations. Genetics 16:97–159.

Yoshiyama RM, Gerstung ER, Fisher FW, Moyle PB. 1996. Historical and present distribution of chinook salmon in the Central Valley drainage of California. Sierra Nevada Ecosystem Project, Final Report to Congress, vol III. Centers for Water and Wildland Resources, University of California, Davis.

Journal of Applied Ecology 2007
44, 1116–1126

Directed connectivity among fish populations in a riverine network

ROBERT S. SCHICK*† and STEVEN T. LINDLEY*
**NOAA Fisheries, Southwest Fisheries Science Center – Fisheries Ecology Division, 110 Shaffer Road, Santa Cruz, CA 95060, USA; and †University Program in Ecology, Duke University, Durham, NC 27708–0328, USA*

Summary

1. The addition of large water storage dams to rivers in California's Central Valley blocked access to spawning habitat and has resulted in a dramatic decline in the distribution and abundance of spring-run chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792). Successful recovery efforts depend on an understanding of the historical spatial structure of these populations, which heretofore has been lacking.

2. Graph theory was used to examine the spatial structure and demographic connectivity of riverine populations of spring-run chinook salmon. Standard graph theoretic measures, including degree, edge weight and node strength, were used to uncover the role of individual populations in this network, i.e. which populations were sources and which were pseudo-sinks.

3. Larger spatially proximate populations, most notably the Pit River, served as sources in the historic graph. These source populations in the graph were marked by an increased number of stronger outbound connections (edges), and on average had few inbound connections. Of the edges in the current graph, seven of them were outbound from a population supported by a hatchery in the Feather River, which suggests a strong influence of the hatchery on the structure of the current extant populations.

4. We tested how the addition of water storage dams fragmented the graph over time by examining changing patterns in connectivity and demographic isolation of individual populations. Dams constructed in larger spatially proximate populations had a strong impact on the independence of remaining populations. Specifically, the addition of dams resulted in lost connections, weaker remaining connections and an increase in demographic isolation.

5. A simulation exercise that removed populations from the graph under different removal scenarios – random removal, removal by decreasing habitat size and removal by decreasing node strength – revealed a potential approach for restoration of these depleted populations.

6. *Synthesis and applications.* Spatial graphs are drawing the attention of ecologists and managers. Here we have used a directed graph to uncover the historical spatial structure of a threatened species, estimate the connectivity of the current populations, examine how the historical network of populations was fragmented over time and provide a plausible mechanism for ecologically successful restoration. The methods employed here can be applied broadly across taxa and systems, and afford scientists and managers a better understanding of the structure and function of impaired ecosystems.

Key-words: California, chinook salmon, connectivity, dispersal, evolutionarily significant unit (ESU), graph theory, *Oncorhynchus tshawytscha*, population spatial structure, restoration

Journal of Applied Ecology (2007) **44**, 1116–1126
doi: 10.1111/j.1365-2664.2007.01383.x

Correspondence: Robert Schick, University Program in Ecology, Box 90328, Levine Science Research Center, Duke University, Durham, NC 27708–0328, USA (tel: + 1919 6138021; fax: + 1919 6848741; e-mail: robert.schick@duke.edu).

Introduction

Effective management of species requires knowledge of population structure, because this is key to understanding how local impacts may affect the larger entity at both ecological and evolutionary time scales (Kareiva & Wennergren 1995; Wennergren, Ruckelshaus & Kareiva 1995; Tilman & Lehman 1997). For example, a metapopulation may have quite different dynamics than a panmictic population of the same aggregate size, depending on factors such as the dispersal rates among populations and internal dynamics of the metapopulation components (Levins 1969; Kareiva 1990; Hanski & Gilpin 1991). Ignoring spatial structure, especially immigration from nearby populations, can impair the management of protected species, such as incorrectly diagnosing population status or the response to habitat restoration (Cooper & Mangel 1999). At longer time scales, the relationship between the structure and dynamics of populations and landscapes may determine the degree to which populations adapt to local conditions (Sultan & Spencer 2002) and how they respond to disturbance (Pickett & White 1985).

In many cases, species conservation problems can be framed in terms of problems with spatial structure, because impacts to species often take the form of lost habitat patches or dispersal corridors. Restoration is aided with a 'guiding image' (Palmer *et al*. 2005), and the virgin state of the system is often used as such. To be most effective, the guiding image should be in the form of a conceptual model that can show system function, system impairment and restoration strategies (Jansson *et al*. 2005). We propose that graph theory provides the tools needed to construct conceptual models for spatially explicit problems in conservation that allow quantitative comparisons of historical, contemporary and potentially restored population structures.

Graphs have been used across a variety of disciplines to study everything from the structure of the World Wide Web to subcellular protein networks. [See any of the following reviews, listed in approximate order of increasing specificity and mathematical complexity: Hayes (2000a, 2000b); Strogatz (2001); Watts (2004); Albert & Barabási (2002); and Newman (2003).] Graph theory is an appealing tool for analysis of population structure for several reasons. First, it allows us to characterize a complex system with a tractable, but explicitly spatial, mechanism (Urban & Keitt 2001; Brooks 2006; Gastner & Newman 2006). Secondly, using graphs we can assess the importance of individual elements in a graph both backwards in time as we examine how the graph, or network, breaks apart (Keitt, Urban & Milne 1997; Bunn, Urban & Keitt 2000; Urban & Keitt 2001) and forward in time to guide a conservation or restoration effort (Palmer *et al*. 2005). Thirdly, a graph is perhaps the simplest spatially explicit representation of a metapopulation (Urban & Keitt 2001; Brooks 2006). Lastly, there is a wealth of graph tools and algorithms that allow different graphs to be analysed and compared.

While graph theory carries with it its own terminology (Harary 1969), many of the terms have direct ecological interpretations. Nodes can represent a range of things, from individuals to populations to patches on a landscape. Edges are the connections between nodes. Construction of a landscape graph typically requires at least two data structures (Urban & Keitt 2001). The first structure includes information about the node's spatial location and some indicator of size. The second structure is a distance matrix between all of the nodes. The *degree* of a node is the number of edges incident to it. A regular graph is one where the edges are bi-directional, i.e. for nodes a,b the connection is $a \leftrightarrow b$ (Fig. 1a). In contrast, a digraph's edges (also called arcs) have direction, i.e. $a \rightarrow b$ (Fig. 1b). For a digraph, *degree* is slightly different: *outdegree* of a point v is the number of points adjacent from a node; and *indegree* is the number adjacent to a node. Logically, *outdegree* and *indegree* correspond to familiar source–sink dynamics with which most ecologists are familiar (Pulliam 1988). The connection between a pair of nodes in a given graph G is based on an adjacency matrix. The adjacency matrix is comprised simply of 0s and 1s, where 0 indicates no connection between a pair of nodes and 1 indicates that a connection, or edge, exists. [To help avoid confusion, we note that nodes can be adjacent (connected) in a graph theoretic sense even if they are not adjacent in a geographical sense.] Lastly, in most instances, populations and metapopulations can be represented realistically as weighted digraphs (Fig. 1c) with different population sizes and the asymmetric connections between them (Barrat *et al*. 2004; Bascompte, Jordano & Oleson 2006). These cartoon graphs serve as the conceptual basis for the connections in larger, more complicated, and in our case, spatially explicit graphs.

While the role of ecological connectivity in regulating and maintaining population distribution and population persistence has been documented in both the terrestrial (Fahrig & Merriam 1985; Taylor *et al*. 1993) and aquatic realms (Wiens 2002), the direction of the connectivity can have important impacts on a given system (Gustafson & Gardner 1996). Therefore, because regular graphs may not capture completely how connectivity influences population structure, we use weighted digraphs (Barrat *et al*. 2004; Bascompte *et al*. 2006) to examine how directed connectivity and asymmetrical dispersal elucidate population structure. Although directed connectivity has been mentioned previously (Gustafson & Gardner 1996; van Langevelde, van der Knaap & Claassen 1998; Urban & Keitt 2001; Schooley & Wiens 2003), its importance for fish populations has not been fully explored. Furthermore, the influence of the dendritic riverine structure on metapopulation persistence and population vulnerability for fish has only been noted relatively recently (Dunham & Rieman 1999; Gotelli & Taylor 1999; Fagan 2002) and no attempt has been made, to our knowledge, to use graphs to represent fish populations in a riverine

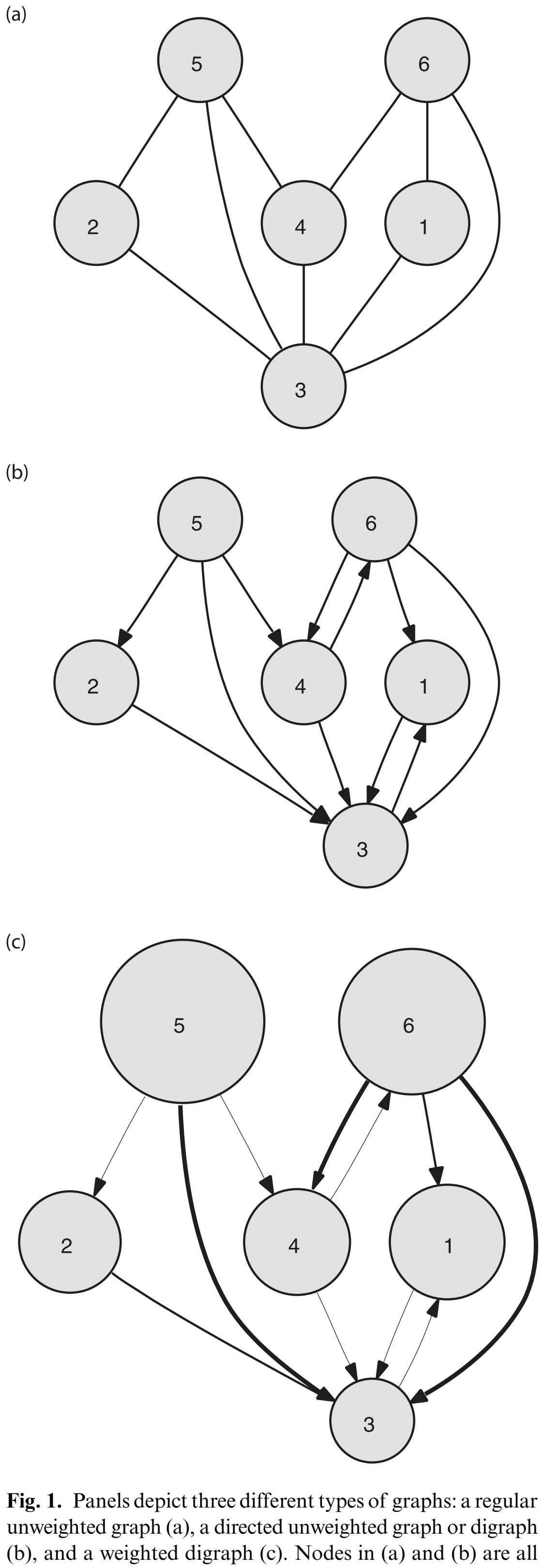

Fig. 1. Panels depict three different types of graphs: a regular unweighted graph (a), a directed unweighted graph or digraph (b), and a weighted digraph (c). Nodes in (a) and (b) are all equal size, while nodes in (c) have different size. Edges in (a) are regular and un-weighted. Edges in (b) are directed, while edges in (c) are both directed and weighted.

setting. The representation of river/stream fish populations as a graph is notably different from most terrestrial graphs, because the dispersal corridors (rivers and streams) are generally fixed and immutable at ecological time scales, i.e. the fish already live in a network.

Endangered salmonid populations are managed as evolutionarily significant units (ESU), which are defined as a salmon population or group of salmon populations that is substantially isolated reproductively from other populations and that contributes substantially to the evolutionary legacy of the species (Waples 1991, 1998). Typically, ESUs are structured internally (Gharrett, Gray & Brykov 2001; Olsen *et al*. 2003; Guthrie & Wilmot 2004) due to the fact that salmon mainly return to their natal rivers after spending several years at sea, but there is some low level of dispersal among the populations that is probably important for ESU persistence. As salmon return to their natal rivers they stray naturally at varying rates (Ricker 1972; Quinn 1993), which allows them to occupy new habitat (Milner & Bailey 1989; Wood 1995) and is the mechanism by which populations are connected. The rate at which salmon stray has proved difficult to quantify, although observed rates in the wild range from 0 to 67% (McElhany *et al*. 2000). Changing the spatial structure through population loss or increased straying must have effects on an ESU, but to date these have not been quantified.

We examine spring-run chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) in California's Central Valley (Fig. 2), which are listed as threatened under the United States' Endangered Species Act. Spring-run chinook salmon are high-elevation mainstem spawners that migrate into the watersheds under high flow conditions in springtime (Yoshiyama *et al*. 2001; Lindley *et al*. 2004). They over-summer in cool temperature pools before migrating out of the pools in the fall to spawn (Lindley *et al*. 2004). After spawning the cool water temperatures delay maturation, and juveniles often remain in the system for a full year (Lindley *et al*. 2004). Spring-run chinook salmon occupied much of the Central Valley, although the installation and continued presence of major dams has blocked and restricted access to much of their historical habitat (Yoshiyama *et al*. 2001; Lindley *et al*. 2004) (Fig. 2). The first of 10 'keystone' dams in the Central Valley, i.e. the lowest-elevation dam that completely blocks upstream habitat, was installed in 1894. The addition of such keystone dams proceeded until 1968, removing a total of 19 populations from the ESU. Lindley *et al*. (2004) describe the putative historical structure of the ESU, which forms the basis for our analysis. We presume this was a viable ESU prior to 1894.

We build and test a dispersal model that accounts for directional connectivity between populations within the historic spring-run chinook salmon ESU, and use graph theoretic methods to test how connectivity influences the spatial structure of populations within the ESU. We focus on (a) the organisms' ability to disperse through fixed edges, (b) on the importance of individual fish populations (nodes) and (c) how the installation and continued presence of dams impacted the ESU. In addition, we examine the structure of the current spring-run chinook salmon ESU. Lastly, we use

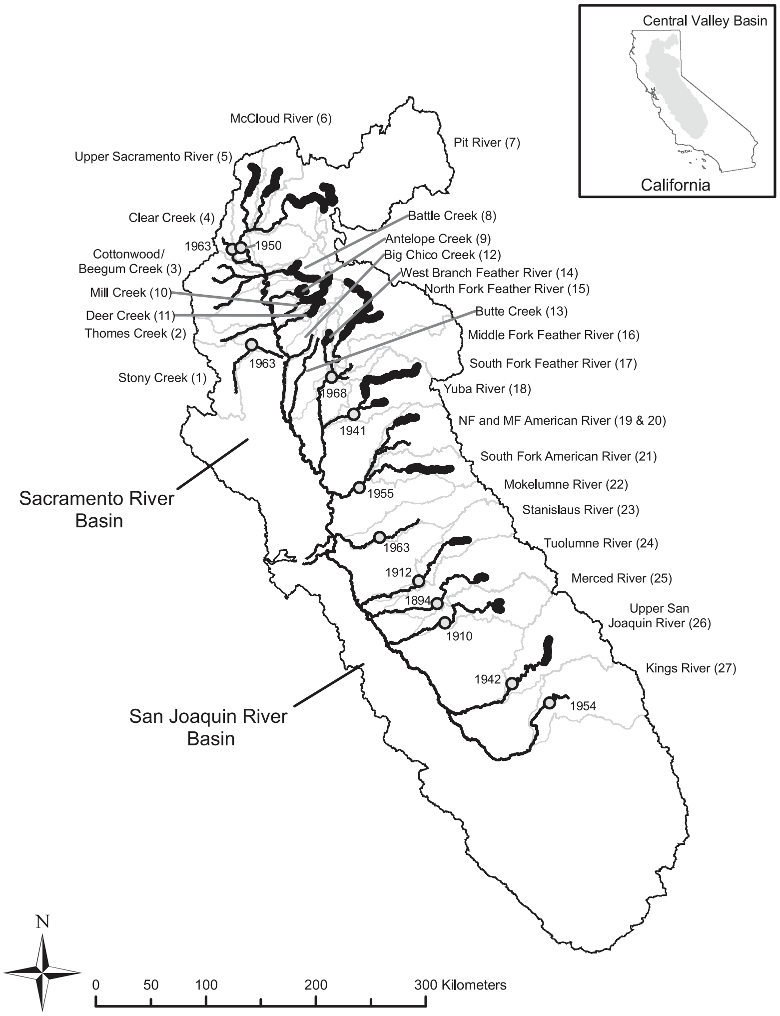

Fig. 2. Basemap of the study region. Depicted are the two river basins in the Central Valley, California (Sacramento River and San Joaquin River) and the major rivers within those basins that historically contained spring-run chinook salmon. The mainstems of the rivers are drawn up to the historical uppermost extent of spring-run chinook salmon as determined by Yoshiyama *et al.* (2001). Inferred spawning habitat above 500 m is shown in thick black lines. Populations are labelled with the river name and with a numerical ID that will be used in subsequent figures. Keystone dams are depicted as light grey nodes and are labelled with the year they were installed. For clarity, the Sacramento River Delta is omitted from the map.

these results – notably changes in graph metrics and in the role of populations – to discuss the persistence and survival of this threatened species. The graph theoretic methods presented herein have broad application across a variety of ecological systems, and can be used in data limited environments to predict population structure, persistence and synchrony.

Materials and methods

To populate the first graph data structure, we initially identified populations in the spring-run chinook salmon ESU that historically contained spawning groups (Lindley *et al.* 2004). The nodes in our graph represent populations; to identify these populations spatially, we located the intersection of the 500 m elevation contour and the mainstem of each river within the ESU. (Yoshiyama *et al.* 2001 identify 500 m as the approximate lower extent of the breeding range for spring-run chinook salmon.) This intersection is then the spatial representation of the node. To represent the size of the population (node) in the historical spring-run chinook salmon ESU, we used a habitat proxy: extent of the mainstem spawning range > 500 m elevation (Yoshiyama *et al.* 2001). For populations whose habitat was below 500 m, e.g. several small populations on the western side of the Central Valley, we used estimated ranges from Yoshiyama *et al.* (2001). Previous studies have shown that spawning habitat, as we have defined it here, correlates significantly with effective population size, N_e (Shrimpton & Heath 2003). To represent the size of the population (node) in the current spring-run chinook salmon ESU, we used the mean number of annual spawners since 1980 in lieu of the habitat proxy for the historical ESU (R. M. Kano, California Department of Fish and Game, Sacramento, CA., USA, unpublished data). [We note that these definitions of node size are different, and comparisons between the historic and current graph were made with an appropriate degree of caution. The correlation between habitat length and number of spawners was negative (–0·301); however, a plot of these revealed the relationship between the two was nonlinear and that this negative correlation was driven by an outlier (Butte Creek). Once Butte Creek was removed, the correlation between habitat length and number of spawners was positive (0·65).]

To create the second graph data structure, we used a network module of a commercially available geographical information system (GIS) package (ArcInfo® workstation version 9·0) to estimate 'as the fish swims' distance between all identified populations. By 'as the fish swims' we mean minimum straight-line distance along the river network, i.e. fish do not explore available tributaries. We used the ArcGIS Network module to estimate this distance between node locations along the river network of the Central Valley (1 : 100 k routed stream layer, version 2003·6, available from CalFish: http://www.calfish.org/DesktopDefault.aspx?tabId = 76, last accessed 18 August 2006). This yielded a full (upper and lower triangles) distance matrix, which served as the second input to our model.

Any two nodes in the graph were deemed connected by an edge if the proportion of incoming fish from one population exceeds a certain threshold level of the total recruitment (local + incoming) in the target population. The edges in the graph were developed from a migration matrix, *N*. To construct *N* we needed the following data structures: (1) a full distance matrix *D* of all the interpopulation 'as the fish swims' distances; (2) a dispersal kernel; (3) a matrix *M* of dispersal probabilities; and (4) a matrix *X* of population size.

We assumed in this analysis that a fraction of fish returning to spawn will stray from their natal stream and that the probability p_{ij} of a fish from node *i* migrating to node *j* is a function of the distance between the populations. While this inter-population distance may seem biologically counterintuitive, we repeated the same analysis using a model where salmon return to their natal watershed with some high fidelity, but make 'wrong' decisions with some small probability. Because the results were quite similar, we chose the more parsimonious model for interpopulation distance, because it rested on fewer unverifiable assumptions. (See supporting material for full characterization of this 'wrong-turn' model and results.)

To estimate p_{ij}, we fitted a dispersal kernel to the interpopulation distances. We used the kernel from Clark, Macklin & Wood (1998):

$$p_{ij} = \frac{c}{2\alpha\Gamma(1/c)} \exp\left(-\left|\frac{d_{ij}}{\alpha}\right|^{c}\right), \qquad \text{eqn 1}$$

where α is a dispersion parameter, c a shape parameter, and d_{ij}, an interpopulation distance measured along the stream network (from a full distance matrix D, described above). α is an estimate of a species dispersal capability, while c controls the shape of the tail in the kernel. To parameterize α we used two different studies on chinook dispersal from McClure *et al.* (2003, unpublished data, available at: http://www.nwfsc.noaa.gov/trt/col_docs/independent-popchinsteelsock.pdf, last accessed 23 August 2006). The first was a within-basin movement study of wild spring-run chinook salmon, which indicated an α = 31·6 km; the second was a cross-basin study of hatchery fish that indicated an α = 166 km. While the first data source is on wild fish, and probably represents a better source, it was limited to one river basin and does not account for basin-to-basin straying. The second estimate of α does account for basin-to-basin straying; however, it is probably biased upwards because of the reduced homing ability of hatchery fish. Therefore we chose the average of the two, or α = 98 km. The nature of the tail is controlled by c, whereby $c = 1$ and $c = 1/2$ correspond to a kernel with an exponential tail and a fat tail, respectively (Clark *et al.* 1998; Clark *et al.* 1999). We chose $c = 1$, where the shape of the kernel is exponential and dispersal probability is controlled by the value of α (personal communication, J. S. Clark, Duke University, Durham, NC 27708, USA).

Whether populations were deemed adjacent depended upon the magnitude of migration between them, the magnitude of total recruitment and a threshold for the ratio of the two. If the percentage of a population's total recruitment coming from immigrating fish from another donor population exceeded some value, these populations were deemed connected (Bjorkstedt *et al.* 2005). To find these connections we first created a dispersal probability matrix M comprised of a mixture model composed of two probabilities: (1) m, defined as straying probability and initialized at 5%; and (2) p_{ij}, as defined above. We then set the off-diagonal elements of M to mp_{ij} and the diagonal elements to 1 – m. Because p_{ij} represented a discrete interpopulation movement, we normalized the off-diagonal probabilities over all possible movements, i.e.

$$M_{i\neq j} = \frac{p_{ij}}{\sum_{j} p_{ij}} .$$

We then used the matrix of population sizes X (described in the previous section) in conjunction with M to define a migration matrix $N = XM$. The diagonal elements of N contained the number of fish resulting from self-recruitment, and the column sums of the off-diagonal elements contained the number of fish immigrating to the populations (*sensu* Bjorkstedt *et al.* 2005). The proportion of recruitment in population i that comes from population j was then calculated in order to examine pairwise directed dependence. If this ratio exceeded some threshold, then population i was dependent upon population j. The relationships among all populations were visualized as a directed graph. Independent populations in the graph were populations that are not dependent upon any others indicated either by populations with either no connections to other nodes, or only outbound connections. In our model, populations were adjacent (connected) if the donor population contributes more than 1% of total recruitment to the recipient. In addition, we preserved the strength of the connection to represent the weighted graph fully.

Lastly, we defined the population's independence (Bjorkstedt *et al.* 2005), or ζ, as:

$$\zeta_i = \frac{\delta_{ii}X_i}{\delta_{ii}X_i + \sum_{i\neq j} \delta_{ij}X_j}, \qquad \text{eqn 2}$$

where X represents population size, and δ_{ij} is local recruitment. We assessed how the trajectory of population independence changed over time by recalculating ζ for the remaining populations after each dam addition.

We examined the source–sink structure (Pulliam 1988) of the ESU by evaluating the importance of individual populations to the historical graph at the ESU scale (Bunn *et al.* 2000; Urban & Keitt 2001). Specifically, we examined node sensitivity for *outdegree* and *indegree* of a given node. *Outdegree* and *indegree* correspond logically to a qualitative representation of source and sink structure (Pulliam 1988), while *node strength* provides a quantitative representation of this structure (Barrat *et al.* 2004; Bascompte *et al.* 2006). We calculated *outdegree* and *indegree* of a given node by summing the rows and columns of the adjacency matrix $A(D)$, respectively. To calculate *node strength*, we summed the row and column sums of the off diagonal elements of N. Note that we assumed all populations have at least some local recruitment and may be more accurately termed pseudo-sinks (Watkinson & Sutherland 1995).

We combined methods from Bunn *et al.* (2000) and Urban & Keitt (2001) with our digraphs to examine the

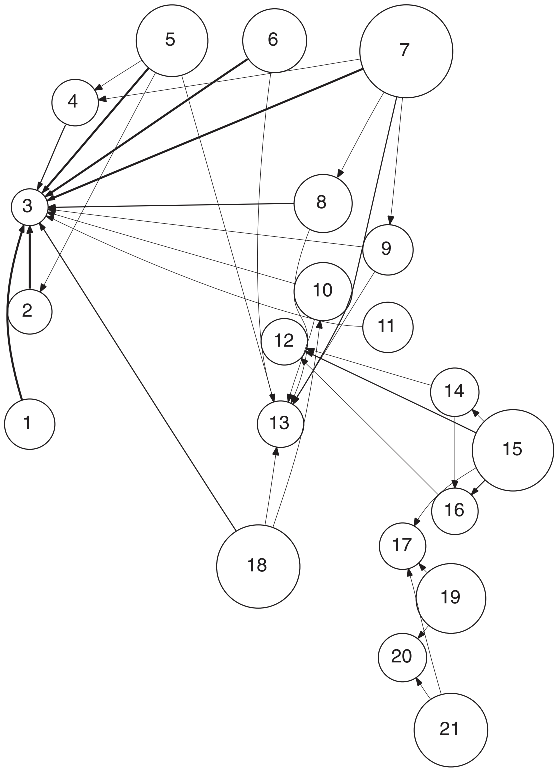

Fig. 3. Digraph for dispersal through the historical spring-run chinook salmon ESU. Because there were no connections into or out of any of the San Joaquin Basin populations (numbers 22–27), they are excluded from the figure. Populations are connected if donor population contributes more than 1% of local recruitment to the receiving population. Increased edge thickness corresponds to increased demographic dependence (1–4·9%, 5–9·9%, > 10%). The size of the nodes corresponds to the amount of habitat present in each watershed (log +1·5 transformed), and the location of the nodes in the figure is an approximation of their true location. Populations are numbered as in Fig. 2.

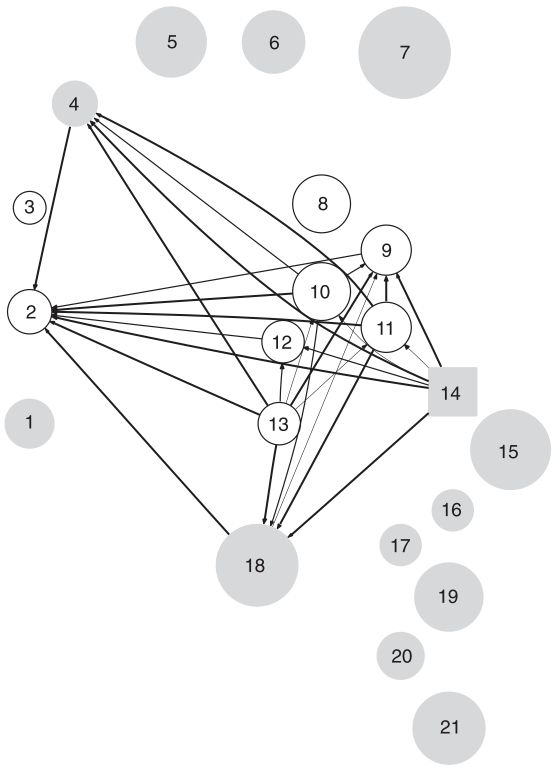

Fig. 4. Digraph for dispersal through the extant populations in the spring-run chinook salmon ESU. In addition the Feather River Hatchery is included in the graph, and is in the same place as the West Branch Feather River (14). Nodes for extinct populations are depicted in grey. Several populations whose historical habitat was blocked by hydropower dams now have some small populations spawning below dams, hence the presence of edges into grey nodes. These include Clear Creek (4) and the Yuba River (18).

effect dam addition had on the structure of the ESU. In addition to observing the actual fragmentation of the ESU, we used our model of connectivity and a series of alternate node removal scenarios (random, removal by largest available habitat and removal by largest node strength) to observe what happened to the graph as populations in the ESU went extinct.

We tested the sensitivity of the model to our assumptions by perturbing each of five model parameters by 10% and tallying the percentage change in the total number of edges in the graph. These parameters included: (1) the α parameter in the dispersal kernel; (2) the percentage of fish straying; (3) that migration is proportional to the interpopulation distance; (4) that population size is proportional to historical spawning extent; and (5) that all fish arriving at a new population recruit into that population (i.e. fitness of natives vs. strays).

Results

The historical digraph G_1 based on the dispersal adjacency matrix outlined above exhibited unbalanced *indegree* and *outdegree*, and contained six entirely disconnected (independent) populations (Fig. 3). All these populations are in the San Joaquin system, where the geography of the river basins is such that the populations are quite far apart (Fig. 2). In addition, the geographically closest of these populations (23–25) are all small enough to preclude outbound/inbound connections (Fig. 2). There are several populations in the Sacramento River Basin whose connections (> 1) were all outbound: Upper Sacramento (5), McCloud (6), Pit (7), Yuba (18), North Fork Feather (15) and the North and South Forks of the American River (19, 21) (Fig. 3). These large source populations, like those in the San Joaquin, are also demographically independent. Stronger demographic connections, on average, exist between nearby populations in which the source population is larger than the pseudo-sink population; as expected, the strength of the connection tends to decay with distance (Fig. 3).

The current graph is smaller than the historic graph, because most spawning habitat for historical populations is now behind dams (Fig. 4). At the ESU scale there are 15 demographic connections above the 10% threshold, four of which are outbound from the Feather River Hatchery (14). Butte Creek (13), a net

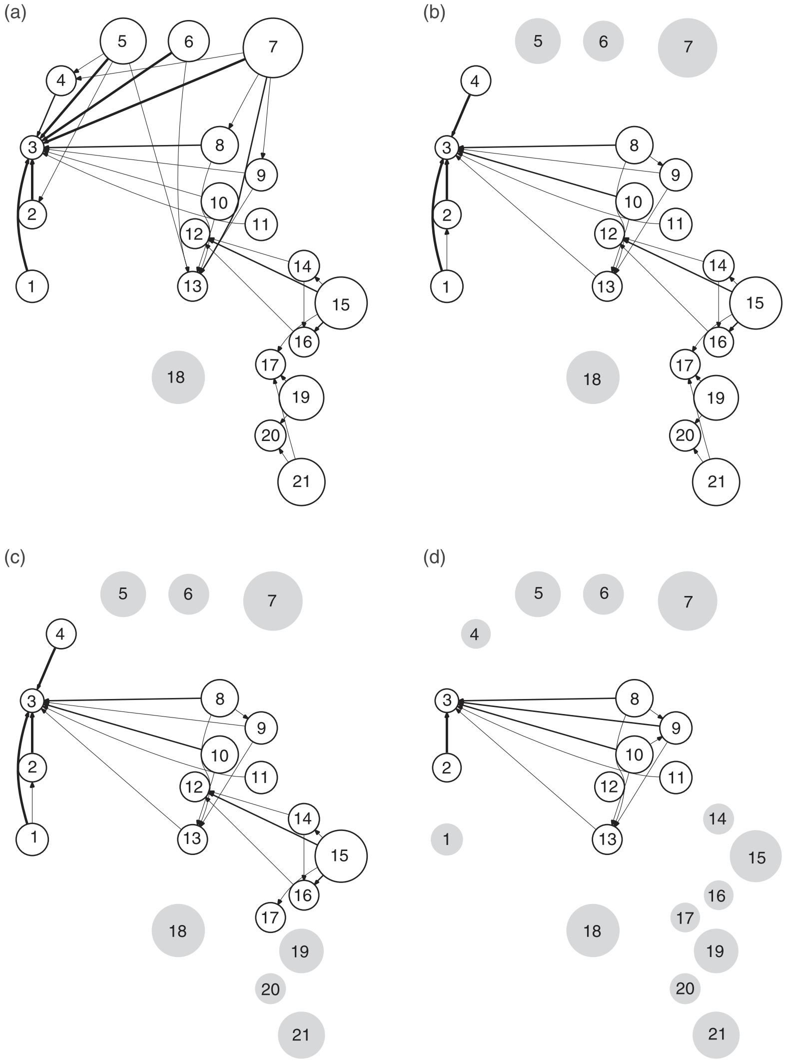

Fig. 5. Four panels depict the addition of dams to certain rivers, and the accompanying change in the graph. Shown are (a) Englebright Dam on the Yuba River (1941), (b) Shasta Dam on the Sacramento River (1945), (c) Nimbus Dam on the American River (1955) and (d) Oroville Dam on the Feather River (1968). Nodes and edges are depicted as in Fig. 3, except for extinct populations whose nodes are in grey.

importer before dam construction (*indegree* = 6, *outdegree* = 1 in Fig. 3), is a net exporter (*indegree* = 0, *outdegree* = 7 in Fig. 4). Both Stony (1) and Beegum Creek (3) had an average of zero reported spawners, hence the lack of connections in either direction (Fig. 4). Lastly, there is only one independent population, Battle Creek (8), in the current graph, while there were nine such populations in the historical graph.

In addition to blocking habitat, dam addition affects the remaining nodes both by increasing demographic independence on average and reducing the strength of the connections between nodes (Fig. 5a–d). As large spatially proximate nodes are removed from the graph, edges with an initial high weight are lost and the weight of certain remaining edges increases as migrants have fewer possible destinations (Fig. 5a–d). For example, when Shasta Dam was constructed in 1945 it blocked access to several major rivers including the Pit, McCloud and the Upper Sacramento (located just above the northernmost dam in Fig. 2), and the results illustrate what a vital source these three rivers were to the overall graph (Fig. 5b). Each of these nodes (especially the Pit River) had a high outdegree, and the removal of these three nodes results in a loss of 12 edges (Fig. 5b). However, the loss also affected the context of populations such as Battle Creek (8), which had an increase in the number of outbound edges, as well as their weight (Fig. 5b–d). The last two panels depict the loss of the American River and the Feather River populations through the addition of Nimbus Dam and Oroville Dam, respectively (Fig. 5c,d). Any dam that blocked access to anadromous habitat in the San Joaquin system had little effect on the remaining populations, because these populations were all quite isolated (nodes not shown).

Independence of smaller populations increases with the loss of large source populations (Fig. 6), suggesting that recolonization rates are lower under the current structure than they were historically. Some losses are worse than others; the addition of Shasta Dam (1942) not only removed many edges (Fig. 5b), but it also caused a dramatic increase in population independence for many of the populations present in the ESU (Fig. 6). Consider, for example, Butte Creek (13), which progresses from $\zeta = 0\cdot77$ in 1850 to $\zeta = 0\cdot87$ in 1968 (Fig. 6).

The median ζ across the ESU shows markedly different patterns when exposed to different node-removal scenarios (Fig. 7). Under the scenario aimed at removing the nodes with the highest node strength, population independence ζ of the remaining populations increased the fastest. The random removal scenario has the next strongest effect, followed by removal based on the largest habitat size of the remaining populations (Fig. 7). The difference between the node-strength and the random removal scenarios is particularly evident after approximately one-third of the habitat has been removed. Population independence ζ increased faster for all of these scenarios, as compared to actual removal (Fig. 7).

Our model was most sensitive to two parameters: (1) uncertainty about the percentage of fish that stray; and (2) to percentage of straying fish that recruit into the recipient population (Table 1). The model was less sensitive to uncertainty in dispersal capabilities of

Table 1. Results from sensitivity analysis. For each parameter listed, we implemented a 10% perturbation and tallied the absolute change in number of edges in the final historical graph. Noted are the number of edges and the absolute percent change. There were 35 edges in the base historic graph

Parameter	No. of edges	% Change
α	37	5·7
% of fish that stray	38	8·6
Habitat size	35	0
Inter-population distance	33	5·7
% Strays recruiting	38	8·6

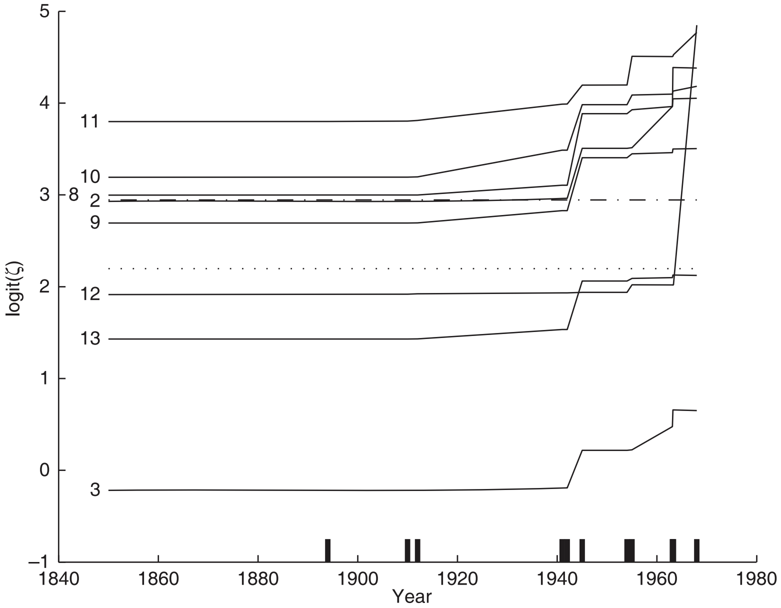

Fig. 6. Independence level (ζ) for each extant population in the ESU from 1850 up to the last dam addition in 1968. Population independence increases as populations are removed from the ESU (dam additions denoted by thick tick-marks on the x-axis). ζ-values are logit-transformed for visual clarity; for reference $\zeta = 0{\cdot}9$ and $\zeta = 0{\cdot}95$ are included as dashed and dash-dot lines, respectively. A dramatic change in population independence is seen after 1945, when the construction of Shasta Dam blocked access to the Pit, McCloud and Upper Sacramento Rivers. Populations are labelled as in Fig. 2.

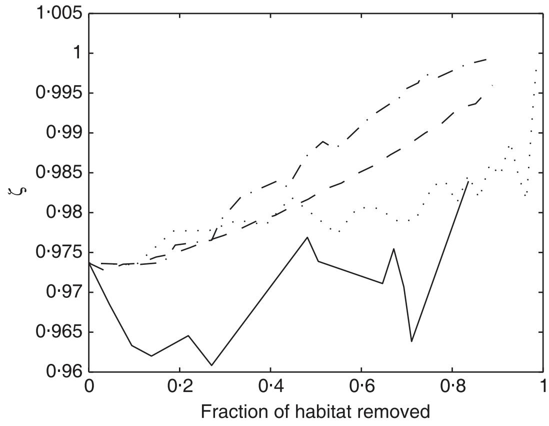

Fig. 7. Effect of node removal on median independence (ζ) of remaining populations in the ESU for four different removal scenarios: actual (solid line), random (dashed line), largest population first (dotted line), population with largest node strength first (dashed–dotted line). Random line represents the mean of 1000 iterations.

chinook and interpopulation distance. The model was not sensitive to our definition of population size. While we present only results for the historical graph (Table 1), these results hold as the graph fragments and the relative impacts of dams are the same as the unaltered empirical graph.

Discussion

Weighted digraphs have enabled us to understand more clearly the population context in the spring-run chinook salmon ESU, because they have shown whether populations are importers, exporters, or functionally independent. The historical digraph had both source and pseudo-sink populations, and a range of demographic connections between populations. The current graph has fewer source populations and fewer independent populations. Additionally, the current graph has populations that switch context from their position in the historical graph, and has more and stronger demographic connections between populations. While the impact of dams on fish populations has long been known, our examination of the sequential dam addition in the Central Valley showed clearly how a single dam can impact almost the entire ESU. This impact meant a loss of source populations to the ESU, resulting in fewer edges and increased isolation for the remaining nodes. This translates to decreased opportunity for recolonization after extinction or disturbance events.

Previous graph theoretic attempts to model how organisms perceive their landscape have relied mainly on regular graphs (Bunn *et al.* 2000; Urban & Keitt 2001; Brooks 2006) (although see Fortuna *et al.* 2006 for a recent example of the utility and strength of a digraph application). Here we have accounted for the strength and directionality of the connections in the graph, and while this is an obvious and intuitive extension of graph theoretic applications that has been mentioned several times in the literature (Gustafson & Gardner 1996; van Langevelde *et al.* 1998; Urban & Keitt 2001; Fagan 2002), we stress its importance in this and future applications. Imagine, for example, the different interpretation of Butte Creek (13) in a regular graph. There Butte Creek might jump out as a stepping-stone population (*sensu* Urban & Keitt 2001); however, it is clear from the digraph that this, in fact, is a pseudo-sink population whose demographic trajectory is influenced by several populations in the graph. Lastly, by accounting for recruitment as a measure of connectivity (*sensu* Bjorkstedt *et al.* 2005), we have extended the purely spatial application of graph theoretic measures and have uncovered not only how nodes are connected spatially, but what that spatial positioning means for the trajectories of populations within the ESU.

Defining what comprises a population remains an active research area in ecology and evolution. Indeed, relatively little work has been conducted on ascertaining what fraction of incoming recruitment affects population trajectories enough to consider them linked (Waples & Gaggiotti 2006). Hastings (1993), in a theoretical system, has shown that the 10% threshold is sufficient to consider population trajectories as linked. However, Lande, Engen & Sæther (1999) showed that under certain circumstances, i.e. weak density regulation, even very small migration rates can help to increase the spatial scale of synchrony. At two extremes, therefore, we can assume independence for populations with no edges or only outbound edges in

Fig. 3, and cannot assume independence for populations with inbound connections over 10% (Fig. 3). Even if absolute independence thresholds are not definitive, relative changes in population independence are clear from the pattern of dam addition that successively fragmented the ESU and isolated remaining populations (Fig. 6).

Graph theoretic applications are appealing from a conservation standpoint because they are relatively simple to implement and they offer critical insight at both the landscape and population level (Urban & Keitt 2001). The graphs herein show interpopulation connectivity across the ESU, population importance, and how the removal of populations over time fragmented the ESU. Because this is a riverine setting, edge removal between two populations means typically that there are no alternate edges between that pair of populations (Fagan 2002). This means that fragmentation events lower down in the trunks of a watershed (Fagan 2002) can have dramatic effects – witness the effect of two single such events (Shasta and Oroville Dams) in our ESU, which removed a total of seven populations from the ESU (Fig. 5b,d). Clearly, the Pit River (7) had a major impact on the ESU, and were it not for the considerable complexities involved with removing major dams like Shasta *and* Keswick (just downstream of Shasta and the one depicted in Fig. 2), this would be an obvious place to highlight conservation and restoration efforts. However, Shasta Dam holds much of Northern California's water and so its removal would have serious implications for both the amount of water and its flow regulation throughout Northern California.

Palmer *et al.* (2005) underscore the need for a guiding image when restoring river ecosystems, and our depiction of the historical graph (Fig. 3) provides such an image. Further, the simulation of node-removal under different scenarios provides information that could be key to managers, as it highlights which restoration methods would bring about a reduction in demographic isolation fastest. While one might assume naively that restoring large populations first would have the greatest affect, that is not the case here (Fig. 7). Clearly, a scenario centred around restoring populations with large node strength first would accomplish this by adding more connections back to the graph (Fig. 7). Somewhat counter-intuitively, ζ decreased initially under the actual removal scenario; however, this is due simply to the spatial arrangement and timing of dam removal in the Central Valley. Notably, the first populations to be removed were in the southern San Joaquin, which meant that while habitat was lost, the resulting graphs were initially more compact and less isolated. Lastly, and perhaps most importantly, our graph framework accomplished what Jansson *et al.* (2005) called for in terms of a conceptual model that shows system function, system impairment and restoration strategies that 'will move the system back to the guiding image'.

Connections are the mechanism by which recolonization can occur following disturbance, and they add stability and resilience to a system. It is intuitive that with more connections the removal of any one edge has less effect on the overall stability of the graph. Given the historical level of connections, then the graph as of 1968 (Fig. 5d) suffers from a lack of connections, and must be viewed as less resilient. This is echoed by the demographic isolation seen in Fig. 6, and adding connections back into the system would decrease demographic isolation and increase stability. There is a limit to this, however, in that a graph can have too many connections. While an increase in connectivity increases the likelihood of rescue (Brown & Kodric-Brown 1977), it also increases both the likelihood of pathogen spread (Hess 1996a) and spatial coupling. Hess (1996a,b) has shown that intermediate levels of connectivity provide a balance between extinction and persistence. With increased spatial coupling, Keeling, Bjørnstad & Grenfell (2004) have shown that synchronous populations are increasingly vulnerable to a similar extinction trajectory. Connections should therefore be viewed in light of a balance between these two opposing forces; simulation and/or analytical studies could help to uncover an optimum level of connectivity for population and ESU persistence.

The conceptual model presented herein has highlighted at least two other areas of future research. First, we might ask what other types of migration models make sense for salmon. We experimented with other models of straying, including implementing a 'wrong-turn' model where returning fish are faced with a series of choices as they migrate back to their natal stream. While this model is potentially more representative of the actual process undergone by a returning adult salmon, its results were qualitatively quite similar (see Appendix S1 in Supplementary Materials) to the more parsimonious distance-based model presented here, and it was less extensible to other systems. Secondly, we might ask how representative this model is for salmon dynamics. It was our intention that this model serve as an illustrative model of salmon connectivity, not necessarily a usable model of metapopulation dynamics. While the sensitivity results indicate that the model is fairly robust to uncertainty, they point to areas of further research. Namely, we need additional information about the percentage of fish that stray and the percentage of strays that recruit into populations.

Remarkable progress has been made in graph theory in just the last 8 years. Ecologists willing to wade into this realm will find that much awaits them in the way of different network structures, rapidly advancing algorithms and a wealth of interesting applications (Proulx, Promislow & Phillips 2005). Here graphs have enabled us to accomplish the following: (1) to enhance our understanding of the overall ESU structure; (2) to examine how ESU structure changed through time; and (3) to understand the historical importance of individual populations. In a data-limited environment, this exercise has shed light on this system from both an ecological and conservation standpoint. Our model of directed connectivity can be extended to many other systems, riverine or otherwise, and we recommend graph theory as an attractive analytical tool for rapid assessment of critical landscapes and endangered populations.

Acknowledgements

We thank Dean Urban, Brad Lamphere, Masami Fujiwara, Eric Treml, Dalia Conde, Chris Brooks and two anonymous reviewers, whose insightful comments considerably strengthened this manuscript. We also thank Ben Best for programming assistance. This work was supported in part by a James B. Duke Fellowship to R. Schick.

References

Albert, R. & Barabási, A.-L. (2002) Statistical mechanics of complex networks. *Reviews of Modern Physics*, **74**, 47–97.

Barrat, A., Barthelemy, M., Pastor-Satorras, R. & Vespignani, A. (2004) The architecture of complex weighted networks. *Proceedings of the National Academy of Sciences USA*, **101**, 3747–3752.

Bascompte, J., Jordano, P. & Oleson, J.M. (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, **312**, 431–433.

Bjorkstedt, E.P., Spence, B.C., Garza, J.C., Hankin, D.G., Fuller, D., Jones, W.E., Smith, J.J. & Macedo, R. (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*. NOAA Technical Memorandum NMFS-SWFSC-382: 1–210. US Department of Commerce, La Jolla, CA.

Brooks, C.P. (2006) Quantifying population substructure: extending the graph-theoretic approach. *Ecology*, **87**, 864–872.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445–449.

Bunn, A.G., Urban, D.L. & Keitt, T.H. (2000) Landscape connectivity: a conservation application of graph theory. *Journal of Environmental Management*, **59**, 265–278.

Clark, J.S., Macklin, E. & Wood, L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs*, **68**, 213–235.

Clark, J.S., Silman, M., Kern, R., Macklin, E. & HilleRis-Lambers, J. (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**, 1475–1494.

Cooper, A.B. & Mangel, M. (1999) The dangers of ignoring metapopulation structure for the conservation of salmonids. *Fishery Bulletin*, **97**, 213–226.

Dunham, J. & Rieman, B. (1999) Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications*, **9**, 642–655.

Fagan, W. (2002) Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology*, **83**, 3243–3249.

Fahrig, L. & Merriam, G. (1985) Habitat patch connectivity and population survival. *Ecology*, **66**, 1762–1768.

Fortuna, M.A., Gómez-Rodríguez, C. & Bascompte, J. (2006) Spatial network structure and amphibian persistence in stochastic environments. *Proceedings of the Royal Society, Series B*, **273**, 1429–1434.

Gastner, M.T. & Newman, M.E.J. (2006) The spatial structure of networks. *European Physical Journal B*, **49**, 247–252.

Gharrett, A., Gray, A. & Brykov, V. (2001) Phylogeographic analysis of mitochondrial DNA variation in Alaskan coho salmon, *Oncorhynchus kisutch*. *Fishery Bulletin*, **99**, 528–544.

Gotelli, N. & Taylor, C. (1999) Testing metapopulation models with stream-fish assemblages. *Evolutionary Ecology Research*, **1**, 835–845.

Gustafson, E. & Gardner, R. (1996) The effect of landscape heterogeneity on the probability of patch colonization. *Ecology*, **77**, 94–107.

Guthrie, C. III & Wilmot, R. (2004) Genetic structure of wild chinook salmon populations of southeast Alaska and northern British Columbia. *Environmental Biology of Fishes*, **69**, 81–93.

Hanski, I. & Gilpin, M. (1991) Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society*, **42**, 3–16.

Harary, F. (1969) *Graph Theory*. Addison-Wesley, Reading, MA.

Hastings, A. (1993) Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology*, **74**, 1362–1372.

Hayes, B. (2000a) Graph theory in practice; part I. *American Scientist*, **88**, 9–13.

Hayes, B. (2000b) Graph theory in practice; part II. *American Scientist*, **88**, 104–109.

Hess, G.R. (1996a) Disease in metapopulation models: implications for conservation. *Ecology*, **77**, 1617–1632.

Hess, G.R. (1996b) Linking extinction to connectivity and habitat destruction in metapopulation models. *American Naturalist*, **148**, 226–236.

Jansson, R., Backx, H., Boulton, A.J., Dixon, M., Dudgeon, D., Hughes, F.M.R., Nakamura, K., Stanley, E.H., Tockner, K. (2005) Stating mechanisms and refining criteria for ecologically successful river restoration: a comment on Palmer *et al*. (2005). *Journal of Applied Ecology*, **42**, 218–222.

Kareiva, P. (1990) Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society, Series B*, **330**, 175–190.

Kareiva, P. & Wennergren, U. (1995) Connecting landscape patterns to ecosystem and population processes. *Nature*, **373**, 299–302.

Keeling, M.J., Bjørnstad, O.N. & Grenfell, B.T. (2004) Metapopulation dynamics of infectious disease. *Ecology, Genetics, and Evolution of Metapopulations* (eds I. Hanski & O. E. Gaggiotti), pp. 415–445. Elsevier, Amsterdam.

Keitt, T.H., Urban, D.L. & Milne, B.T. (1997) Detecting critical scales in fragmented landscapes. *Conservation Ecology*, **1.** Available at: http://www.ecologyandsociety.org/vol1/iss1/art4/ (accessed 19 August 2007).

Lande, R., Engen, S. & Sæther, B.-E. (1999) Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. *American Naturalist*, **154**, 271–281.

van Langevelde, F., van der Knaap, W.G.M. & Claassen, G.D.H. (1998) Comparing connectivity in landscape networks. *Environment and Planning, B, Planning and Design*, **25**, 849–863.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the of the Entomological Society of America*, **15**, 237–240.

Lindley, S.T., Schick, R.S., May, B.P., Anderson, J.J., Green, S., Hanson, C., Low, A., McEwan, D., MacFarlane, R.B., Swanson. C. & Williams, J.G. (2004) Population structure of threatened and endangered chinook salmon ESUs in California's Central Valley Basin. NOAA Technical Memorandum NMFS-SWFSC-360: 1–56. US Department of Commerce, La Jolla, CA.

McElhany, P., Ruckelshaus, M., Ford, M., Wainwright, T. & Bjorkstedt, E. (2000) *Viable Salmonid Populations and the Recovery of Evolutionarily Significant Units*. NOAA Technical Memorandum NMFS-SWFSC-42: 1–156. US Department of Commerce, Seattle, WA.

Milner, A. & Bailey, R. (1989) Salmonid colonization of new streams in Glacier Bay National Park. *Alaska Aquaculture and Fisheries Management*, **20**, 179–192.

Newman, M. (2003) The structure and function of complex networks. *SIAM Review*, **45**, 167–256.

Olsen, J., Miller, S., Spearman, W. & Wenburg, J. (2003) Patterns of intra- and inter-population genetic diversity in Alaskan coho salmon: implications for conservation. *Conservation Genetics*, **4**, 557–569.

Palmer, M.A., Bernhardt, E.S., Allan, J.D., Lanke, P.S., Alexander, G., Brooks, S., Carr, J., Clayton, S., Dahm, F.S.J., Galat, C.N., D.L., Loss, S.G., Goodwin, P., Hart, D.D., Hassett, B., Jenkinson, R., Kondolf, G.M., Lave, R., Meyer, J.L., O'Donnell, T.K., Pagano, L. & Sudduth, E. (2005) Standards for ecologically successful river restoration. *Journal of Applied Ecology*, **42**, 208–217.

Pickett, S.T.A. & White, P.S. (1985) Patch dynamics: a synthesis. *The Ecology of Natural Disturbance and Patch Dynamics* (eds. S.T.A. Pickett & P.S. White), pp. 371–384. Academic Press, Inc., Orlando, FL.

Proulx, S., Promislow, D. & Phillips, P. (2005) Network thinking in ecology and evolution. *Trends in Ecology and Evolution*, **20**, 345–353.

Pulliam, H. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652–661.

Quinn, T. (1993) A review of homing and straying of wild and hatchery-produced salmon. *Fisheries Research*, **18**, 29–44.

Ricker, W. (1972) Hereditary and environmental factors affecting certain salmonid populations. *The Stock Concept in Pacific Salmon* (eds R. Simon & P. Larkin), pp. 27–160. H. R. MacMillan Lectures in Fisheries. University of British Columbia, Vancouver, BC.

Schooley, R.L. & Wiens, J.A. (2003) Finding habitat patches and directional connectivity. *Oikos*, **102**, 559–570.

Shrimpton, J.M. & Heath, D.D. (2003) Census vs. effective population size in chinook salmon: large- and small-scale environmental perturbation effects. *Molecular Ecology*, **12**, 2571–2583.

Strogatz, S. (2001) Exploring complex networks. *Nature*, **410**, 268–276.

Sultan, S.E. & Spencer, H.G. (2002) Metapopulation structure favors plasticity over local adaptation. *American Naturalist*, **160**, 271–283.

Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993) Connectivity is a vital element of landscape structure. *Oikos*, **68**, 571–573.

Tilman, D. & Lehman, C. (1997) Habitat destruction and species extinctions. *Spatial Ecology* (eds D. Tilman & P. Kareiva), pp. 233–249. Princeton University Press, Princeton, NJ.

Urban, D. & Keitt, T. (2001) Landscape connectivity: a graph-theoretic perspective. *Ecology*, **82**, 1205–1218.

Waples, R. (1991) Pacific salmon, *Oncorhynchus* spp. and the definition of 'species' under the Endangered Species Act. *Marine Fisheries Review*, **53**, 11–22.

Waples, R. (1998) Evolutionarily significant units, distinct population segments, and the Endangered Species Act: reply to Pennock and Dimmick. *Conservation Biology*, **12**, 718–721.

Waples, R.S. & Gaggiotti, O. (2006) What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, **15**, 1419–1439.

Watkinson, A.R. & Sutherland, W.J. (1995) Sources, sinks and oseudo-sinks. *Journal of Animal Ecology*, **64**, 126–130.

Watts, D. (2004) The 'new' science of networks. *Annual Review of Sociology*, **30**, 243–270.

Wennergren, U., Ruckelshaus, M. & Kareiva, P. (1995) The promise and limitations of spatial models in conservation biology. *Oikos*, **74**, 349–356.

Wiens, J.A. (2002) Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology*, **47**, 501–515.

Wood, C. (1995) Life history variation and population structure in sockeye salmon. *Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation*, American Fisheries Society Symposium 17 (ed. J.L. Nielsen), pp. 195–216. American Fisheries Society, Bethesda, MD.

Yoshiyama, R.M., Gerstung, E.R., Fisher, F.W. & Moyle, P.B. (2001) Historic and present distribution of chinook salmon in the Central Valley drainage of California. *Fish Bulletin 179: Contributions to the Biology of Central Valley Salmonids*, vol. 1. (ed. R.L. Brown), pp. 71–176. California Department of Fish and Game, Sacramento, CA.

Received 21 December 2006; accepted 27 June 2007
Editor: Marc Cadotte

Supplementary material

The following supplementary material is available for this article.

Appendix S1. Description and graphical results of the 'wrong-turn' model.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01383.x
(This link will take you to the article abstract).