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 popu-

lations 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.

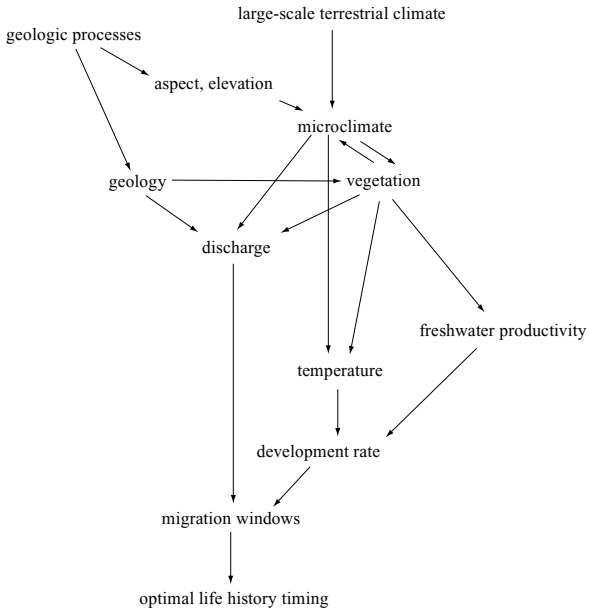

Figure 1. A simplified conceptual model of how aspects of the environment interact to influence the optimal timing of life history events such as spawning and juvenile emigration. Arrows indicate direct effects of one variable on another.

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

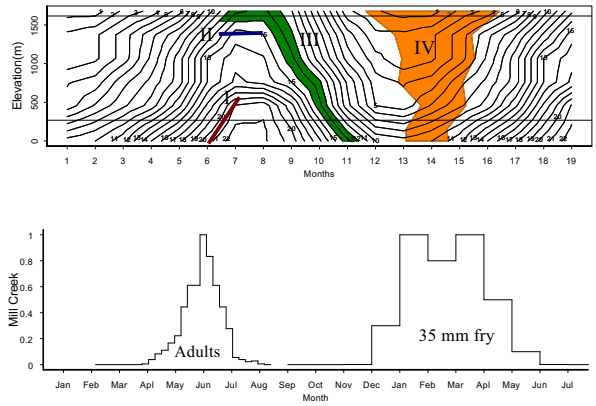

Figure 2. Effect of temperature on timing of spawning migration and fry emergence. Upper Panel shows the isotherm (°C) contours representative of northern Sierra Nevada streams. Line I depicts the thermal boundary for upstream adult migration. Line II depicts the thermally derived elevation where adults 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.

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

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 genentic 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.

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.

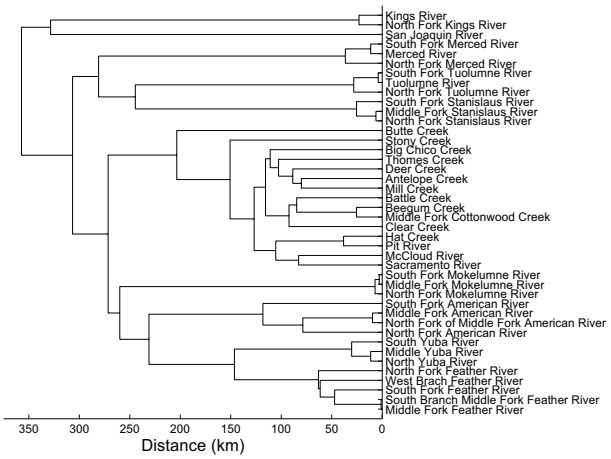

Figure 3. Neighbor-joining tree, based on distance along streams between 500 m elevation points, of watersheds that historically contained spring-run chinook salmon.

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).

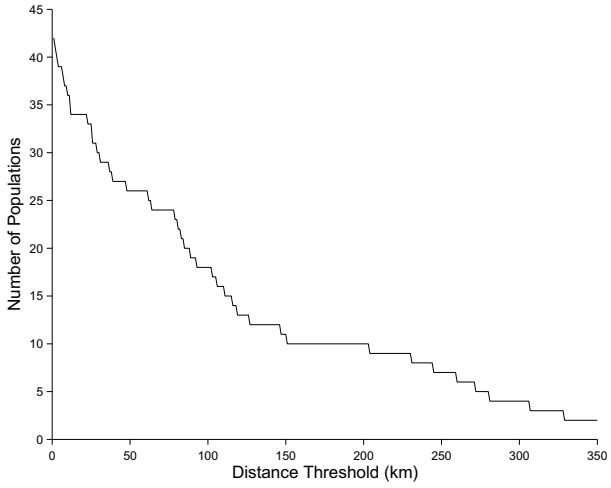

Figure 4. The number of population groups separated by dispersal distances. Distance measure is distance between 500 m elevation along the stream route.

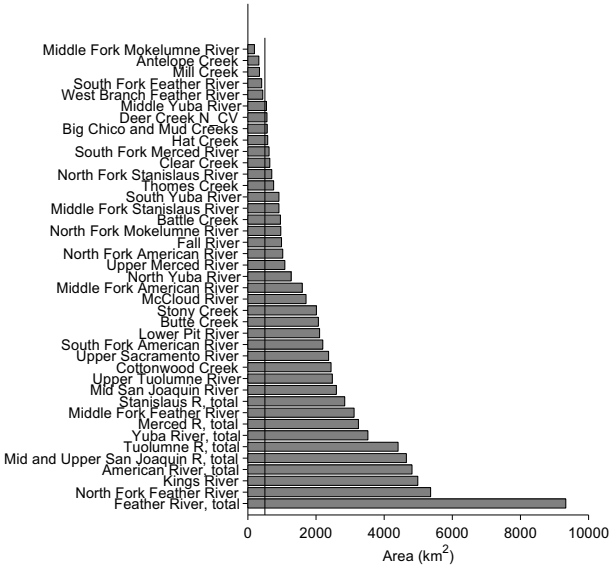

Figure 5. Area of Sacramento-San Joaquin watersheds that currently or historically contained spawning groups of spring-run chinook salmon, according to Yoshiyama et al. (1996). The vertical line marks 500 km^2.

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-

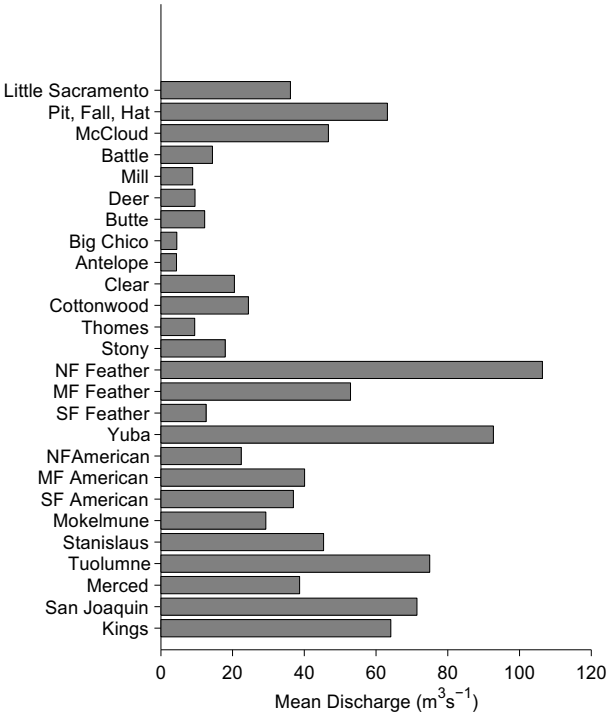

Figure 7. Mean annual discharge rate of Central Valley watersheds historically known to contain spring-run chinook salmon or winter-run chinook salmon.

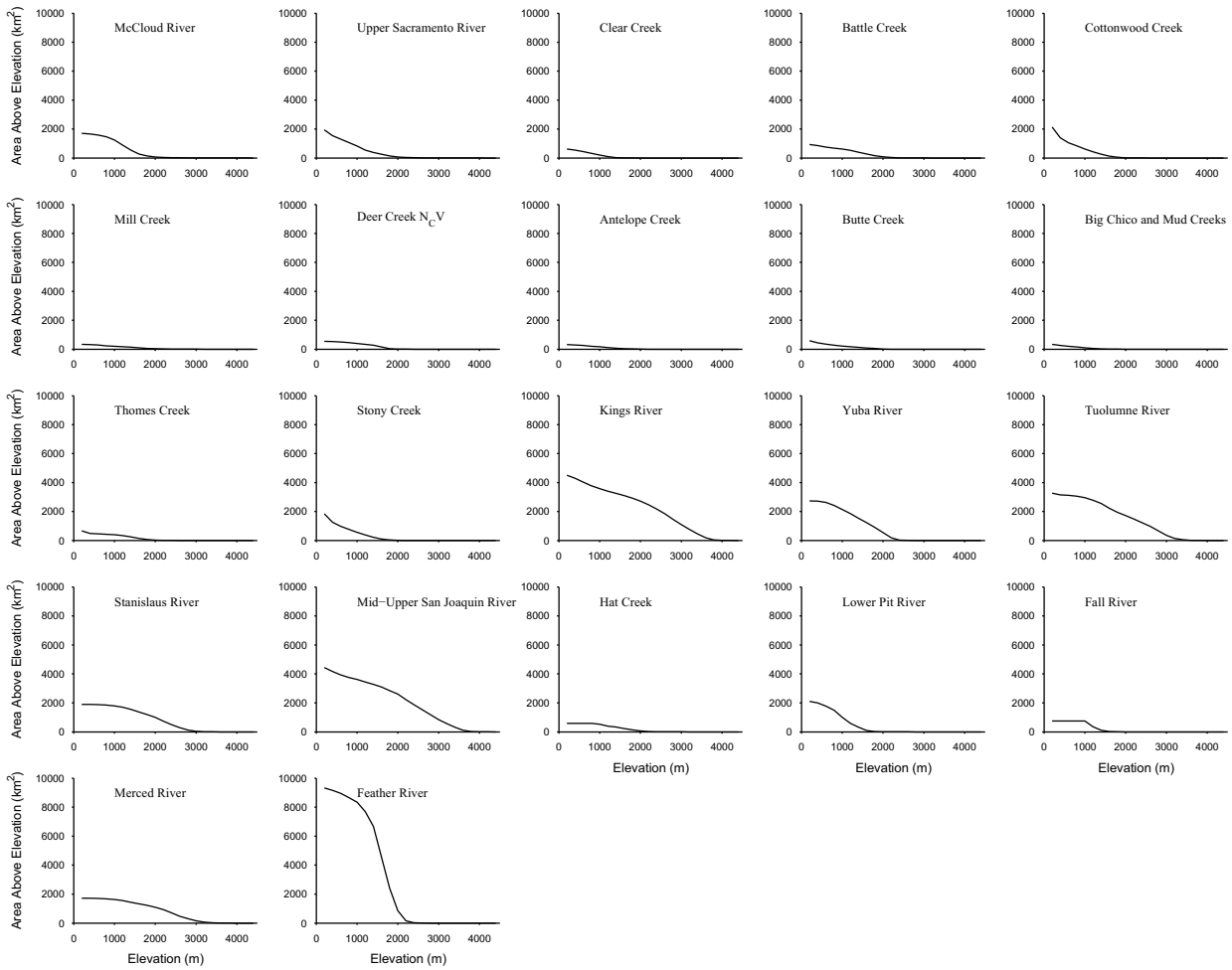

Figure 6. Area-elevation relationships of Central Valley watersheds historically known to contain spring-run chinook salmon or winter-run chinook salmon.

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.

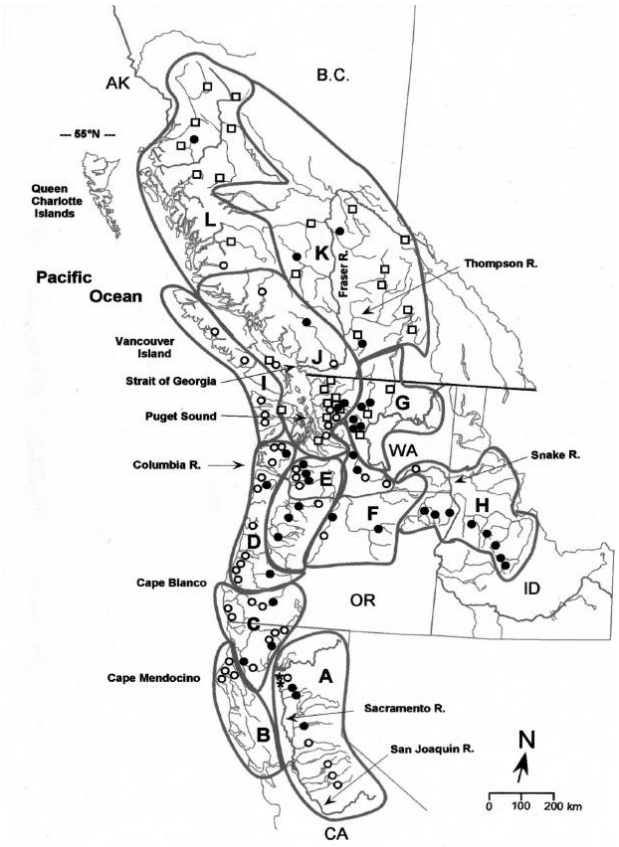

Figure 8. Populations sampled for genetic and life history data in Waples et al. (2004). Populations are coded by adult run time: closed circle = spring; open square = summer; open circle = fall; asterisk = winter. Twelve geographical provinces (A-L) used in the analysis of genetic and life history data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

3.3.2 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.

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.

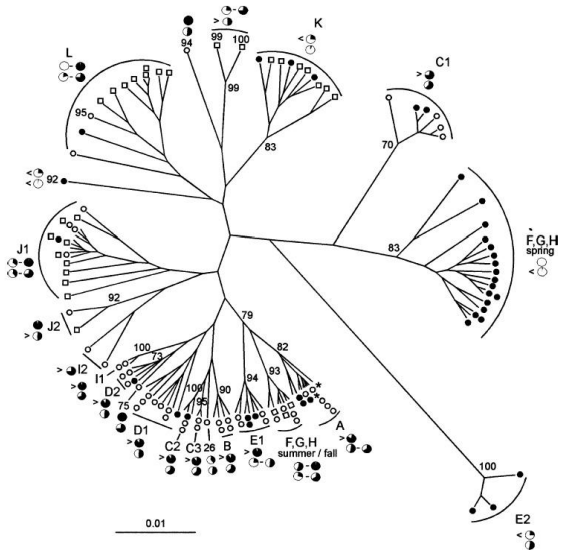

Figure 9. UPGMA phenogram of genetic distances (Cavalli-Sforza and Edwards) among 118 chinook salmon populations. Bold letters and numbers indicate provinces and areas, respectively, identified in Figure 8. Population symbols indicate adult run timing: closed circle = spring; open square = summer; open 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).

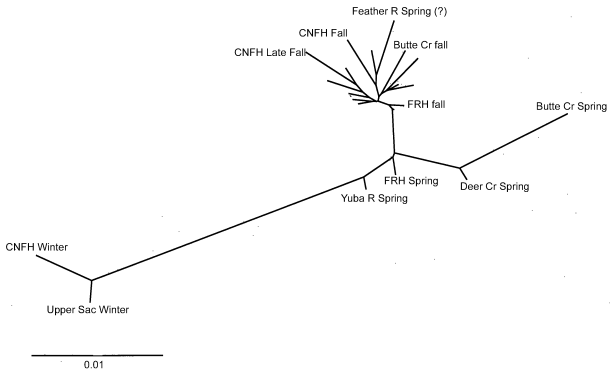

Figure 10. Neighbor joining tree (Cavalli-Sforza and Edwards chord distances) for Central Valley chinook populations, based on 24 polymorphic allozyme loci (unpublished data from D. Teel, NWFSC). Unlabeled branches are various fall-run chinook populations. CNFH = Coleman National Fish Hatchery; FRH =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

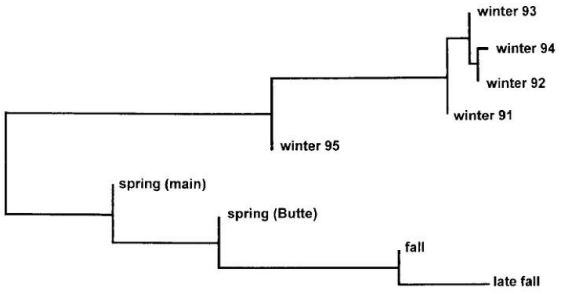

Figure 11. Phenogram based on Nei's genetic distance (D) demonstrating the relationships of Central Valley chinook runs.

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

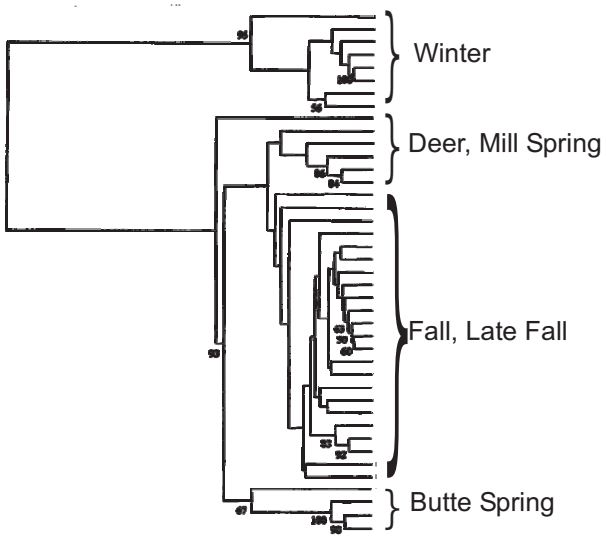

Figure 12. UPGMA dendrogram of Cavalli-Sforza and Edwards chord distances based on 5 microsatellite loci. Numbers at branch points indicate bootstrap percentages. Figure adapted from Banks et al. (2000).

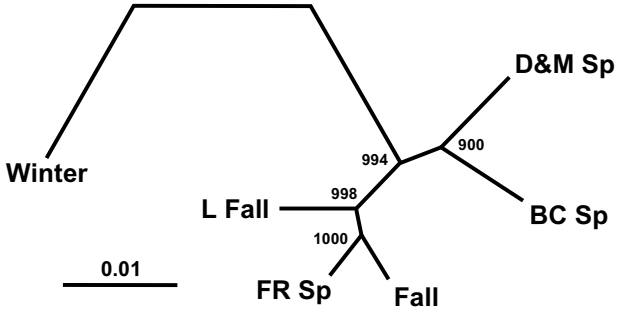

Figure 13. Neighbor joining tree (Cavalli-Sforza and Edwards chord distances) for Central Valley chinook populations, based on 12 microsatellite loci. D&M = Deer and Mill Creek; BC = Butte Creek; FR = Feather River; Sp= spring chinook; L Fall = late-fall chinook; Winter = winter-run chinook salmon. The 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

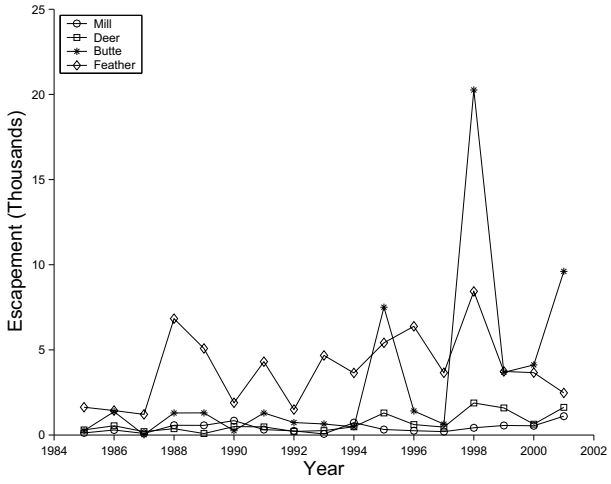

Figure 14. Estimated escapement of spring-run chinook in Mill, Deer, Butte creeks and the Feather River.

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).

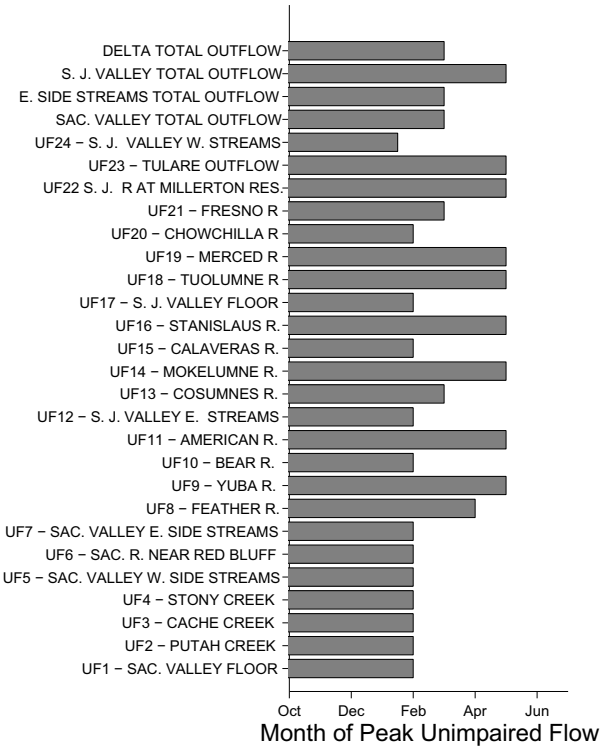

Figure 16. Month of peak discharge for the Sacramento and San Joaquin rivers and assorted tributaries, prior to development of on-stream reservoirs.

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).

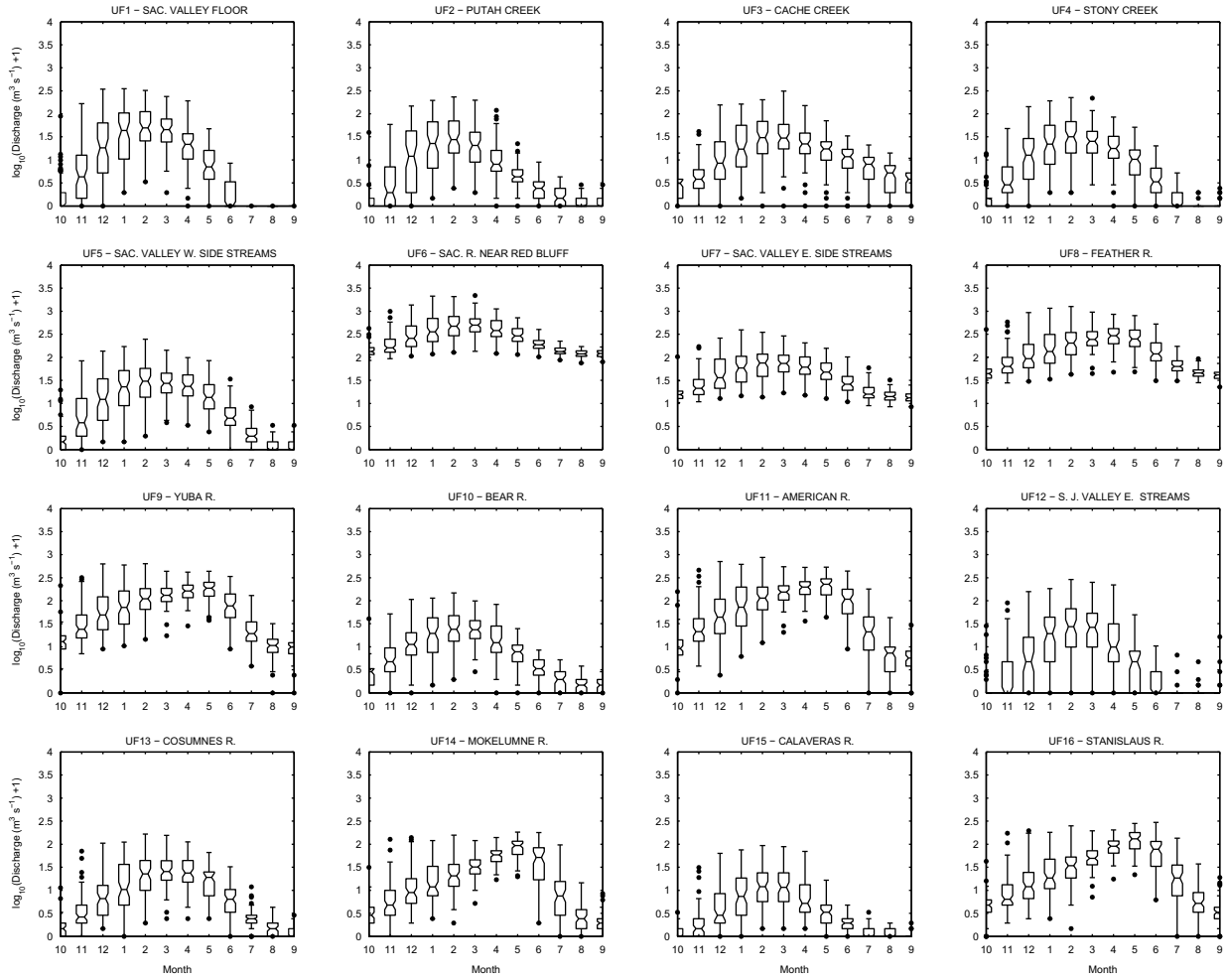

Figure 15. Estimated monthly discharge of the Sacramento and San Joaquin rivers and assorted tributaries, prior to development of on-stream reservoirs. Center of notch indicates median; notch represents standard error of median; box covers interquartile range; whiskers cover 1.5 $\times$ interquartile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

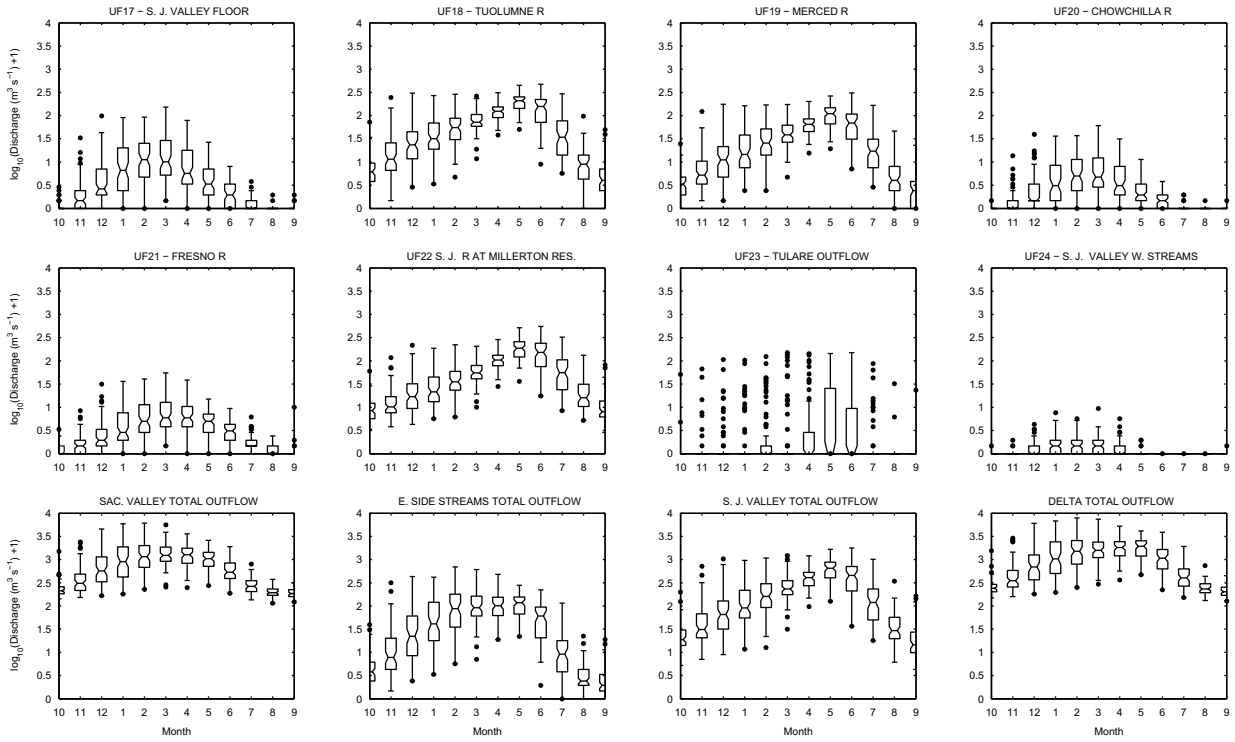

Figure 15. Continued. Estimated monthly discharge of the Sacramento and San Joaquin rivers and assorted tributaries, prior to development of on-stream reservoirs. Center of notch indicates median; notch represents standard error of median; box covers interquartile range; whiskers cover 1.5 $\times$ interquartile 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.

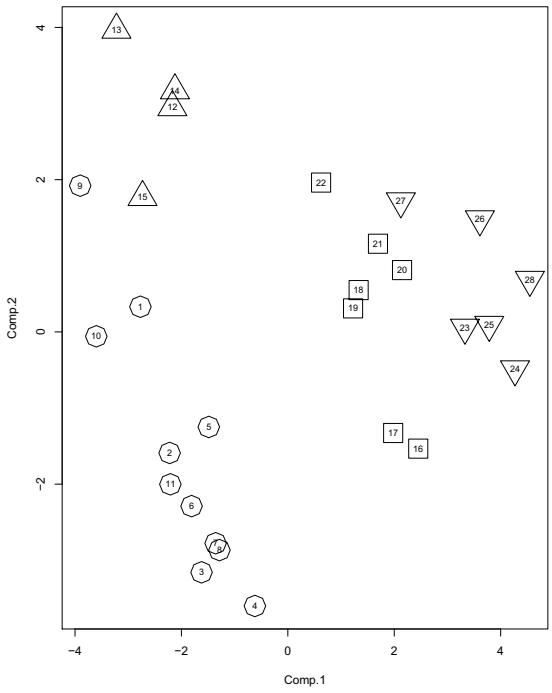

Figure 17. Principle components analysis of environmental attributes. Symbols denote regions: ◯–Southern Cascades; □–Northern Sierra; △– Coast range; ▽– Southern Sierra. Numbers indicate stream: 1–Upper Sacramento; 2–Lower Pit; 3–Fall; 4–Hat; 5–McCloud; 6–Battle; 7–Mill; 8–Deer; 9–Butte; 10–Big Chico; 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.

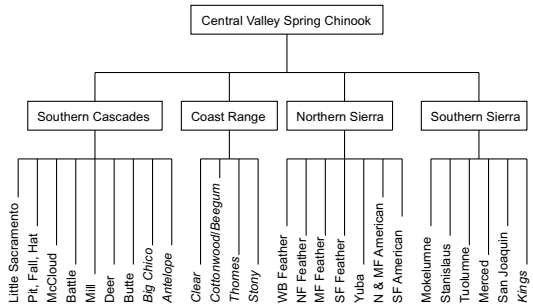

Figure 18. Historical structure of the Central Valley spring-run chinook salmon ESU. Independent populations are in regular type; dependent populations are in italics. In this figure, Mill and Deer creek spring-run chinook salmon populations are indicated as independent, although the TRT will also consider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

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

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

(≈ 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.

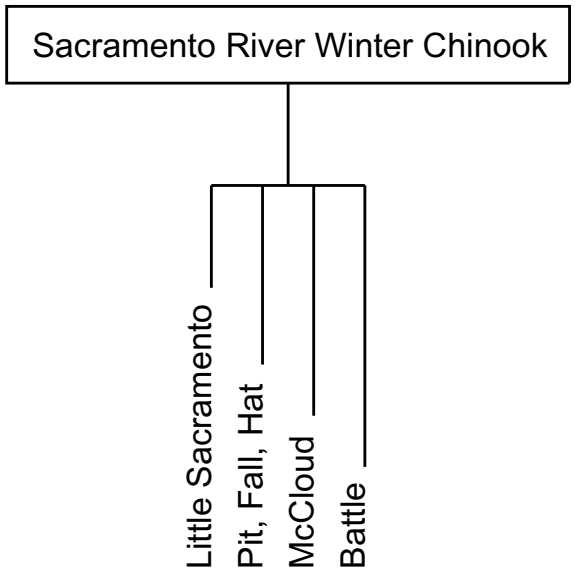

Figure 19. Historical structure of the Sacramento River winter-run chinook salmon ESU.

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).

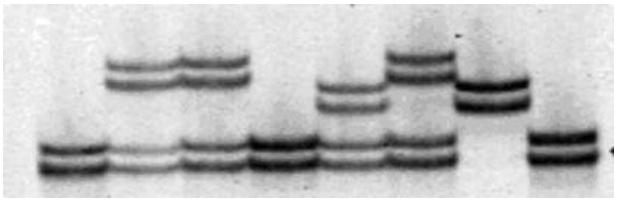

Figure 20. Microsatellite variation where each allele is portrayed by two bands, each representing one of the two strands of a DNA molecule. Vertical sets of bands are derived from single individuals. Individuals with two bands are homozygous for the same allele, receiving the same from both parents 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.

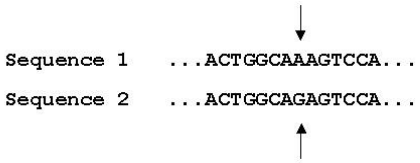

Figure 21. DNA sequence variation. The principle type of DNA variation is in the sequence of nucleotides found at some location (locus) in the genome. Mutations give rise to the replacement of one of the four nucleotides (guanine - G, adenine - A, cytosine - C, and thymine - T) with another. In this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

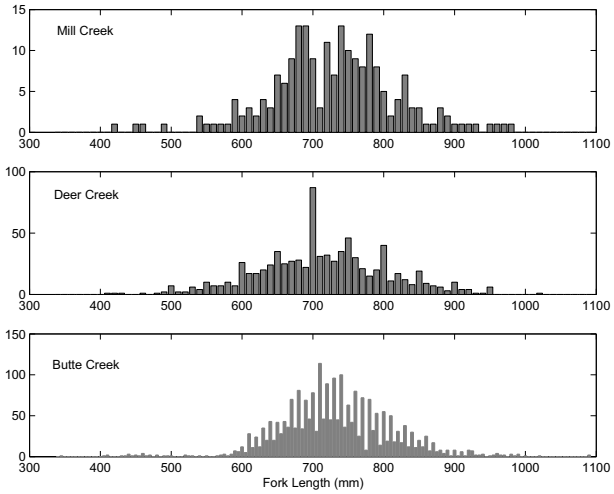

Figure 23. Size distribution of spawning adult spring-run chinook salmon in Mill, Deer and Butte creeks.

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).

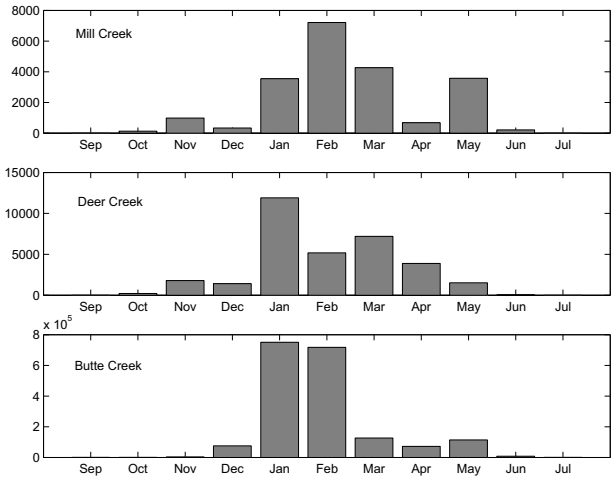

Figure 24. Mean monthly catches of juvenile spring-run chinook salmon in rotary screw traps in Mill, Deer and Butte creeks.

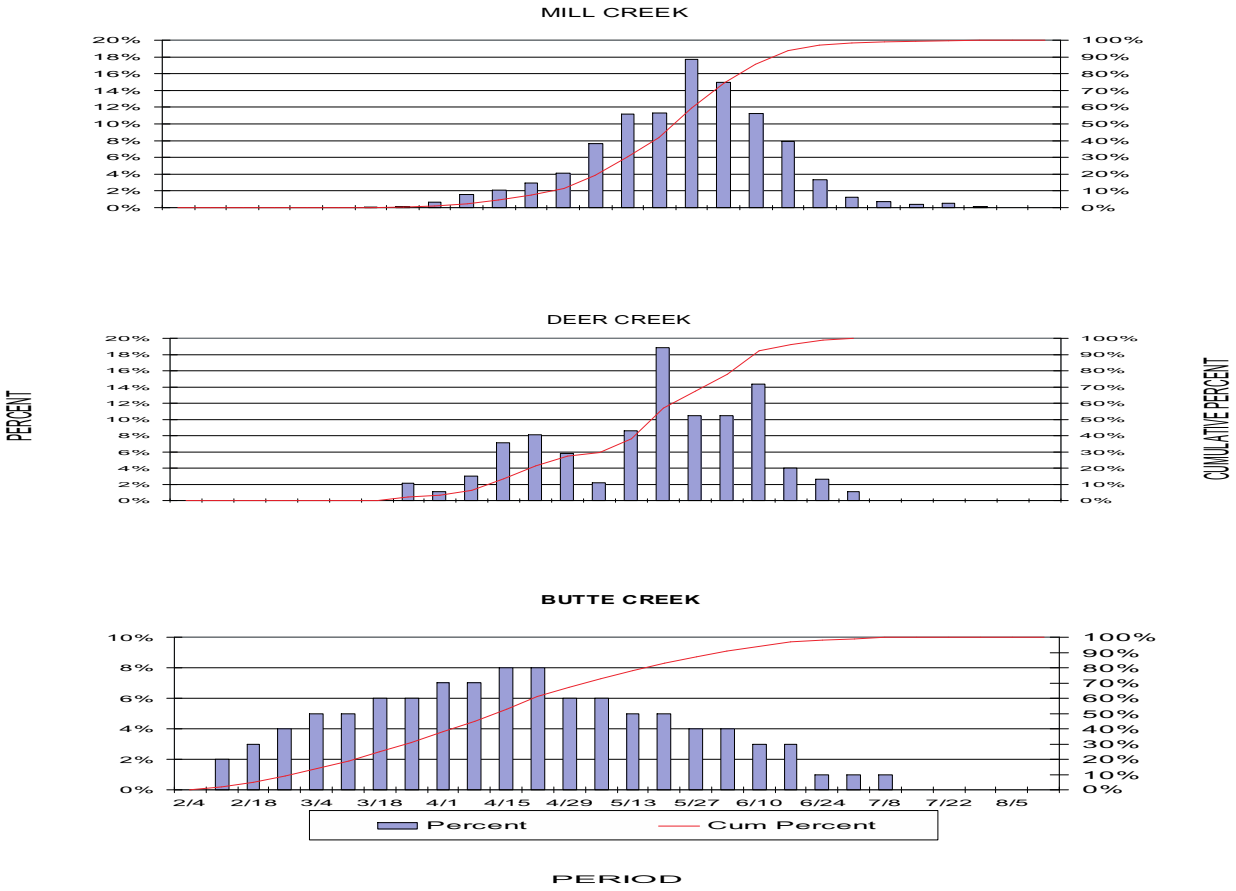

Figure 22. Weekly migration of spring-run chinook salmon into Mill, Deer and Butte creeks. Bars show the percentage of migrants migrating in that week; the line shows the cumulative percent migration.

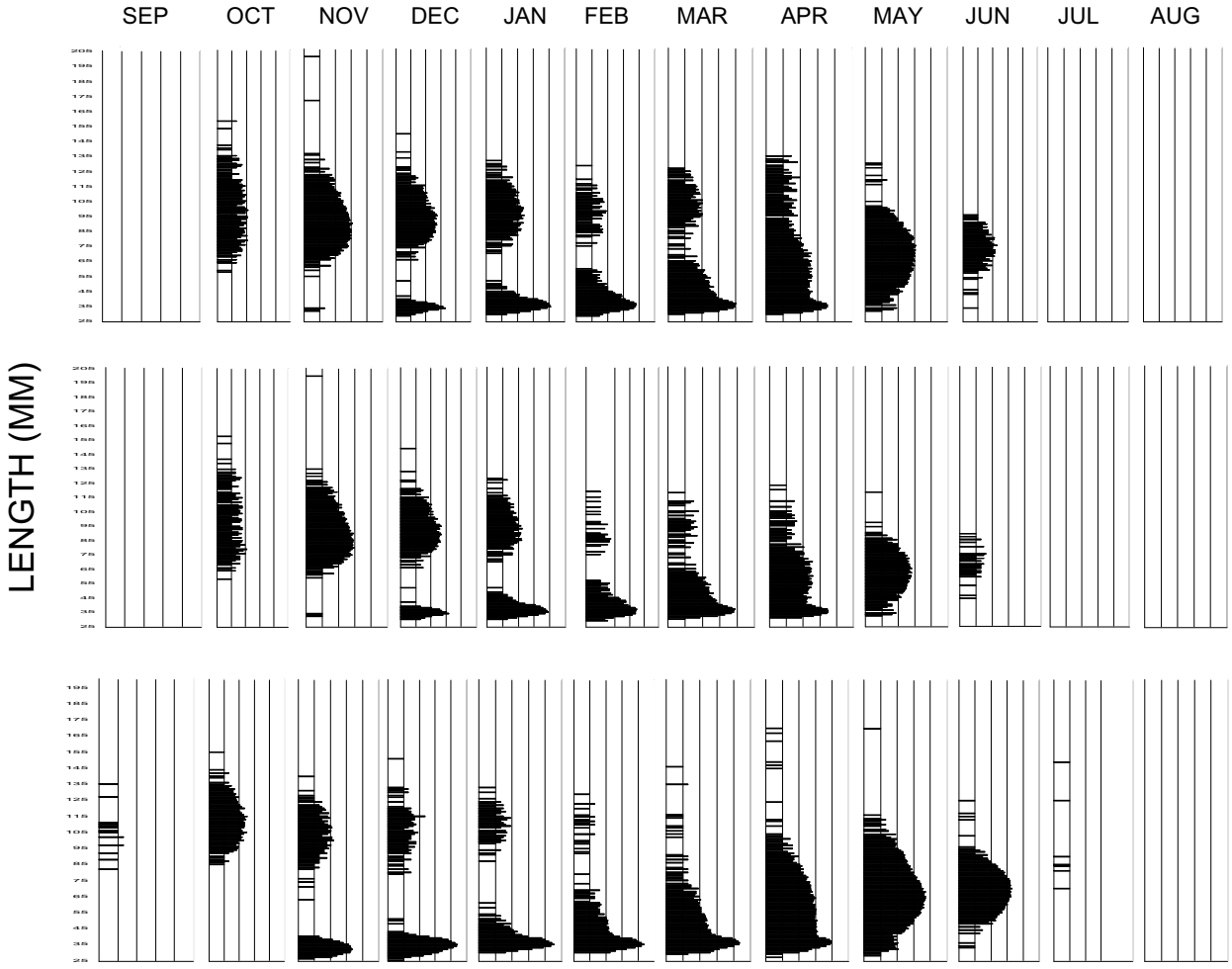

Figure 25. Size distribution of juvenile spring-run chinook salmon migrants in Mill (top), Deer (middle) and Butte (bottom) creeks. The x-axis is on the $\log_{10}$ scale. Data from C. Harvey-Arrison and T. McReynolds, CDFG.

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

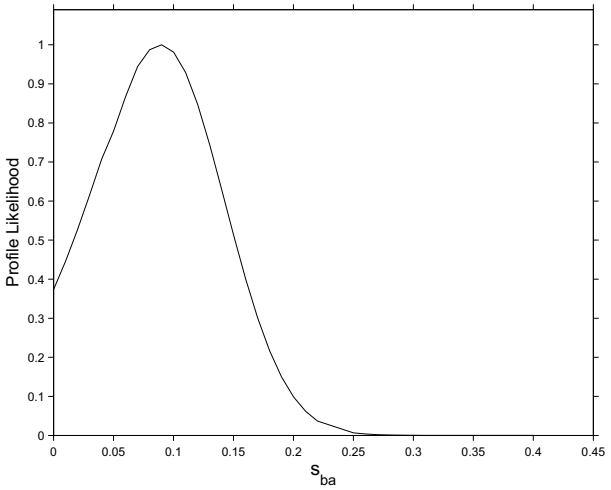

Figure 26. Profile likelihood of the migration parameter describing the fraction of fish moving from Deer to Mill Creek.

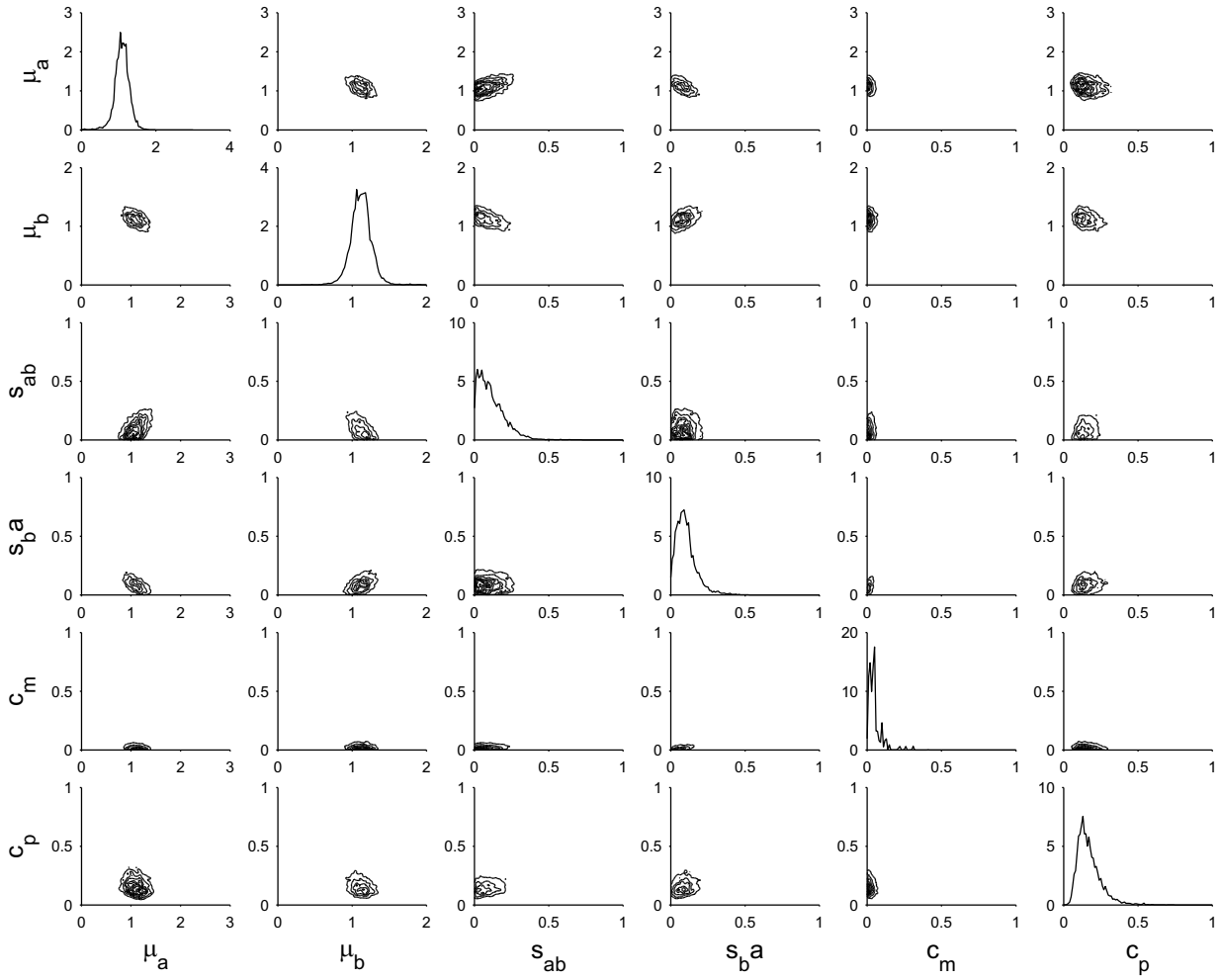

Figure 27. Marginal (on diagonal) and bivariate densities of parameter estimates.

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 ($> \pm 0.1$) 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. Soule, 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.

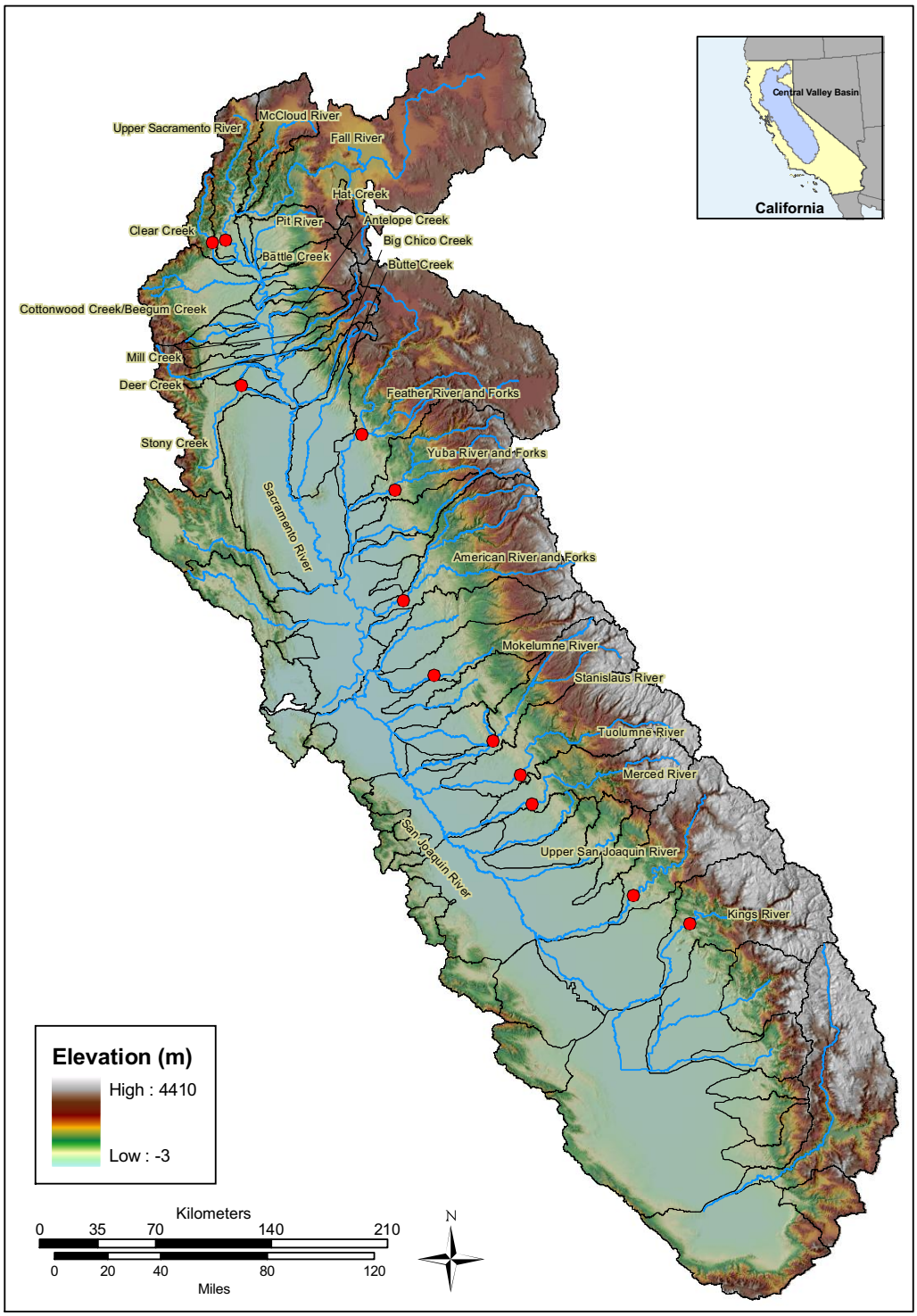

Plate 1. Map of the Central Valley basin, showing elevation, major rivers and streams (blue lines) and their associated watersheds (black lines), and major barriers to fish passage (red dots).

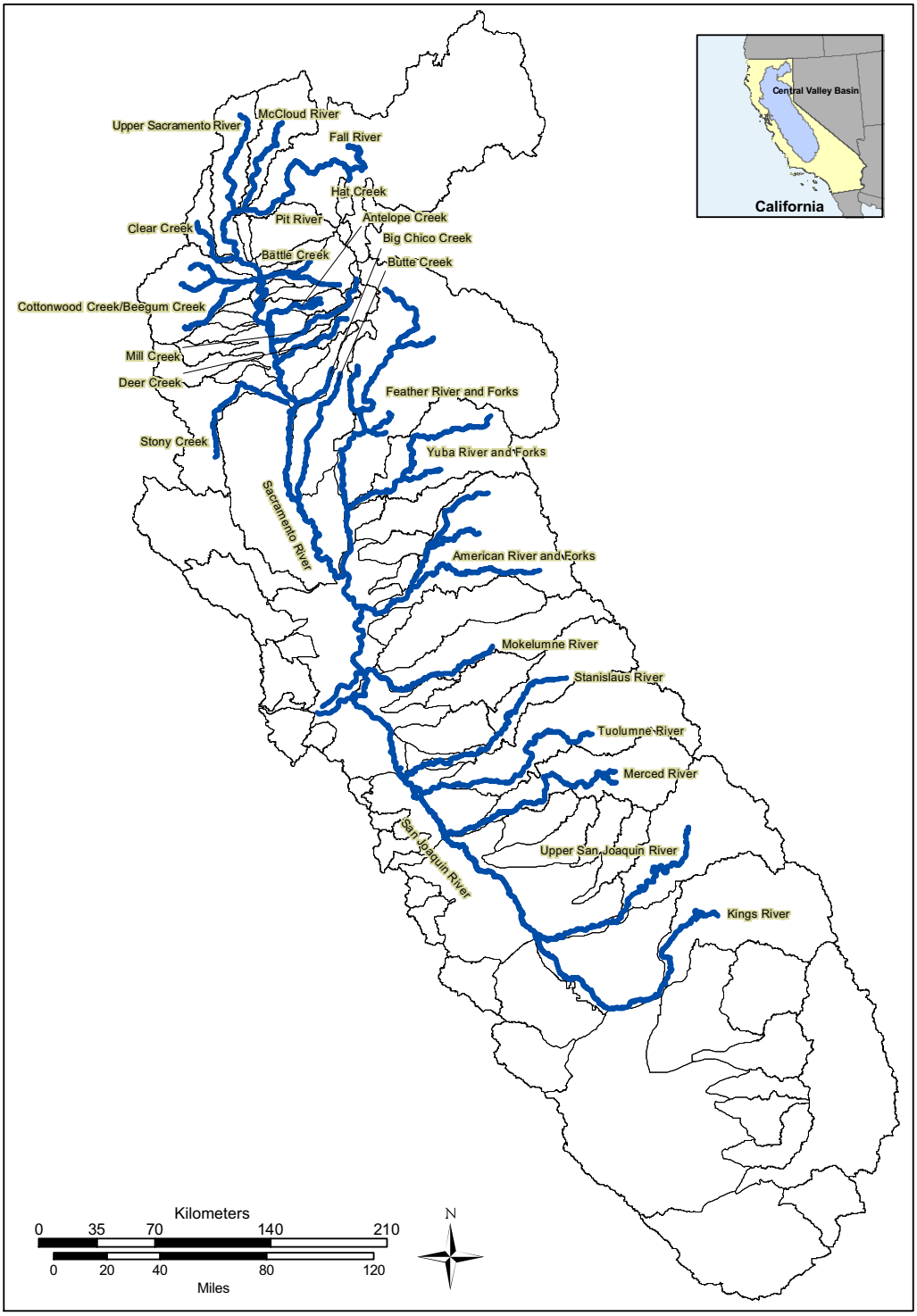

Plate 2. Historic distribution of spring-run chinook salmon in the Central Valley. Distribution information from Yoshiyama et al. (1996).

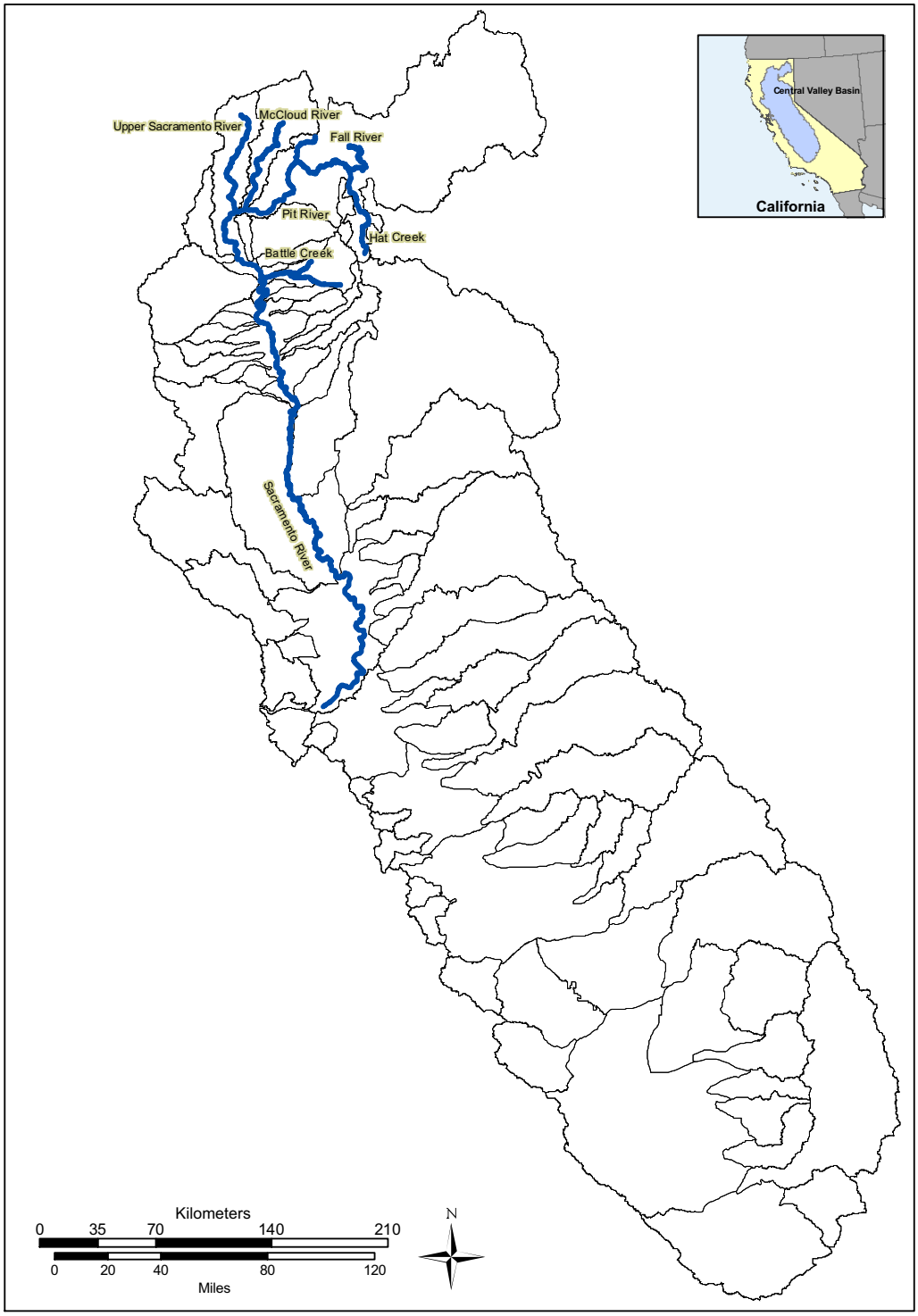

Plate 3. Historic distribution of winter-run chinook salmon in the Central Valley. Distribution information from Yoshiyama et al. (1996).

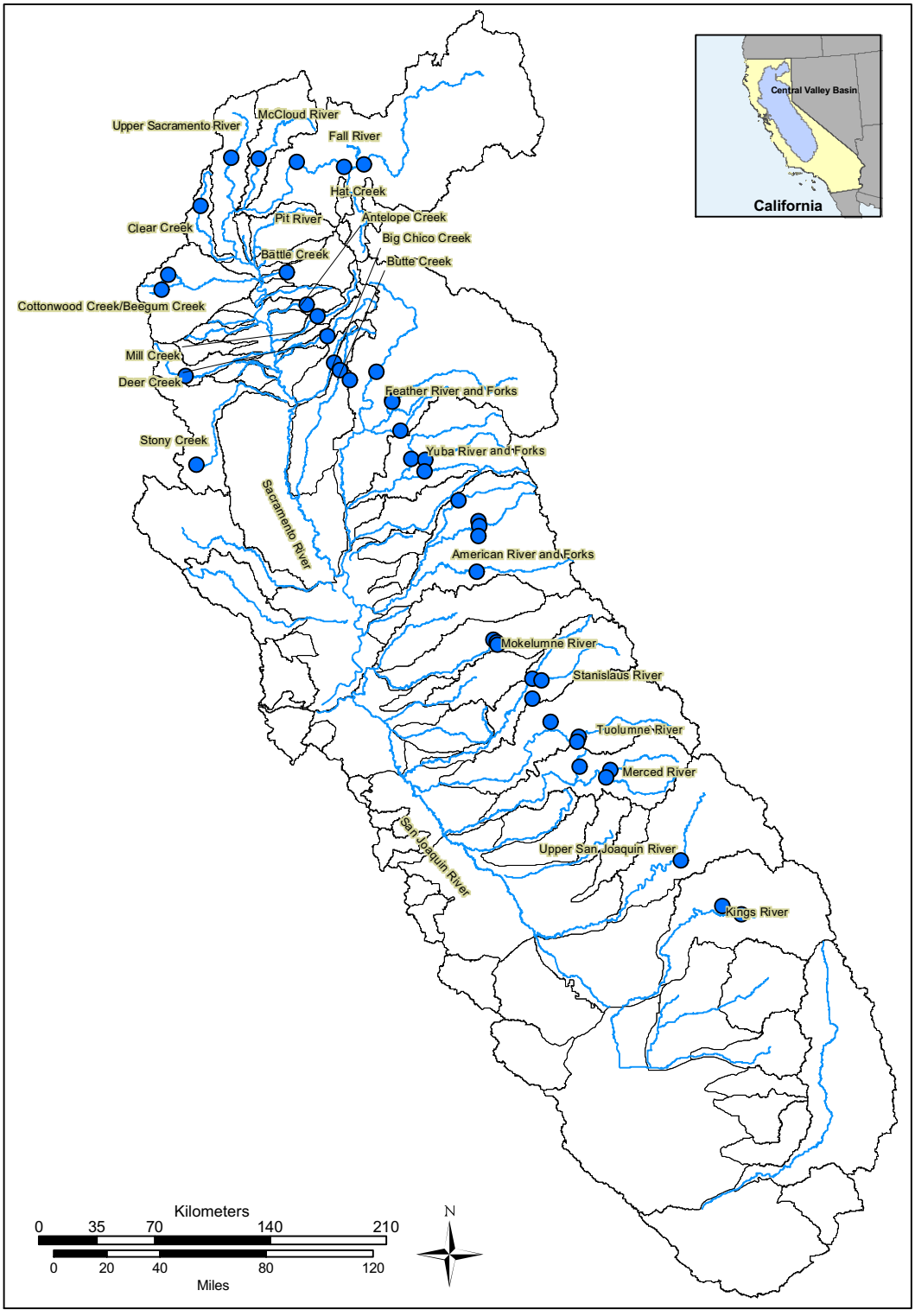

Plate 4. Points used to calculate distances among watersheds.

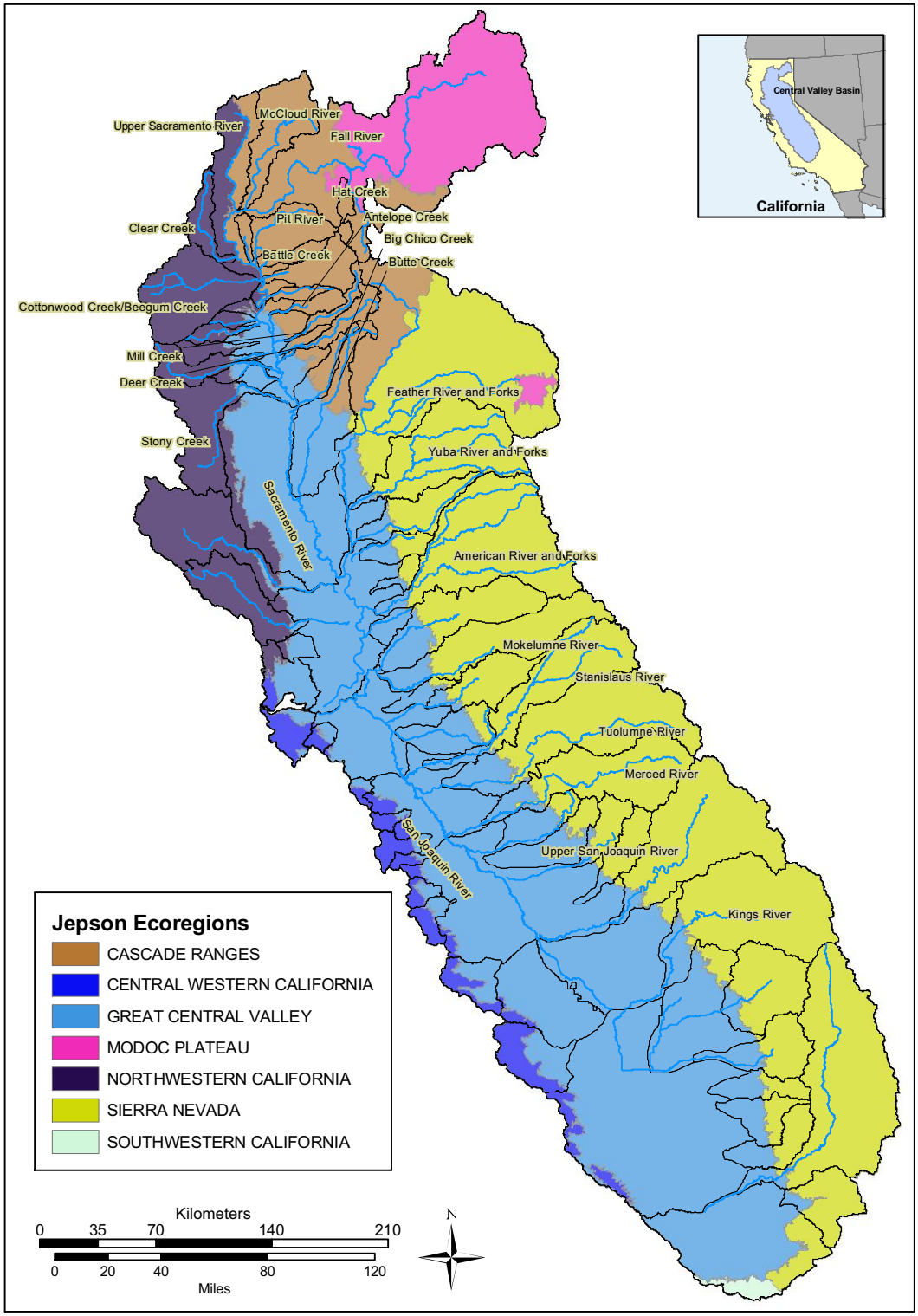

Plate 5. Floristic regions of the Central Valley basin.

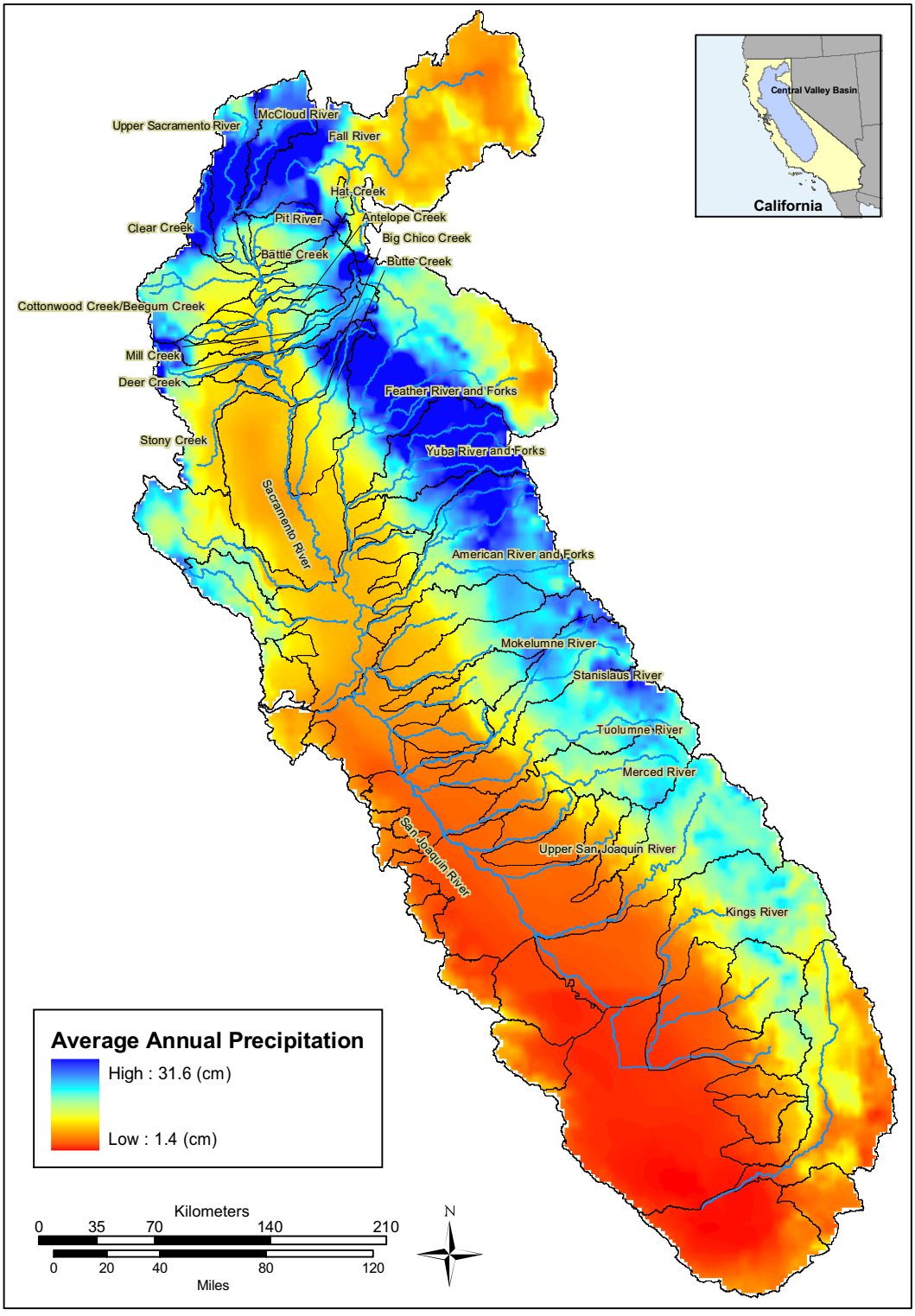

Plate 6. Average annual precipitation.

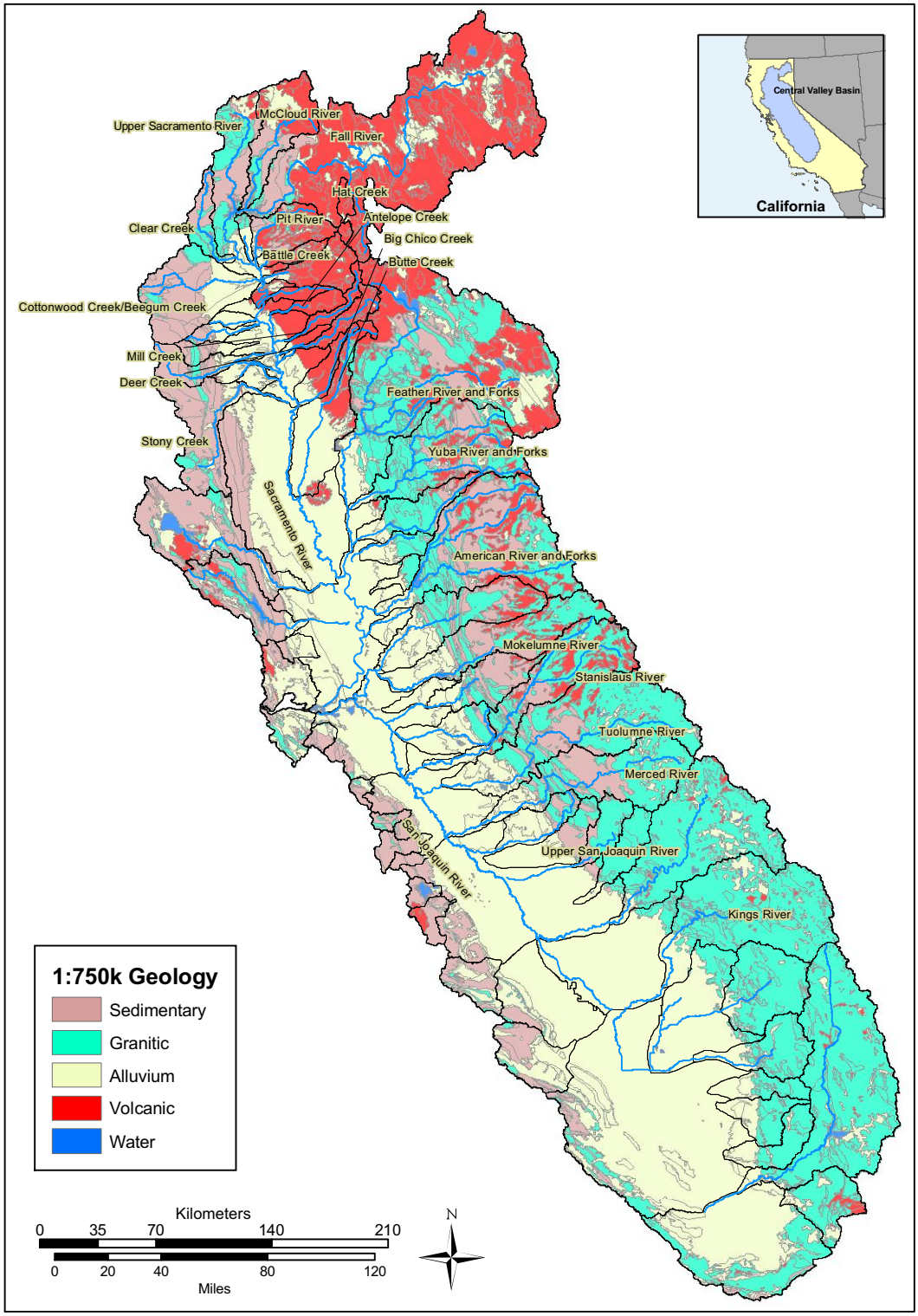

Plate 7. Geology of the Sacramento-San Joaquin basin.

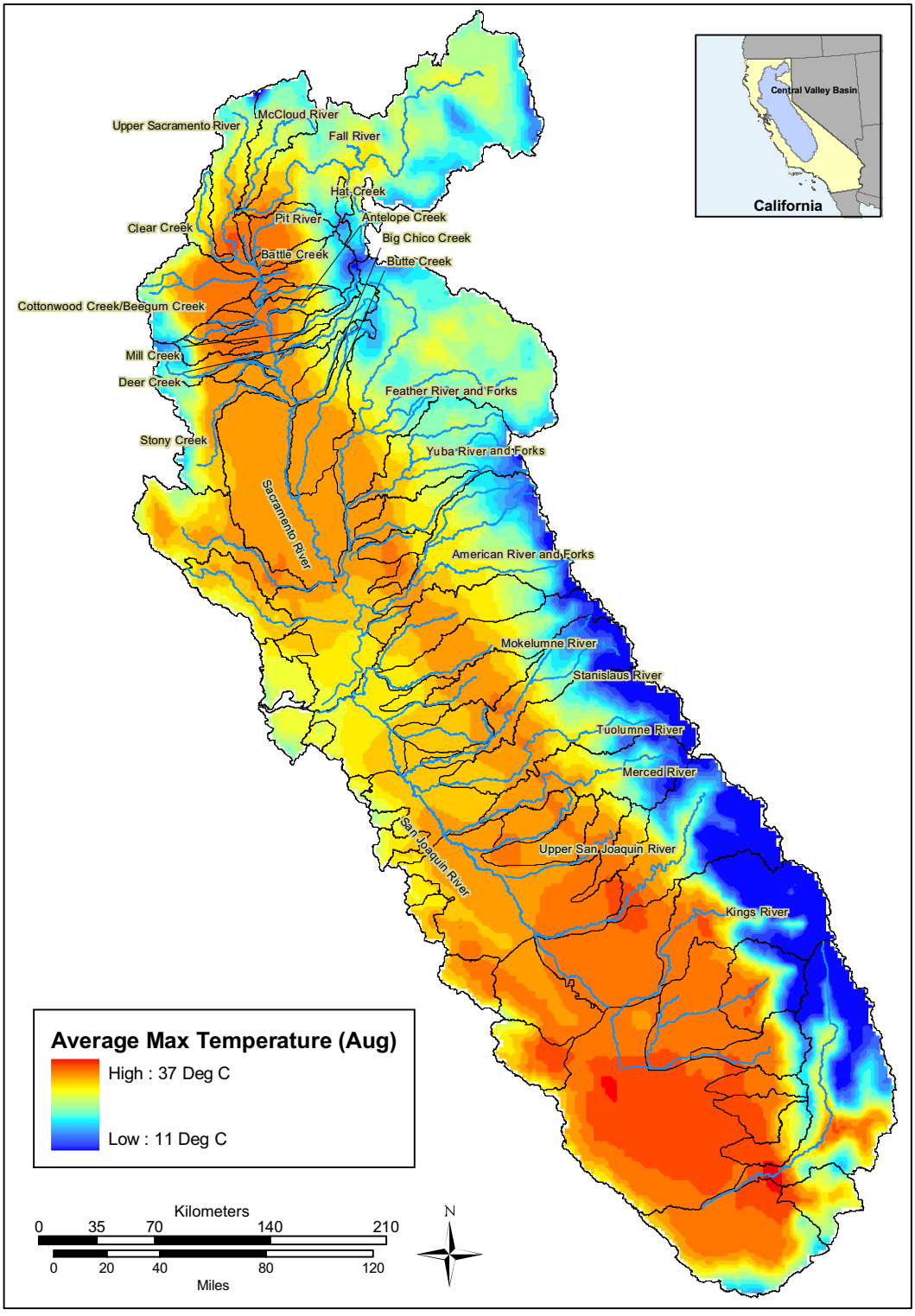

Plate 8. Average maximum August temperature.

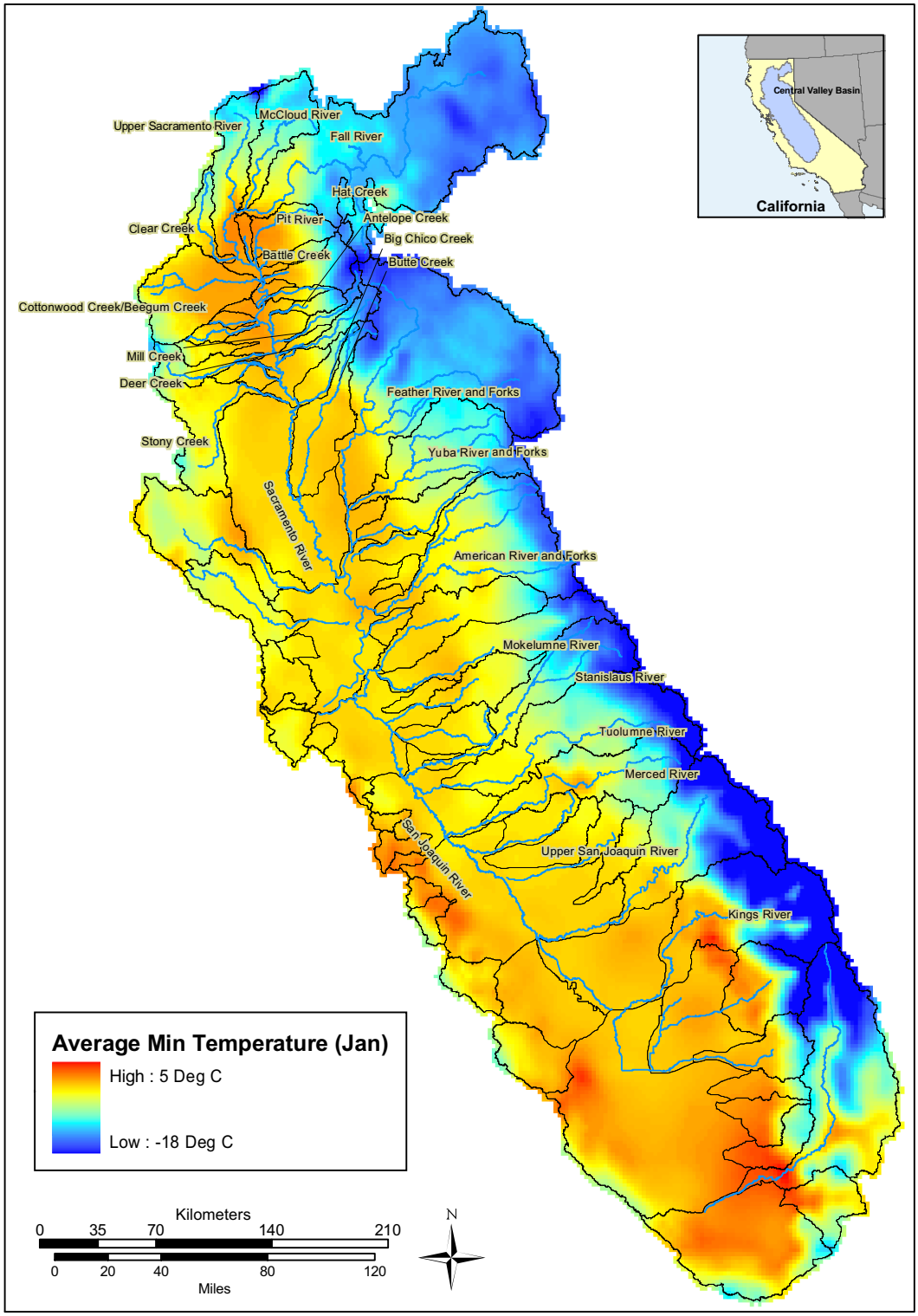

Plate 9. Average minimum January temperature.

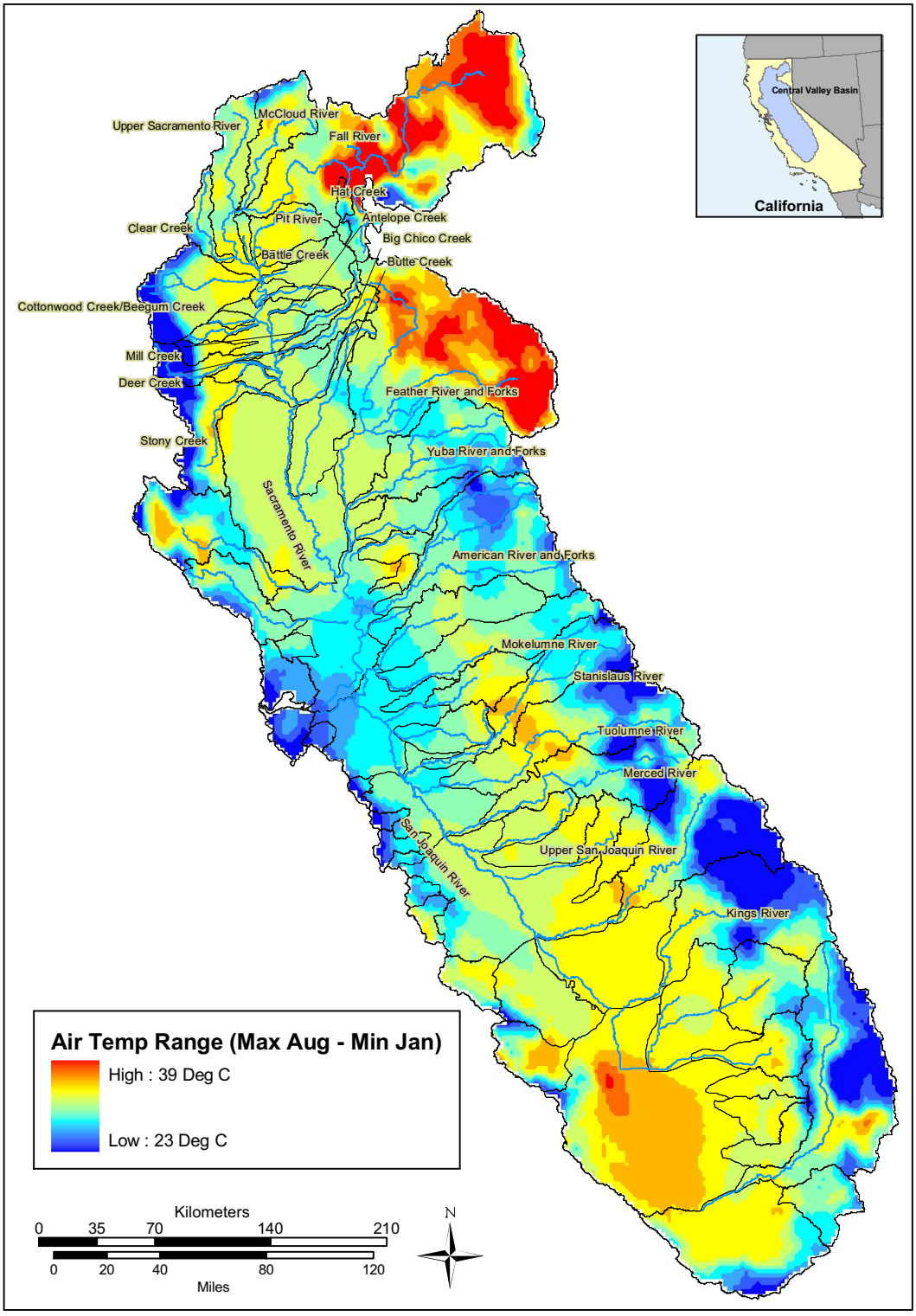

Plate 10. Temperature range (average maximum August temperature - average minimum temperature in January.