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Part 1. Introduction

The aim of the Federal Endangered Species Act (ESA) is to recover species that would otherwise go extinct, and to this end it requires the Federal government to prepare recovery plans. A recovery plan outlines a strategy for lowering extinction risk to an acceptable level, and has two components: a technical part and a policy part.

The technical part evaluates information on the species itself, and especially the changes in abundance, distribution, habitat condition, *etc.*, that would reduce the extinction risk. The policy part determines which of the risk-reducing changes are desirable and feasible, outlines the steps necessary to bring them about, and estimates their cost. For West Coast salmon and steelhead, these two parts are formally labeled "Phase I" technical recovery and "Phase II" implementation by the National Marine Fisheries Service.

This report concerns Phase I, and applies a formal evaluation framework developed elsewhere (McElhaney *et al.* 2000, Bjorkstedt *et al.* 2005) to the problem of delineating *Oncorhynchus mykiss* populations in the South-Central/Southern California Coast recovery domain. These populations inhabit the set of coastal river basins encompassed by the Pajaro basin in the north and the Tijuana basin in the south, hereafter referred to as the study area (Figure 1). According to a coast-wide status review of steelhead described by Busby *et al.* (1996), the study area is inhabited by two Evolutionarily Significant Units (ESUs) of *O. mykiss*.

The ESU concept comes from Waples (1991), who considered a group of *O. mykiss* to comprise an ESU if 1) they were substantially reproductively isolated from other conspecific population units, and 2) they represented an important component of the evolutionary legacy of the species. The distinct Mediterranean ecology of the study area, and its division into two faunal provinces on either side of Point Conception, led Busby *et al.* (1996) to designate two important components of the evolutionary legacy of the species, with geographic ranges as in Figure 1; some genetic considerations also played a role in this analysis.

Figure 1. The study area and the geographic ranges of its steelhead ESUs.

These units were named the South-Central California Coast Steelhead ESU and the Southern California Coast Steelhead ESU, and we follow this convention here.

The steelhead (anadromous) portion of each ESU is currently listed on the US Endangered Species List as a threatened or endangered Distinct Population Segment, or DPS (*Federal Register* 70: 67130 [2005] & 71: 834 [2006]). Anadromous fish are those that spend some part of their adult life in the ocean, in contrast to non-anadromous fish that spend their entire lifecycle in freshwater systems. Both forms occur in the study area. Formally, the steelhead DPS of *O. mykiss* includes only those individuals whose freshwater habitat occurs below impassible barriers, whether artificial or natural, and which exhibit an anadromous life-history. Operationally, distinguishing listed from non-listed *O. mykiss* can rely on features such as relative size, smolting behavior, feeding activity, length of migratory movement, and number of eggs produced by females, but cannot rely on reproductive isolation between the anadromous and non-anadromous forms (See *Federal Register* 71: 834 [2006]). Thus, listed anadromous forms and unlisted non-anadromous forms can co-exist in the same ESU or even the same population, and indeed there is evidence suggesting both kinds of co-existence (or polymorphism) are present in the

study area. This means that discussions of population delineation and distribution necessarily involve considering both forms of *O. mykiss* jointly in natural units of ecological organization (populations and ESUs).

The authors of this report are members of a Technical Recovery Team (TRT), convened to advise NMFS on technical aspects of recovery in the study area. This report has two goals: to describe the normal (reference) condition of each ESU; and to identify existing and potential populations of steelhead that could form the basis for recovery.

It should be noted at the outset, however, that these two goals are burdened with numerous uncertainties and judgment calls on the part of the authors. The uncertainty stems from several interacting factors:

1) The extremely large and heterogeneous planning area, comprising the south-west range limit for the species. Environmental heterogeneity appears to constrain the distribution of the species at a number of spatial scales, making the task of describing this distribution somewhat complex.

2) Most of the information about the species in the study area comes from anecdotal reports (descriptive in nature) or from studies conducted at restricted spatial scales (individual reaches, or at best, large sections of individual watersheds).

3) The task of delineating populations and characterizing recovery potential is largely reliant on quantitative data samples from across the planning domain. Since such information is unavailable, we are confined to the less satisfactory exercise of A) applying simplistic yet uniform methods over large spatial extents, and B) describing existing small-extent studies, and making uncertain inferences of their implications for the larger ESU. For the most part, these two approaches lack the level of quantitative description that is necessary for making concrete recommendations.

There is a natural tension between the simple broad-extent, coarse-resolution mode of analysis and the small-extent, high-resolution mode of analysis alluded to above. In describing both modes, we hope to provide a useful reference for recovery efforts, and to clarify the relative utility of future research on *O. mykiss* that might be conducted in the study area.

1.1. First Goal: Normal Condition as a Reference Point

Recovery is defined by the National Marine Fisheries Service as "the process by which listed species and their ecosystems are restored and their future is safeguarded to the point that protections under the ESA are no longer needed" (NMFS 2004). Such restoration first requires a description of the normal condition to which the species is to be restored. For ESU structure, normal condition is most conveniently described in terms of individual populations: where they are located, how resilient each one is to extinction, and so forth. In this context, "normal condition" can have at least two meanings, the simplest being the original population structure of the ESU prior to the arrival of non-native Americans. This concept has three problems in our case: 1) settlement-era accounts of steelhead are extremely sparse (Titus *et al.* 2003); 2) the abundance of steelhead during the settlement era may have been unusually high due to the preceding demise of Native Americans (a key predator) from small pox (see Keeley 2002b), and 3) the climate of southern California has been changing, getting wetter and warmer since the ending of the "Little Ice Age" in the 19th Century (Millar and Woolfenden 1999; Haston and Michaelsen 1997; Scuderi 1993). *O. mykiss* are probably especially vulnerable to climate change in the study area, as it contains their southern range limit. Presumably the species is near the limits of its tolerance for warm or dry conditions, and small changes in climate may well translate to large changes in potential steelhead distribution. This would cause the 19th Century to be a misleading reference point.

The other meaning of "normal condition" would be the hypothetical present-day state of each ESU if non-native Americans had had no significant impact on the fish. Though a hypothetical construct, this concept of "unimpaired population structure" is in many ways more useful for recovery because it can be studied using data collected from relatively unimpaired stream systems in the present climate[1]. Moreover it is directly relevant to

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[1] Unimpaired is a relative term, since the natural function of most and perhaps all streams in the study area has been affected to some degree by human immigrants

recovery under current climatic patterns. However, "unimpaired" should not be taken to mean "static," as unimpaired condition involves dynamical regimes that are characteristic of a given ecosystem (such as terrestrial fire regimes or marine ecosystem responses to decadal climate patterns (*e.g.* Mantua and Hare 2002).

Here, the overall focus will be on the unimpaired population structure rather than the original structure, since it is the most relevant reference point for recovery planning. However, due to ongoing climate change, the difference between unimpaired structure today and 50 yrs hence could be quite large—perhaps much greater than the difference between now and 200 yrs in the past.

In addition to unimpaired structure and original structure, there are two other useful reference points, current structure of the ESU, and ESU viability (Table 1). The level of recovery necessary to achieve ESU viability is not addressed in this report, but will be discussed at length elsewhere.

1.2. Second Goal: Identify Populations for Recovery Planning

In a scientific review focused on recovery planning for west coast salmonids, McElhany *et al.* (2000) concluded that independent viable populations are the basic components of a viable ESU. Independence and viability are defined thus:

"A viable salmonid population is an independent population of any Pacific salmonid that has a negligible risk of extinction due to threats from demographic variation (random or directional), local environmental variation, and genetic diversity changes (random or directional) over a 100-year time frame" (McElhany *et al.* 2000:2)

"The crux of the population definition used here is what is meant by 'independent.' An independent population is any collection of one or more local breeding units whose population dynamics or extinction risk over a 100-year time period is not substantially altered by exchanges of individuals with other populations." (McElhany *et al.* 2000:3)

Table 1. Reference points in ESU recovery.

Term	Definition
Original population structure	The population structure of the ESU at the arrival of permanent settlers of European descent (*c.* 1769 – 1850)
Unimpaired population structure	The hypothetical present-day structure of the ESU if non-native Americans had had no significant impact on the fish.
ESU viability	The hypothetical state(s) in which extinction risk of the ESU is negligible.
Current population structure	The current population structure of the ESU (*c.* 1970 – 2005).

To use these concepts, it is necessary to divide each ESU into individual populations and assess the independence and viability of each.

The reason for taking these steps is that certain populations may not be viable even in their original or unimpaired state. This could occur for example in small coastal basins that do not provide enough habitat to support a large, persistent steelhead run, and rely on periodic immigration for long-term presence. A possible example is the steelhead in Topanga Creek, which though common in the 1960s were not observed during the 1980s and most of the 1990s, but later reappeared near the end of the century (Dagit and Webb 2002). A reasonable interpretation of these data is that the local population went extinct, but later was re-established by steelhead from elsewhere. Topanga Creek is a small stream system, presumably with a small carrying capacity for steelhead. In general, small populations are expected to turnover in the manner of Topanga Creek steelhead, so the data are not surprising. However, one would not want to base a recovery plan on populations that are, even if completely recovered, so small or so unstable that they are vulnerable to local extinction. Thus, the second goal of this re-

port is to identify populations that have the inherent potential to be well-buffered from extinction if restored to their unimpaired state. Consequently, our primary tasks in this report are:

1) Identify all the original steelhead populations in the study area, and determine which ones are extant;
2) Delineate the potential unimpaired geographic extent of each population;
3) Estimate the potential viability of each population in its (hypothetical) unimpaired state; and
4) Assess the potential demographic independence of each population in its unimpaired state.

1.3. Life-History Plasticity

Before going further, it may be informative to review what is known about life-history plasticity of the steelhead in California, as it is somewhat complex and intricate but very key to understanding the rest of the document.

These fish are flexible in their approach to life—they can complete their life cycle completely in freshwater, or they can migrate to the ocean after 1 – 3 yrs, and spend 2 – 3 years in the marine environment before returning to spawn. The fish pursuing the former life history trajectory is commonly called a rainbow trout in our study area, and the latter is called a steelhead, but it has become clear in recent years that this terminology is misleading in its simplicity.

For one thing, rainbow trout sometimes have steelhead as progeny, and vice versa. These facts have been demonstrated by studying the otolith microchemistry of *O. mykiss*. Otoliths are small ear bones that lay down growth increments that are the ichthyological equivalents to tree rings. Moreover, the isotopic composition of the increments depends on whether the fish inhabited fresh or salt water at the time the increment was laid down. As a result, mass-spectrometry can be used to reconstruct the isotopic timeline, and therefore the freshwater-marine timeline, of a given fish's life history. The isotopic composition of the otolith primordium is determined by the habitat of the mother, and this allows a comparison of parent-offspring life histories. Zimmerman and Reeves (2000) used techniques such as this to uncover occasional life-history "switching" in certain *O. mykiss* populations in Oregon. The steelhead in our study area have not yet been examined in this way, but numerous anecdotes indicate that life-history switching is probably widespread. We do not know what cues it.

For another thing, there is a third group of life history strategies, that we here call "lagoon-anadromous." Bond (2006), working at a study site in northern Santa Cruz County, has recently shown that each summer a fraction of juvenile steelhead over-summered in the estuary of their natal creek. Like elsewhere in California, this estuary was cut off from the ocean during the summer by the formation of a sandbar spit, and thus is more properly referred to as a seasonal lagoon. Bond (2006) showed unequivocally that juvenile steelhead do very well if they over-summer in the lagoon—many grow fast enough to migrate to the ocean their first year, and most enter the ocean at a larger size than fish coming from the freshwater portion of the stream system. Large size enhances survival in the ocean, and thus the lagoon-reared fish tend to be disproportionately represented in the adult spawning population (Bond 2006).

Within each of the three basic life-history groups (freshwater resident, lagoon-anadromous and fluvial-anadromous), there is additional variation: Juveniles may spend 1 – 3 yrs in freshwater, 1 – 2 yrs in the lagoons, and adult steelhead may spend from 2 – 3 yrs in the ocean before returning to spawn. Finally, unlike other Pacific salmon, some adults survive their first spawning and return to the ocean to wait for next year. A graphic overview of this life-history diversity, along with some of the specialized terminology, is given in Figure 2.

On top of all this, there are examples of finer-scale habitat switching, such as multiple movements between lagoons and freshwater in the course of a single summer; and also so-called "ad-fluvial" populations that inhabit reservoirs but spawn in tributary creeks. *O. mykiss* are flexible in their approach to life.
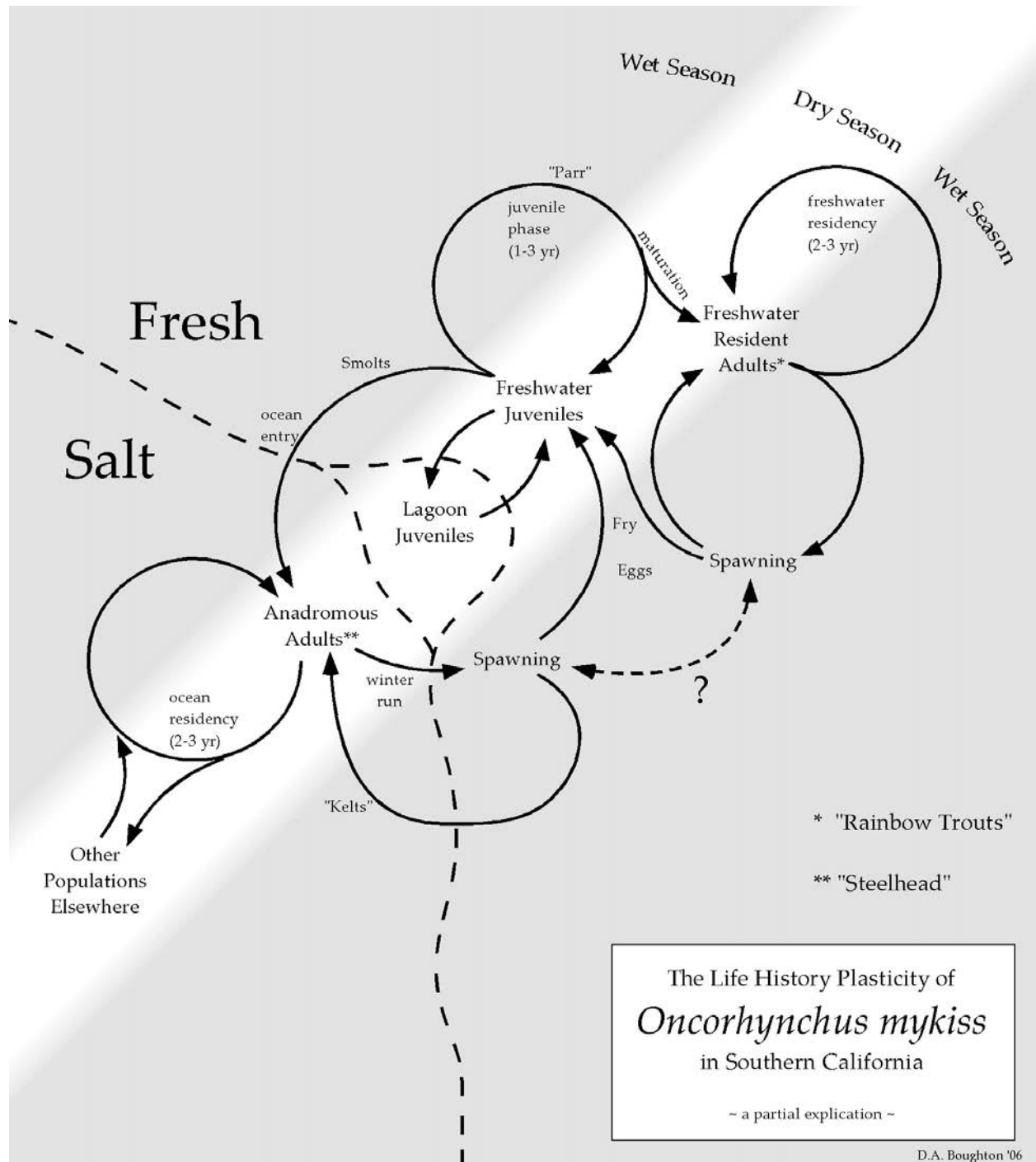
Figure 2. A synopsis of life-history trajectories believed to occur in the study area. Relative frequency of each trajectory is not known.

1.4. Available Information

We briefly review the available data that bear on the distribution, abundance, and potential habitat of steelhead in the study area, because these data are the ultimate basis for identifying and characterizing populations.

Usefulness of the available data are based on relevance, credibility, and geographic consistency. A discussion of relevance we defer to the next section. Credibility of information is considered relatively high when information has been published and peer-reviewed. Much other information is available as reports that have not necessarily been through a formal peer-review process or even made publicly available. Due to paucity of information we found it useful to cite many such reports, but were faced with the task of judging their credibility. To do so, we adapted recommendations from Walton (1997), a practical philosophical treatise on judging the validity of expert opinions (for more detail, see §10.4, p. 104).

The geographic consistency of a given source of information is what allows the broad-extent, coarse-resolution analyses that we alluded to in the introduction.

1.4.1. Data on Distribution and Abundance

Data on run size—the number of adult steelhead spawning in a particular stream during a particular winter—would be extremely relevant but are almost non-existent for the study area (as well as most other parts of California). The notable exception is the Carmel River, for which run size has been monitored since 1964 at the fish ladder on San Clemente Dam (with a gap from 1978 – 1987; see Snider 1983, Williams 1983, and Monterey Peninsula Water Management District website[2]). The count is incomplete because some proportion spawns downstream of the dam; expert opinion puts the proportion somewhere in the range of 10% - 50%.

There are also accounts of "typical" historical run size for many of the domain's largest basins. The accounts are generally based on expert opinion rather than data (Boughton 2005), and there is

[2] http://www.mpwmd.dst.ca.us

little agreement among today's experts as to their accuracy. For the smaller basins, and the basins south of Los Angeles, there are usually no credible estimates of historical run size at all.

A number of single-basin studies of fish distribution have been made in recent years, including Smith's (2002) summary of the upper Pajaro River system; Alley's (2001) monitoring on Santa Rosa Creek in San Luis Obispo County; Payne and Associates' (2001, 2004) survey around Morro Bay and San Luis Obispo Creek; the informative survey of the Salinas basin by Casagrande *et al.* (2003); the thesis of Douglas (1995) on O. mykiss in the Santa Ynez basin; Kelley's (2004) assessment of the Santa Clara basin; the assessment by Stoecker and the CCP (2002) on the Santa Barbara Coast and Stoecker and Stoecker (2003) on the Sisquoc River; Allen's (2004) assessment of the Ventura River basin; a study of steelhead habitat in the Santa Monica Mountains (California Trout 2005); Kelley and Stoecker's (2005) assessment of recovery opportunities in the Santa Clara River, and Spina and Johnson's (1999) examination of Solstice Creek in the Santa Monica Mountains (for more information, refer to the descriptive summary starting on page 11). Though these types of studies provide insight into the status of particular basins, they do not cover all steelhead-bearing watersheds and are thus not definitive. Also, since each has a unique set of goals and study design, they are not always comparable.

A simple but useful type of information is occurrence data, also called "presence-absence" data. Occurrence data are sparse for pre-history; the authoritative reference is Gobalet *et al.* (2004), who used archaeological records to establish the occurrence of *Oncorhynchus mykiss* in 25 coastal localities between San Francisco and Mexico. The southern-most was Los Peñasquitos Creek in San Diego County, confirming that the species occurred at least this far south prior to European settlement.

Titus *et al.* (2003) have made a concerted effort to track down occurrence data in the historical record. Most of this record consists of field notes from CDFG biologists active in the early 20th Century. Also, Sleeper (2002) and Franklin (1999) gathered oral accounts from elderly citizens of

Orange/San Diego Counties and the upper Salinas Valley, respectively. These three manuscripts summarize eyewitness accounts of steelhead, mostly from the early-to-mid 20th Century, by which time much environmental change had occurred resulting from the decline of the large Native American population and the arrival of Europeans in the 18th and 19th centuries (See §10.2 on p. 98). Even so, the accounts provide much credible information about the geographic distribution of steelhead at the resolution of named creeks. Franklin (1999) and Sleeper (2002) had an emphasis on observations of adults; Titus *et al.* (2003) tended to emphasize juveniles. Recently, Kelley and Stoecker (2005) provided a table summary of early steelhead reports within the Santa Clara River basin.

For the immediate past, there are numerous sources of occurrence data. The basin-scale studies mentioned above have numerous data, assignable to particular reaches on particular dates. Boughton *et al.* (2005) made an assessment of occurrence across the entire domain; reports such as those by Payne and Associates (2001, 2004) contain useful accounts; and occurrence data are also preserved in the research collections of the California Academy of Science and the Los Angeles County Museum. Many of the occurrences specify latitude and longitude; or give detailed locality descriptions. These data, though collected rather haphazardly through the years, appear to be the best fish data we have in terms of overall credibility, geographic extent, and geographic resolution.

1.4.2. Genetic Data

Since the late 1980's, a number of studies have been conducted to elucidate the genetic structure of steelhead populations in the study area. Early studies used electrophoretically detectable protein differences (allozymes). More recently, studies have employed molecular genetic analyses, assaying variation in mitochondrial DNA (mtDNA) sequence, and variation in tandem-repeat copy number of microsatellite loci.

Berg and Gall (1988) surveyed 24 polymorphic allozyme loci from populations throughout California, including a small number of populations

from the study area. They discovered considerable variability among California populations, but did not discern a clear geographic pattern to the variation.

Busby *et al.* (1996) report a large-scale study of 51 allozyme loci in 113 populations, including 22 from California, four of which were specifically from the study area. A high level of genetic variability was found in the California coastal populations. The most remarkable feature of the data was a cline in frequency of the "70" allele at the fructose–biphosphate aldolase-3 (FBALD-3) locus. The allele occurred either rarely, or not at all, in steelhead samples from coastal Oregon and the Klamath Mountains province, but its frequency in the samples increased north to south down the California coast, and was the only allele present in the southernmost sample at Gaviota Creek. Busby *et al.*(1996) noted that finding an allozyme allele fixed in some populations, but entirely absent in others, is unprecedented in salmon, except when comparing populations at the extreme ends of their ranges.

Over all loci, however, there was not a clear pattern of population affiliation among the populations south of the Eel River. For example, a multidimensional scaling plot showed that the two southernmost populations in the study (Arroyo Hondo and Gaviota Creek) were not closely related to each other even though they are located near one another and are divergent from most other California populations. This was attributed to four possibilities: 1) the extreme and variable habitat conditions of southern California promote local adaptation, and hence isolation, between southern steelhead populations, 2) increased reliance on freshwater residency and maturation in the south leads to increased isolation between populations, 3) small population size allows genetic drift–the change of allele frequencies due to the random nature of genetic inheritance–to proceed more rapidly in the southern populations, and 4) haphazard sampling (*i.e.* non-random, non-systematic sampling of fish in space and time).

In the 1990s, Nielsen began a series of investigations into the molecular genetic diversity and biogeography of steelhead in our study area. Nielsen *et al.* (1994) assayed genetic variation in

mtDNA and a single microsatellite locus in 468 coastal *O. mykiss* sampled from 31 populations throughout California. Allele frequencies differed enough between populations to reject the hypothesis that steelhead throughout southern California are freely interbreeding. Nielsen *et al.* (1994) offered two explanations for this: 1) genetic drift has caused populations in southern California to differ from one another and from the rest of the California populations, or 2) the southern steelhead are descended from an ancient lineage that survived the Pleistocene in a refugium in the Gulf of California. The authors noted that the data were insufficient to reject either explanation, but predicted that if explanation 2 were true, then a high degree of genetic diversity should be observed in our study area.

Nielsen *et al.* (1997) compared genetic diversity in mtDNA and three microsatellite loci in *O. mykiss* from five habitats with varying degrees of hatchery influence and accessibility to the ocean. Samples were drawn from streams with and without access to the ocean, reservoirs, and hatcheries, and from sea-run adults and outmigrating smolts (the anadromous group). Based on the presence of rare haplotypes, mtDNA diversity was found to be highest among the anadromous fish (however, this result may be an artifact of the small number of anadromous fish sampled), and lowest among the hatchery trout. A similar pattern was observed at the three microsatellite loci.

Additionally, certain "uniquely southern" haplotypes absent in rainbow trout hatchery strains occurred at moderate frequency in rainbow trout from freshwater habitats–both with and without ocean access–throughout the study. This suggested that some rainbow trout populations in southern California, despite years of stocking with hatchery strains, still possess genetic heritage from wild southern steelhead. It was pointed out, however, that rainbow trout from streams with open access to the ocean were more closely related to the anadromous fish than were fish from closed habitats or reservoirs, suggesting that trout that still have access to the ocean may retain a greater degree of southern steelhead heritage. While these are interesting suggestions, the authors emphasized that studying direct introgression between

hatchery fish and remnant southern steelhead populations is difficult because of their shared evolutionary history, and, hence, genetic similarity between coastal steelhead and some hatchery populations.

Nielsen *et al.* (1998) documented D-loop variation in mtDNA from 5 species of *Oncorhynchus* and reported that coastal *O. mykiss* carried the highest haplotype diversity (number of haplotypes) found in the study. However, this could be an artifact of sample size: their sample sizes were largest for coastal steelhead and no attempt was made to account for sample size in the number of haplotypes observed. They also found that southern steelhead and a trout from Mexico comprised the most genetically separated *O. mykiss* populations. However, this claim was based on a single genetic locus (the mtDNA) and had low statistical support. As the authors noted, "population differentiation based on putatively neutral genetic variation holds only speculative value in drawing evolutionary inference at the fine scale of intraspecific or subspecific analyses."

In Nielsen (1999), 11 microsatellites were typed from a small number of anadromous fish collected over 8 years from southeast Alaska to Malibu Creek. Several alleles were recorded in northern and southern California populations that were not previously reported in populations of steelhead in Washington. In fact, at nine of the 11 loci, alleles were observed in California that were outside the size range of alleles observed in Puget Sound.

Nielsen (1999) deemed it unlikely that wider allele size ranges would occur in California if steelhead survived the late Pleistocene in a single northern refugium, and then colonized rivers to the south in California, Thus, she argued that "we are left with one alternative to explain the unique genetic diversity observed...the vicariance model of genetic variation," and that "Perhaps some of the genetic diversity in southern steelhead represents lineage effects from populations that evolved from a Gulf of California refugium, rather than reflecting particular processes in a marginal population with common ancestry from a Beringia refugium" (p. 456). This is a compelling hypothesis, and accords somewhat with Behnke's (1992)

view that "coastal rainbow trout diverged from the redband line...possibly during the late Pleistocene...and perhaps in California" (p. 20), but it remains unknown whether the data presented in Nielsen (1999) are sufficient to reject the possibility that southern steelhead may, in fact, have descended with northern populations from a common refugium. There is not a standard statistical test for such a proposition.

Several other analyses in Nielsen (1999) gave a mixed picture of the distinctness of southern steelhead: first, a neighbor-joining tree based on delta-mu, microsatellite distances supported separation of southern steelhead from the rest of the populations in the study with the low (not statistically significant) bootstrap value of 57%. The weak statistical support may be due to the small sample sizes. And second, evidence was presented of isolation by distance, but the signal was diminished with the southern steelhead included in the data, possibly because the southern steelhead are not in genetic equilibrium due to a recent genetic bottleneck.

1.4.3. Landscape Data

Environmental science now has available to it a vast array of mapped information, deployed as computerized Geographic Information Systems (GIS). This kind of data is usually produced by some combination of remote sensing, field studies, and geographic modeling. A classic example of a such information is the Digital Elevation Model (DEM), which represents the Earth's surface as a grid of 30m x 30m cells (sometimes 10m x 10m), and specifies the mean elevation of each cell. Older DEMs are basically digitized versions of USGS topographic maps; new DEMs are generated from NASA's Shuttle Topography Radar Mission (STRM).

A DEM is the basis for many derivative datasets that are relevant to steelhead recovery. For example, an algorithm can use the topographic information to identify stream networks and automatically map them. This is useful for high-order streams that are not well portrayed in the original USGS maps, although the algorithm does not perform particularly well in flat areas, such as alluvial valleys. Two other applications useful for steelhead are the use of DEMs to delineate catchment basins; and to estimate valley width. The latter is the lateral area around a stream channel in which the channel can migrate over time due to erosion and depositional processes.

There are numerous other sorts of geoenvironmental data available, describing land cover, geology, *etc*. Those geoenvironmental datasets that are relevant to steelhead ecology are useful, because they are generally credible and have broad geographic extent. However, in many cases the resolution of the data can be limiting.

1.4.4. Climate Data

Daly *et al.* (1994) describe a model for mapping climate data in a GIS framework. In particular, based on a mechanistic understanding of how broad-scale climate patterns interact with topography, they developed a model that allowed them to use data from the US network of weather stations (precipitation, temperature) to create complete maps of certain climate norms, such as mean annual temperature, mean annual precipitation, mean monthly precipitation, and so forth. Since we expect that both temperature and precipitation are key limiting factors for steelhead distribution in our study area, we expect these datasets to be useful. They are available online at the Spatial Climate Analysis Service[3]. Some pertinent examples of the data are in Plate I through Plate VI at the end of this report. Detailed overviews of this approach to climate modeling can be found in Daly *et al.* (1994, 2001 and 2002).

1.4.5. Data on Stream Discharge

The United States Geological Service maintains data from numerous stream gauges within the study area, some of which provide useful historical context[4]. For example, one gauge has been in continuous operation on the Arroyo Seco, a tributary of the Salinas River, since 1901. These datasets consist of mean daily discharge for the period of record at each gauge.

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[3] http://www.ocs.orst.edu/prism/

[4] http://waterdata.usgs.gov/ca/nwis/nwis

Needless to say, water flow is fundamental to the occurrence of *O. mykiss*, and in southern California it is so variable that it cannot be taken for granted. Gauges are widespread in the study area, but their distribution is irregular and hence their geographic consistency is only moderate. Even so, these data are potentially useful in three respects. The first is that discharge data describe, to some degree, what is occurring upstream and downstream. In this sense gauge data have greater geographic extent than just the point at which the data were collected.

The second respect in which the data are useful is for fitting models that *are* geographically consistent. For example, Burnett *et al.* (2002) used gauge data in Oregon to predict discharge in ungauged reaches, so as to assess the potential distribution of coho salmon (*Oncorhynchus kisutch*). The predictors in their model were geoenvironmental coverages with high geographic consistency—namely, contributing watershed of each reach in a GIS stream network, and a coverage of mean annual precipitation. To the extent that discharge can be regressed on these two datasets, they can be combined with USGS discharge data to make a predictive map. The map is spatially consistent, relevant, and credible because its accuracy can be assessed using standard statistical procedures. Beighley et al. (2005) describe a more refined approach for constructing rainfall-run-off models for a portion of the study area.

The third respect in which the data are useful is that they provide information on migratory accessibility for the fish. In arid regions where rainfall is variable within and among years, it is thought that discharge is so variable that it does not provide reliable access for steelhead migrating to or from the ocean. USGS gauge data provide a means to compare the migration reliability of streams empirically.

When using gauge data to interpret patterns of discharge, it is important to recognize some limitations of stream gauges. One key limitation is
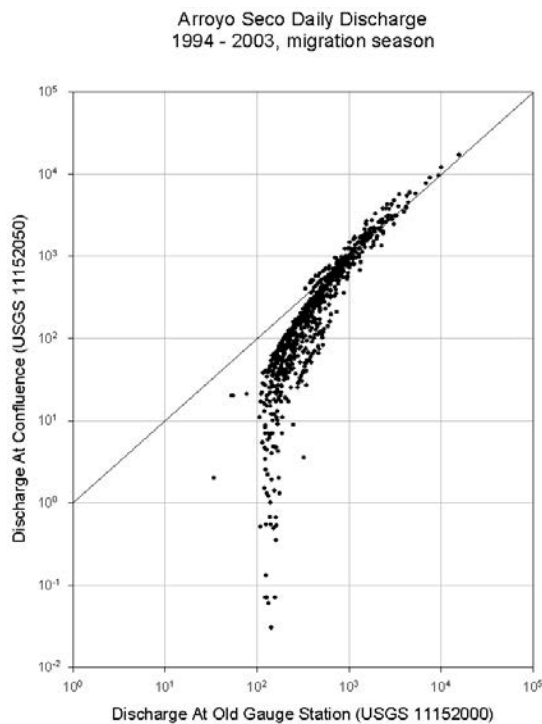
Figure 3. Daily mean discharge during the steelhead migration season (Jan – May), for two gauges on the Arroyo Seco, a steelhead stream in the Salinas basin. The old gauge (11152000) is situated where the Arroyo Seco leaves the Sierra de Salinas and enters the broad alluvial Salinas Valley. The other gauge (11152050) is located 17 km downstream, near the confluence with the mainstem Salinas. Between the two sites, a significant proportion of discharge is lost under low-flow conditions, as indicated by the downward-curve of the cloud of datapoints. Presumably the "lost" water enters the Salinas aquifer underlying the alluvial valley. Data are in cubic feet per second.

that stream gauges omit data on groundwater or hyporheic flow. In some cases losses to, or gains from, groundwater can be quite substantial, especially at low flow (Figure 3). In addition, many USGS gauges are not designed to accurately record low flows (2 – 5 cfs), and because of irregular maintenance some are not always operable. In consequence, estimates of low flows are sometimes biased low or erroneously reported as zero.

Part 2. Identifying the Original Steelhead Populations

The stream systems of the study area are arrayed as a string of 173 coastal basins, bounded by the Pajaro Basin in the north and the Tijuana Basin in the south. This study area encompasses about half the California coast, a span that includes redwood forests, oak savannah, chaparral and high desert. The study area is rather large and has exceptional ecological diversity. For ease of presentation, we divide it into three sections of about equal geographic area (Figure 4). The SCCC section is inhabited by the South-Central California Coast Steelhead ESU. The NOLA and SOLA sections are both inhabited by the Southern California Coast Steelhead ESU, although as we shall see there is more steelhead information about the NOLA section. Below we give an overview of each section.

2.1. SCCC Section

The SCCC section is inhabited by the South-Central California Coast Steelhead ESU. The sections' two northernmost basins—the Pajaro River system and Salinas River system—are also the two largest basins in the entire study area (Figure 5). A distinctive feature of both is their penetration to the interior of the coastal mountain ranges, which is significantly more arid and seasonal than the coastal slopes (see Plate I, Plate IV). Another distinctive feature is the long alluvial lower stretches of the mainstem Pajaro and Salinas. It is suspected that during severe droughts, these lower channels may have caused problems for fish passage (especially for smolts) and therefore were a source of stochasticity that made inland populations less stable.

A segment of the Pajaro system drains the southern end of the Santa Cruz Mountains, an area of dense redwood forest and cool mountain creeks. For more information on the Pajaro, see Stanley *et al.* (1983) and Smith (2002); for the Salinas see Casagrande *et al.* (2003).

South from the Salinas estuary, a notable system is the Carmel River basin, larger than the coastal systems of the Big Sur to the south, but

Main Sections of the Study Area
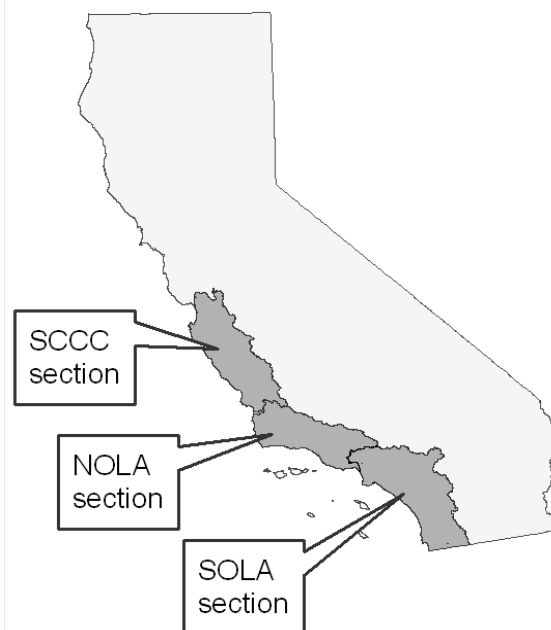
Figure 4. Short-hand acronyms for sections of the study area discussed in the text. SCCC = South-Central California Coast; NOLA = North of Los Angeles; SOLA = South of Los Angeles.

nowhere near the size of the neighboring Salinas Basin. The Carmel is a well-known steelhead stream (Snider 1983), and continues to be actively managed by various entities. Unlike the systems of the Big Sur to the south, the lower reaches of the Carmel have an alluvial character somewhat like the Pajaro and Salinas.

The Big Sur coastal area is south of Carmel and has a moderate climate—cool foggy summers and warm wet winters. Vegetation consists of oak parklands and chaparral, but also stands of Douglas fir and small pockets of redwoods. The stream systems occur as numerous small coastal basins draining the steep Pacific-facing slopes of the Santa Lucia Mountains. Along with the southern Santa Cruz Mountains, the central Big Sur is one of the two distinctly wet places in the study area (Plate IV).
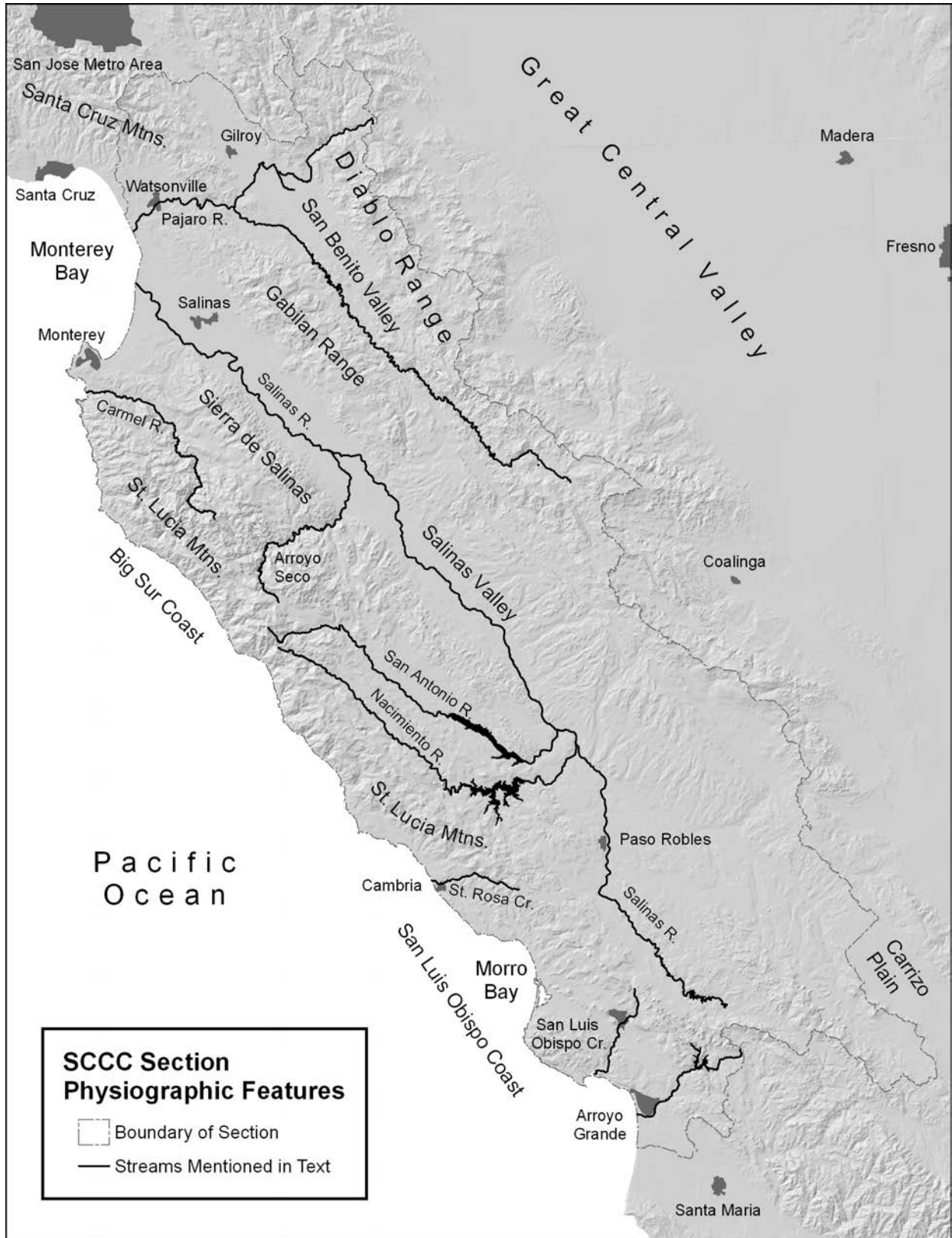
Figure 5. SCCC Section, showing principal streams, towns, and mountain ranges.

In the vicinity of the Monterey-San Luis Obispo county line, the steep coastal slopes of the Big Sur give way to marine terraces as the Coast Range heads slightly inland. This pattern of terrace backed by mountains is typical of the coastal streams of San Luis Obispo County. Examples are Santa Rosa Creek in north county, San Luis Obispo Creek in central county, and Arroyo Grande in south county (Alley 2001, Payne and Associates 2003). Arroyo Grande was mentioned by David Starr Jordan as a popular angling spot for *O. mykiss* in the early 20th Century (Titus *et al.* 2003). All these systems tend to be slightly larger than those of Big Sur and penetrate further inland; they also differ in that their lower mainstems tend to be low-gradient channels through raised marine terraces. To the extent that these lower mainstems retain perennial flow better than the upper tributaries, they serve as important over-summering habitat for juvenile steelhead (Payne and Associates 2003).

The Salinas basin is large, and its magnitude is perhaps brought home by the fact that its headwaters are adjacent to the headwaters of the Arroyo Grande. Several significant tributaries of the Salinas River drain the backside of the Big Sur, each with a watershed area comparable to that of the Carmel River. The furthest north is the mis-named Arroyo Seco, which joins the mainstem Salinas near the ruins of the old Mission Soledad. Further upstream are the paired Nacimiento and San Antonio Rivers, both of which join the mainstem at the Camp Roberts Military Reservation. These systems are true perennial rivers, in contrast to the desert washes that drain the eastern side of the Salinas Valley. Casagrande *et al.* (2003) provide a useful overview of the Salinas system.

2.2. NOLA Section

So far we have been describing basins inhabited by fish of the South-Central California Coast Steelhead ESU. Starting with the Santa Maria system, the basins are inhabited by the Southern California Coast steelhead ESU. It is useful to divide this area into a "north-of-Los-Angeles" section and a "south-of-Los-Angeles" section (NOLA and SOLA, respectively).

The most northerly basin in the NOLA section is drained by the broad Santa Maria River, running past the town of the same name (Figure 7). The Santa Maria River itself is a relatively short connection between the ocean and its two major tributaries—the Sisquoc and Cuyama Rivers. Both of these systems, as well as the large Santa Ynez system just to the south, drain the steep slopes of the Transverse Ranges before running through wide alluvial valleys to the ocean. Their headwaters drain the coolest, wettest area in the NOLA section (Plate II, Plate V), the rugged montane highlands around Monte Arido. Stoecker and Stoecker (2003) give an overview of steelhead in the Sisquoc system, and Douglas (1995) and Carpanzano (1996) describes distributional studies of *O. mykiss* in the Santa Ynez system.

South of the Santa Ynez River mouth, the coast makes a right-angle turn to the east at Points Arguello and Conception. From here to Ventura, the Santa Barbara coast is drained by a set of small, south-facing coastal basins. These systems all have their headwaters in the Santa Ynez Mountain range that parallels the coast at this point; their lower sections run through the small coastal terrace sandwiched between the ocean and the range. One noteworthy exception to the pattern is Gaviota Creek, which actually penetrates the Santa Ynez Mountains and drains a small part of its north slope. Stoecker and the CCP (2002) provide a useful introduction to steelhead in the Santa Barbara coastal area.

Continuing down the coast, the pattern of very small basins is interrupted near the coastal town of Ventura, which is flanked on either side by the mouths of two large and well-known steelhead rivers. The first of these is the south-running Ventura River, whose headwaters drain the south slopes of the same cool and wet Monte Arido highlands drained on the west by the Santa Ynez and Sisquoc Rivers (Plate II). The second is the west-running Santa Clara River, which drains a large and arid area stretching all the way to Soledad Pass just south of Palmdale.

The available evidence suggests that steelhead have been limited to the western part of the Santa Clara basin (Kelley 2004). Noteworthy in this part of the basin are two large tributaries—Sespe and

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Piru Creeks--that arc around to the west, draining the north-west slopes of the same cool-wet Monte Arido highlands mentioned earlier. These two streams and their tributaries are thought to contain most of the steelhead habitat in the Santa Clara system, though two other creeks, Santa Paula and Hopper, also contain significant steelhead habitat. Moore (1980a), Kelley (2004) and Kelley and Stoecker (2005) provide overviews of Santa Clara steelhead, and Dvorsky (2000) describes a focused study of geomorphic influences on *O. mykiss* distribution in Sespe Creek.

Finally, at the southern end of the NOLA section are the Santa Monica Mountains, drained by a series of small south-facing basins somewhat like those on the Santa Barbara coast, but drier (Plate V). Of these basins, Malibu Creek is similar to Gaviota Creek in that it penetrates the mountain range and drains a portion of its north slope. The rest of the north slope is drained by Calleguas Creek, which runs west to the ocean; and the headwaters of the Los Angeles River, which runs around the eastern flank of the mountain range. The southern-most steelhead creek in the NOLA section is Topanga Creek, which harbors a small steelhead population (Dagit and Webb 2002).

2.3. SOLA Section

At the town of Santa Monica, the coast departs from the feet of the mountains. More than half of the large, thick alluvial fan now inhabited by 20 million people was deposited in recent geological times (Gumprecht 1999), from sediments washing out of the rapidly growing mountains to the north.

For steelhead, this means that there are no mountain streams close enough to the coast to benefit in summer from the ocean's climatic cooling effect. The tall mountains apparently have cool temperatures suitable for steelhead and trout, but are further inland, at the far ends of the Santa Ana and San Gabriel River systems (Plate III, Plate VI).

The aridity of the region probably hinders the migration of steelhead up and down the mainstems. For example, the southern-most of the cool-wet areas is the San Jacinto mountain range southwest of Palm Springs. Its western faces are drained by the San Jacinto River, which theoretically
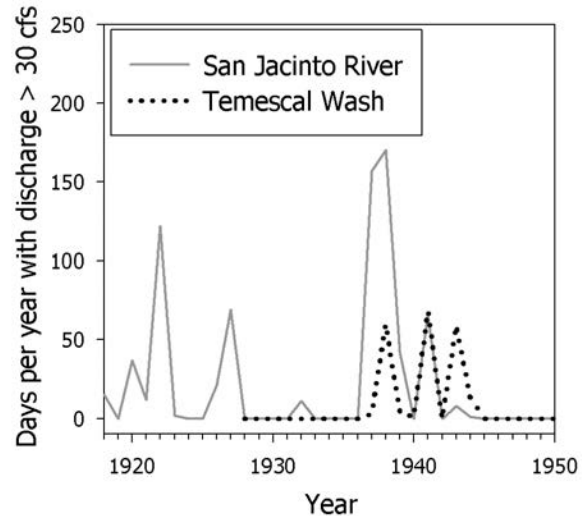
Figure 6. Days per year in which mean discharge exceeded 30 cfs under a natural flow regime, for the potential migration corridor draining the San Jacinto Mountains. The period illustrated is prior to the use of the San Jacinto River as an aqueduct, initiated in 1956.

drains to the Pacific Ocean via Lake Elsinore, Temescal Wash and thence the Santa Ana mainstem. In fact it does so only in very wet years (Figure 6).

The wettest spot in the entire SOLA study area, for the period 1961 – 1990, is the northwest part of the Santa Ana basin, specifically the Cucamonga Wilderness west of Cajon (clearly visible in Plate VI). During the 20th Century, discharge in the principle creeks appears to have been more reliable here than in the San Jacinto River mentioned above (Figure 9). Yet Figure 9 clearly shows that many years had virtually no discharge and hence few migration opportunities.

South of the Santa Ana basin are a series of elongated basins draining Orange and western San Diego Counties. Climate maps suggest that August air temperatures here are typically at least 20° C (Plate III), so the maintenance of cool stream temperature, where it occurs, seems likely to depend on non-climatic factors, such as inputs of groundwater. There is, remarkably enough, a well-documented steelhead population in one of the smaller of these coastal basins, San Mateo Creek (Hovey 2004). Estimated size of the breeding population (never accurately determined) was thought to be less than 70 individuals by Hovey (2004).
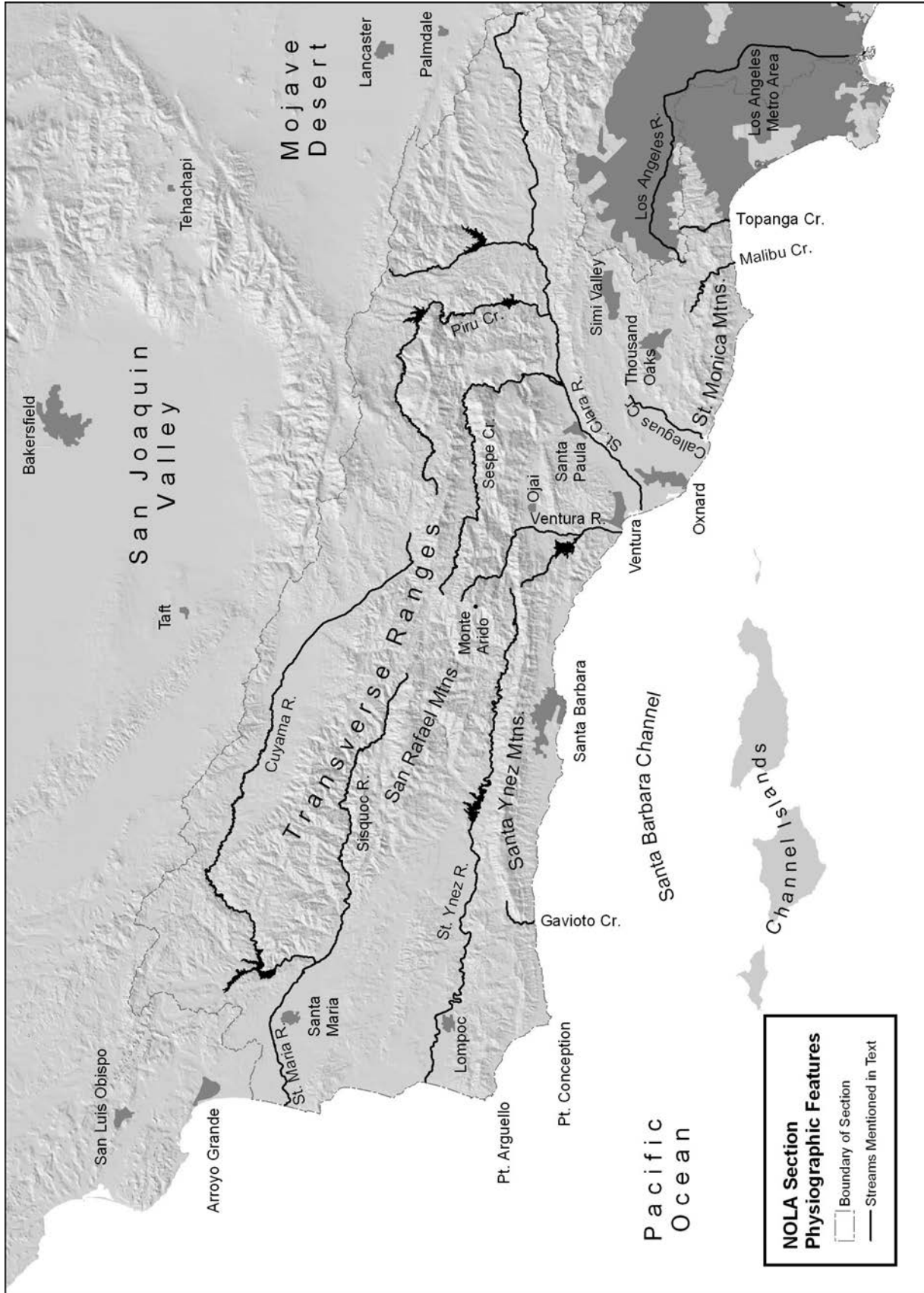
Figure 7. NOLA Section, showing principal streams, towns, and mountain ranges.
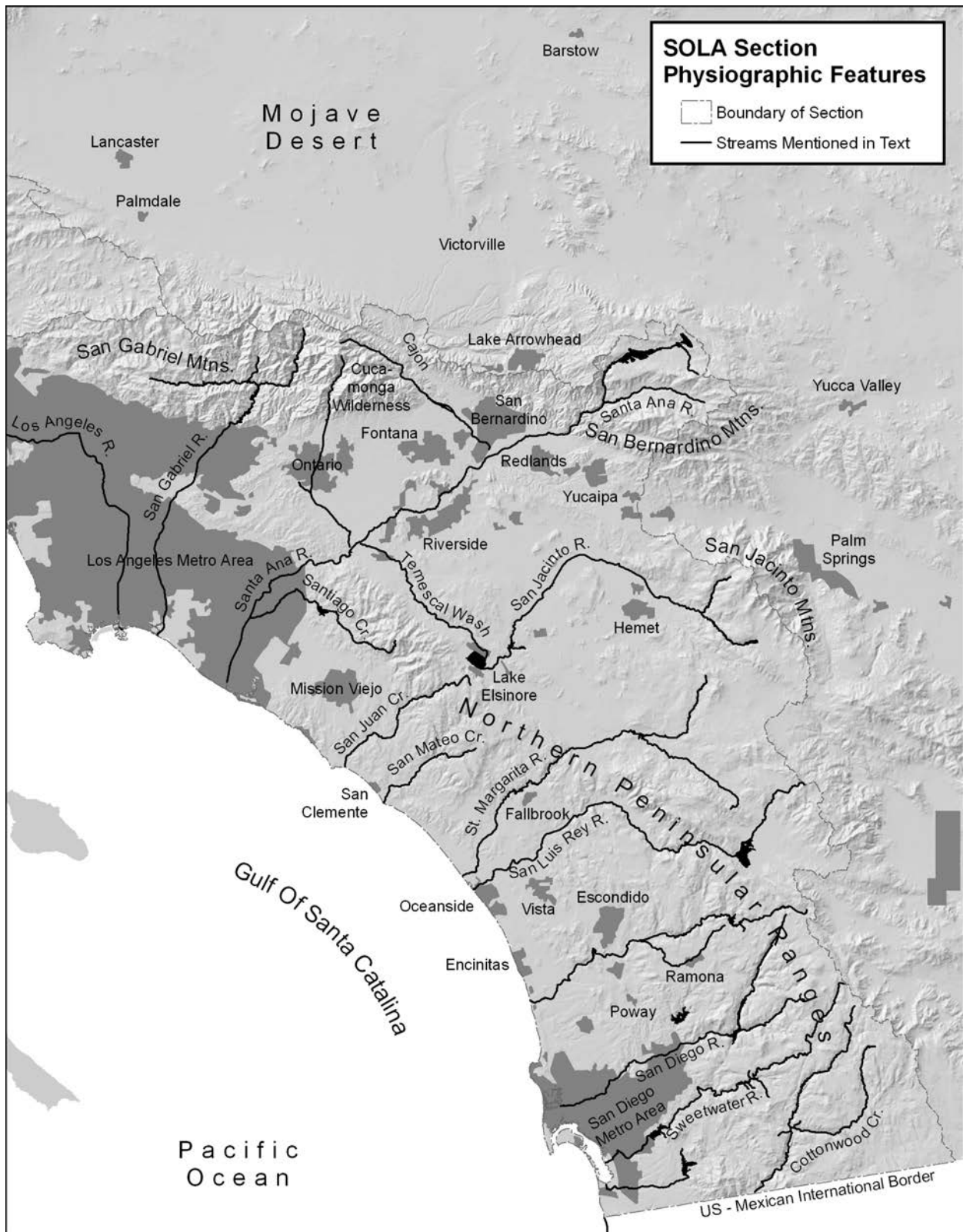
Figure 8. SOLA Section, showing principal streams, towns, and mountain ranges.
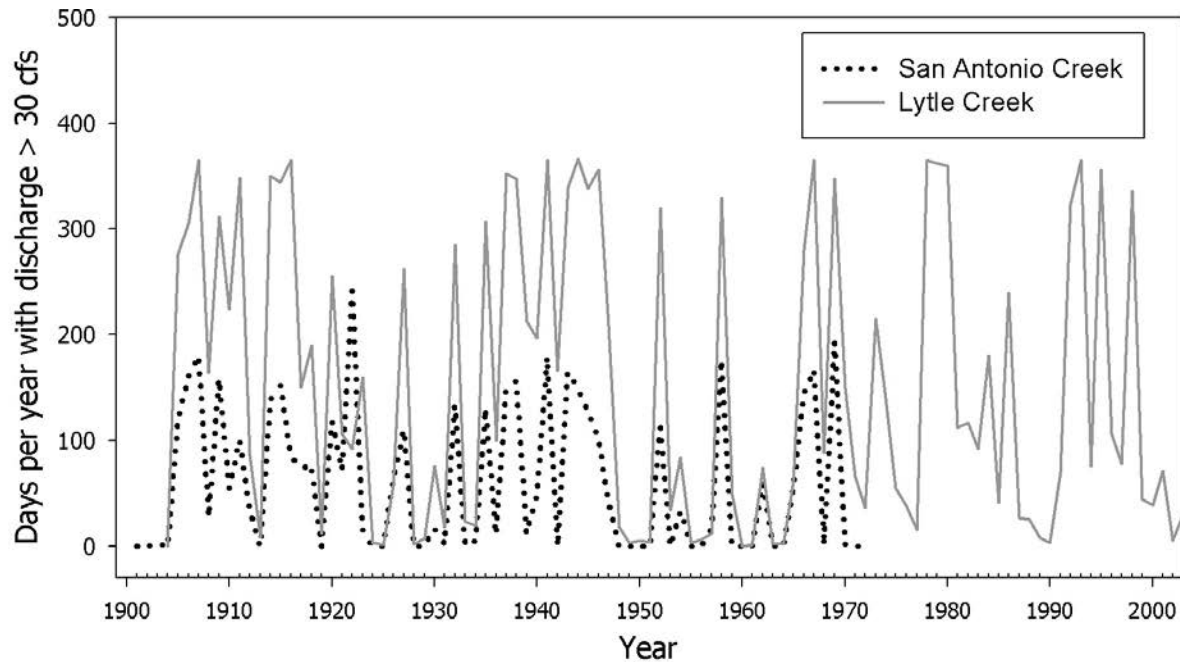
Figure 9. Discharge patterns of two creeks draining the Cucamonga Wilderness, both tributaries of the Santa Ana River. Many years appear to have insufficient flow for migratory access by steelhead.

The original distribution of *O. mykiss* in the SOLA section, prior to European colonization, is not well known; in this report we have summarized in the appendix (§10.3, p. 101) some of the historic record that is known to us.

2.4. A Working Definition of Population

On page 3 we described viable, independent populations as the primary components of a recovery plan, where "viable" and "independent" were defined as in McElhany *et al.* (2000). However, before we apply these concepts we need a working definition of the term "population" itself. We adopt the following convention:

A population is a group of fish and their progeny that share a reasonable expectation of interbreeding, judged by their likelihood of co-occurrence in a stream segment during the winter migration season.

In the study area most of the coastal basins are small enough that one could reasonably expect all the fish inhabiting a particular basin to constitute a single population. In addition to this there are environmental forces encouraging the fish to move around the basin and commingle. For example,

Payne and Associates (2001) conducted an extensive study of juvenile distribution in the San Luis Obispo Creek system during summer 2001. Their data suggest that the juveniles from all over the watershed tend to congregate in the lower part of the mainstem creek during the summer because this reach has reliable discharge. Many of the tributaries of the mainstem dry up during the summer (*e.g.* Figure 3 in Payne *et al.* 2004), and in dry years may not support breeders during the winter. This pattern appears to us to be typical for the study area, and may sometimes force the spatial co-occurrence of breeders originating from different tributaries. This suggests that as a general rule all the *O. mykiss* in a coastal basin should be grouped into a single population.

Can we expect fish in different coastal basins to interbreed? This would require either juvenile movement through the ocean—believed to be extremely rare—or adult dispersal.

When steelhead return to freshwater to spawn, they occasionally stray to the mouths of non-natal systems, a phenomenon known as dispersal. However, biologists generally believe dispersal to be a somewhat rare event. The historical basis for this belief in coastal California is a study by Shapovalov and Taft (1954), who in the 1950s

studied the steelhead populations in Scott and Waddell Creeks, two small neighboring coastal systems in northern Santa Cruz County (mouths 7 km apart). In an intensive tagging study, they determined that only about 2-3% of a run ascended the neighboring stream rather than their natal stream. The general assumption today appears to be that this figure may be biased high—because streams whose mouths are further apart on the coast are assumed to exchange even smaller percentages; and because Scott Creek had a hatchery and hatchery fish are believed to exhibit higher–than-natural dispersal rates.

Rarity of dispersal is corroborated by recent genetic studies. Garza *et al.* (2004) describe a genetic tree of relatedness for steelhead from 41 basins throughout coastal California. They found a pattern of isolation-by-distance among the basins, and also that the terminal branch lengths of the tree tended to be much longer (and better supported) than the internal branch lengths. This last result suggests that each basin has a fairly distinct genetic population, and has relatively small amounts of genetic exchange with neighboring basins.

Based on these studies, a "one basin = one population" rule is a reasonable working hypothesis.

However, dispersal rate may vary geographically due to local adaptation, and this could cause much movement between individual coastal basins under some circumstances. Theoretical work on the evolution of dispersal suggests that high dispersal is most likely to evolve when the benefits of not dispersing are unreliable (Johnson and Gaines 1990). This is a definite possibility in the study area—stream discharge and thus migration access appears to be less reliable in the study area than in northern California or the Pacific Northwest; and this would tend to select for an opportunistic flexibility in the homing tendencies of salmonids. No such tendency has been demonstrated for the steelhead in the study area. One piece of information that suggests such a tendency is the rapid return of steelhead to the Carmel River after the river was "re-watered" in the mid 1990s. However, these data could also be interpreted as regeneration of the anadromous form of the fish

by freshwater residents in the headwater tributaries (which did not dry up).

Streams in the study area typically have sandbar barriers at their mouths during the dry season, transforming the estuary to a freshwater lagoon. In years with low rainfall, these barriers are commonly observed to persist throughout the rainy season as well, and this too suggests that migration access is unreliable and forces the steelhead to be flexible and opportunistic in their migration behavior.

If the steelhead in the study area have unusually high and opportunistic dispersal patterns, it might tend to knit the steelhead of multiple basins together into a single population—in other words, an exception to the one-basin-one-population rule. The situations in which this scenario seems most plausible are 1) sets of small neighboring basins, such as in Big Sur, the southern Santa Barbara coast, and the Santa Monica Mountains; and 2) neighboring basins with unreliable flow, such as those in the SOLA section of the study area.

There is also the possibility that some of the larger basins may contain more than one population. This is especially likely for the very large Salinas Basin, and in §2.6 and §10.1 we examine this question more carefully.

For recovery-planning overall we suggest a prudent approach: In the short term, adopt the one-basin-one-population rule as a default. But, for particular basins in which a compelling argument suggests an alternative population structure, assume the alternative structure. Over the longer term, it would be useful to conduct research on the movement patterns of steelhead, particularly in the Big Sur, Santa Barbara Coast, and in the steelhead-inhabited parts of the SOLA section of the study area.

2.5. Historic Steelhead Populations

Given the "one-basin-one-population" rule, it is straightforward to make an accounting of original populations using historical accounts from Titus *et al.* (2003), Franklin (1999), Stoecker and CCP (2002), and Sleeper (2002). These accounts provide evidence for occurrence in 87 of the 173
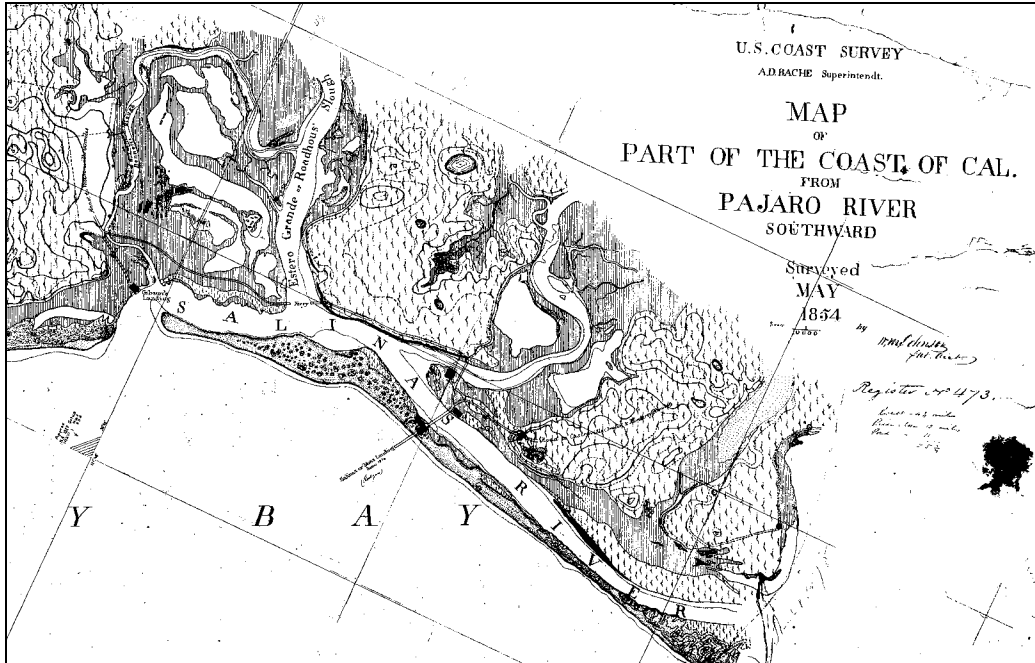
Figure 10. The mouth of the Salinas River at Elkhorn Slough in 1854. Elkhorn Slough is labeled "Estero Grande or Roadhouse Slough" on the map.

basins in the study area(listed in Table 2 on p. 21). Two points are worth bearing in mind.

The first point is that the list of original populations in Table 2 are mostly based on observations of juvenile *O. mykiss* in so-called "anadromous waters" at some point during the 20th Century (Titus *et al.* 2003). Anadromous waters are reaches believed to be accessible to fish swimming upstream from the ocean during their migration season (Jan. – May). However, *O. mykiss* in such reaches may not necessarily be expressing the anadromous life-form at a given time—they may be freshwater residents.

The second point is that absence from the list means absence of evidence for fish; not necessarily absence of the fish themselves. There had been no recent systematic attempt to locate steelhead in all of the 173 coastal basins until 2002, at which point Boughton *et al.* (2005) managed to survey 132 of them. In the process they discovered *O. mykiss* in four coastal basins not mentioned in Titus *et al.* (2003) or other sources. The newly-documented steelhead basins were Malpaso Creek, Vicente Creek, and Villa Creek in Monterey County (Boughton *et al.* 2005); and Los Osos Creek in San Luis Obispo County (Payne and Associates 2001).

In some basins, Boughton *et al.* (2005) did not observe *O. mykiss*, and if the basin had a historical account of the fish they classified the population as extirpated or as excluded from their habitat by anthropogenic barriers (Table 2). The extirpation classification was based on spot checks of the best-occurring summer habitat in the basin. "Best-occurring" was a subjective designation stemming from field reconnaissance by an experienced team of researchers; the subsequent spot-check consisted of a snorkel survey along a 100m transect. Naturally, this rapid-assessment technique may miss some extant populations. Still, Boughton *et al.* (2005) found that if juvenile steelhead were found at all, they tended to be observed within the first 30m of the survey transect. This suggests that juvenile populations tend to fall into two categories: dense enough to be easily detected in a 100m transect, or completely absent. In 17 cases Boughton *et al.* (2005) were able to conduct replicate spot-checks in different parts of a basin, always finding the same result as the initial spot-check. Consequently, Boughton *et al.* (2005) suggested the rapid-assessment technique probably had a reasonably low error rate, and most of the apparent extirpations were true extirpations.

Even so, a more intensive study might turn up additional extant populations, either because error rates were higher than thought, or because some of the vacant basins were subsequently colonized. For example, the latter may have occurred in the San Juan system in Orange County. Boughton *et al.* (2005) conducted four separate spot checks in this basin in 2002 and reported no evidence of juvenile steelhead; since that time several people have reported sporadic adult migrants[1]. There are no reports so far of successful reproduction (*i.e.*, juveniles).

Some of the migration barriers reported by Boughton *et al.* (2005) may turn out, after more intensive study, to be better described as migration impediments. Since many of these streams have extant populations of *O. mykiss* above these impediments, these populations might justifiably be reclassified from freshwater-resident to possibly anadromous. Unfortunately, the passability of small instream barriers by adult steelhead appears to be an intricate and poorly understood subject. Opinion varies widely about the abilities of steelhead with respect to barriers and impediments.

In addition to the historical steelhead basins listed in Table 2, we also list so-called non-historical basins in Table 3. These are basins for which no one has yet described observations of *O. mykiss*, according to Boughton *et al.* (2005), Titus *et al.* (2003), Stoecker & CCP (2002), Sleeper (2002), and Franklin (1999). Ed Henke, of Ashland Oregon, has reportedly compiled historical accounts for some of these basins but has not yet made them public.

One basin in Table 3 deserves special mention. Elkhorn Slough, listed as one of the 173 coastal basins, could reasonably be viewed as a part of the Salinas River system. When first mapped in the 19th Century the current northwest arm of the slough was actually the mouth of the river, and the slough proper was a side-bay on river-right (Figure 10). At that time the slough proper was relatively shallow at low tide (deepest: 1.5m; Van Dyke *et al.* 2005), and might have served as an important steelhead rearing area. During the past millennium, the mouth of the Salinas has probably alternated repeatedly between its 1854 location and its present-day location 8 km south (Gordon 1996).

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[1] M. Larson, personal communication, CDFG.

Table 2. Coastal basins historically occupied by steelhead, with data on recent occupancy in anadromous waters[1]

S.-Central California Coast Steelhead ESU		Southern California Coast Steelhead ESU	
Coastal Basin (N to S)	Extant?[3]	Coastal Basin (N to S)	Extant?[3]
Pajaro River	Y	Santa Maria River	Y
Salinas River	Y	Santa Ynez River	Y
Carmel River	Y	Jalama Creek	Negative obs.
San Jose Creek	Y	Canada de Santa Anita	Y
Malpaso Creek[2]	Y	Canada de la Gaviota	Y
Garrapata Creek	Y	Canada San Onofre	Negative obs.
Rocky Creek	Y	Arroyo Hondo	Y
Bixby Creek	Y	Arroyo Quemado	Barrier
Little Sur River	Y	Tajiguas Creek	Barrier
Big Sur River	Y	Canada del Refugio	Negative obs.
Partington Creek	Y	Canada del Venadito	Barrier
Big Creek	Y	Canada del Corral	Barrier
Vicente Creek[2]	Y	Canada del Capitan	Negative obs.
Limekiln Creek	Y	Gato Canyon	Not determined
Mill Creek	Y	Dos Pueblos Canyon	Barrier
Prewitt Creek	Y	Eagle Canyon	Not determined
Plaskett Creek	Y	Tecolote Canyon	Barrier
Willow Creek - Monterey	Y	Bell Canyon	Barrier
Alder Creek	Y	Goleta Slough Complex	Y
Villa Creek – Monterey[2]	Y	Arroyo Burro	Barrier
Salmon Creek	Y	Mission Creek	Y
San Carpoforo Creek	Y	Montecito Creek	Y
Arroyo de la Cruz	Not determined	Oak Creek	Barrier
Little Pico Creek	Not determined	San Ysidro Creek	Y
Pico Creek	Not determined	Romero Creek	Y
San Simeon Creek	Y	Arroyo Paredon	Y
Santa Rosa Creek	Y	Carpinteria Salt Marsh Complex	Barrier
Villa Creek - SLO	Y	Carpinteria Creek	Not determined
Cayucos Creek	Negative obs.	Rincon Creek	Barrier
Old Creek	Dry	Ventura River	Y
Toro Creek	Y	Santa Clara River	Y
Morro Creek	Y	Big Sycamore Canyon	Negative obs.
Chorro Creek	Y	Arroyo Sequit	Y
Los Osos Creek[2]	Y	Malibu Creek	Y
Islay Creek	Y	Topanga Canyon	Y
Coon Creek	Y	Los Angeles River	Barrier
Diablo Canyon	Y	San Gabriel River	Barrier
San Luis Obispo Creek	Y	Santa Ana River	Barrier
Pismo Creek	Y	San Juan Creek	Negative obs.
Arroyo Grande Creek	Y	San Mateo Creek	Y
		San Onofre Creek	Dry
		Santa Margarita River	Negative obs.
		San Luis Rey River	Barrier?
		San Diego River	Barrier
		Sweetwater River	Barrier
		Otay River	Barrier
		Tijuana River	Not determined

[1] Historical data: Titus *et al.* (2003); Sleeper (2002); Franklin (1999). Recent data: Boughton *et al.* (2005)

[2] No data on historical occurrence, but recent occurrence documented by Boughton *et al.* (2005).

[3] "Negative obs." means juveniles were observed to be absent during a spot-check of best-occurring summer habitat in 2002. "Dry" indicates the stream had no discharge in anadromous reaches during the summer of 2002. "Barrier" indicates that all over-summering habitat was determined to be above an anthropogenic barrier, believed to be impassable. See Boughton *et al.* (2005) and notes on page 19 for details.

Table 3. Coastal basins with no evidence[1] of historical or extant populations of *O. mykiss* in anadromous waters.

South-Central California Coast Steelhead ESU	Southern California Coast Steelhead ESU	
Coastal Basins (N to S)	**Coastal Basins (N to S)**	
Elkhorn Slough	Shuman Canyon	Santa Monica Canyon
Del Rey Creek	San Antonio Creek	Solstice Canyon
Seal Rock Creek	Honda Creek	Corral Canyon
Pescadero Canyon Creek	Wood Canyon	Trancas Canyon
Gibson Creek	Damsite Canyon	Escondido Canyon
Soberanes Creek	Canada del Cojo	Ramirez Canyon
Doud Creek	Barranca Honda	Zuma Canyon
Sycamore Canyon	Canada de la Llegua	Ballona Creek
Grimes Canyon	Arroyo San Augustin	Dominquez Channel
Hot Springs Canyon	Arroyo El Bulito	San Diego Creek
Lime Creek	Canada del Agua	Los Trancos Canyon
Kirk Creek	Canada de la Cuarta	Muddy Canyon
Wild Cattle Creek	Canada de Alegria	Moro Canyon
Soda Spring Creek	Agua Caliente	Emerald Canyon
Arroyo de los Chinos	Canada del Molino	Laguna Canyon
Oak Knoll Creek	Las Llagas Canyon	Aliso Creek
Little Cayucos Creek	Las Varas Canyon	Salt Creek
Willow Creek - SLO	Sycamore Creek	Canada de Segunda Deshecha
Little Irish Canyon	Toro Canyon Creek	Las Pulgas Canyon
Irish Canyon	Los Sauces Canyon	Aliso Canyon
Wild Cherry Canyon	Hall Canyon	Loma Alta Creek
Pecho Creek	Arundell Barranca	Buena Vista Creek
Rattlesnake Canyon	Calleguas Creek	Agua Hedionda Creek
	La Jolla Canyon	Canyon de las Encincas
	Little Sycamore Canyon	San Marcos Creek
	Carbon Canyon	Escondido Creek
	Las Flores Canyon	San Dieguito River
	Piedra Gorda Canyon	Los Penasquitos Creek
	Pena Canyon	Rose Canyon
	Tuna Canyon	Tecolote Creek
	Santa Ynez Canyon	Chollas Creek
		Telegraph Canyon

[1] No evidence of occurrence does not imply evidence of no occurrence; the latter would require a "negative observation;" *i.e.* evidence that the species was looked for but not found.

2.6. Three Discrete Populations in the Salinas System

The Salinas Basin appears to possess five distinct steelhead areas—Gabilan Creek, Arroyo Seco, the San Antonio River, the Nacimiento River, and the upper Salinas system south of San Miguel. The large size of the basin suggests that these steelhead areas may be sufficiently isolated to contain multiple populations—a possible exception to the one-basin/one-population assumption. A detailed assessment of this hypothesis is in §10.1 (p. 92 of the Appendix); here we summarize the main conclusions.

Gabilan Creek should be considered a distinct population, due to its unique connection with the ocean via Tembladero Slough and the Old Salinas River channel which connects Elkhorn Slough to the current estuary of the Salinas River. The steelhead habitat is high in the headwaters of the system, quite isolated from the other steelhead areas by low-gradient sloughs in the lower Salinas Valley.

Arroyo Seco should probably be considered a distinct population, for three reasons. First, it is separated from the other steelhead areas by a long stretch of the mainstem Salinas that does not appear particularly hospitable to juvenile movement. This appears to be an isolating mechanism. Second, there is no evidence that under natural hydrologic conditions, low streamflow prevented adults from homing to Arroyo Seco (This would potentially force them to spawn elsewhere in the basin, presumably in the other steelhead areas). Third, the consequences of making a "lumping" mistake (erroneously treating Arroyo Seco as not distinct) appear to be greater than making a "splitting" mistake (erroneously treating it as distinct).

Nacimiento, San Antonio, and upper Salinas Rivers should be considered to jointly share a single distinct population. There is evidence that under natural hydrologic conditions, low streamflow often prevents adult migrants from returning to a particular stream, forcing them to spawn in one of the other two steelhead areas comprising the population. Under natural hydrologic conditions, the discharge from the Nacimiento River appears to be the most reliable, so usually it would be fish natal to the San Antonio or upper Salinas that would be forced by low flows to spawn in the Nacimiento. Thus we refer to this population as "*Nacimiento et al.*"

This three-population scheme for the Salinas Basin is based on indirect evidence pertaining to steelhead movement patterns. Data on fish movement between the five steelhead areas would give a clearer and more accurate picture of the population structure of the Salinas Basin. More detail on the indirect evidence and its evaluation is given in the appendix, §10.1 (p. 92).

At present the mainstem of the Salinas River does not appear to comprise suitable spawning or rearing habitat for steelhead, and this is partially the basis for considering the basin to have several discrete populations in major sub-drainages. However, the mainstem prior to Spanish settlement may have been quite different ecologically, having a well developed riparian forest; a higher water table providing cool water inflows to the mainstem; a less incised channel; and substrates coarser than the sand and silt that now predominate. These conditions would have been more conducive to steelhead spawning and rearing than the current state of the river. The evidence that the mainstem was once more suitable for steelhead is discussed in the Appendix (§10.2, p. 98).

Part 3. Extant Populations

In 2001, Boughton *et al.* (2005) undertook a survey of the original populations listed in Table 2 (p. 21), to determine which had extant anadromous components. In 2002 a similar survey was conducted in the sub-basins of the two largest systems, the Salinas and Pajaro. Overall, 92 historical steelhead basins and sub-basins were identified, and occurrence was estimated in 86 of them through a combination of literature review, field re-connaissance, and snorkel surveys (spot checks) in the best-occurring habitat. Six basins were inaccessible for various reasons and were not surveyed. The survey also assessed occurrence in 55 coastal basins that lacked any historical account of steelhead occurrence, and detected the species in 5 of them.

The survey indicated that between 58% and 65% of the historical steelhead basins currently harbor *O. mykiss* populations at sites with migration connectivity to the ocean. Most of the apparent losses of steelhead occurred in the south (Figure 11).

Sixty-eight percent of the apparent basin-wide losses of steelhead were associated with anthropogenic barriers to fish migration (dams, flood-control structures, culverts, etc.; termed "barrier exclusions" in Figure 11). According to a regression analysis, the barrier exclusions were statistically associated with highly-developed watersheds (percent cover by urban and agricultural development). The remaining losses of steelhead (not associated with migration barriers) had no statistical association with percent development in the watershed; they tended to occur in basins with relatively warm climate (mean annual air temperature as inferred using the parameter-elevation regressions on independent slopes model; Daly *et al.* 1994).

The lowest rate of basin-wide steelhead loss (zero) was along the Big Sur coast. Every one of the 21 original populations between the towns of Carmel and Cambria had extant *O. mykiss* in anadromous waters, and 3 additional populations were also detected by Boughton *et al.* (2005).
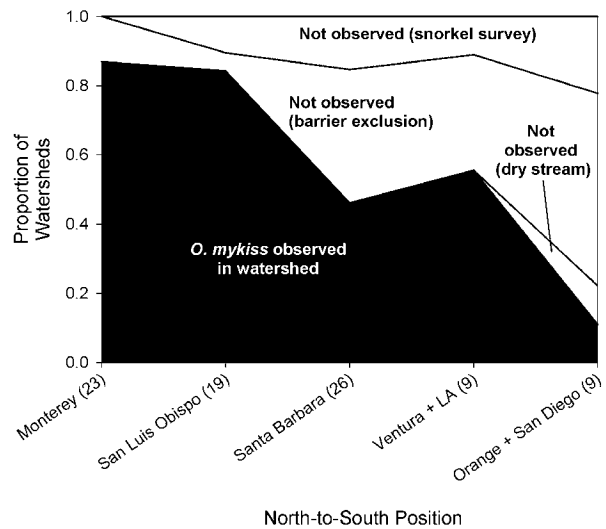
Figure 11. Basin-level occurrence of steelhead by county (sub-basins in the Pajaro and Salinas systems). Occurrence is shown only for systems with evidence for previous occurrence of *O. mykiss* in anadromous reaches. Numbers of basins per county are in parentheses on the x-axis. Figure from Boughton *et al.* (2005).

Nearly all of these occupied basins are extremely small in area, but are located in one of the wettest and coolest parts of the study area. The region is sparsely settled, and the steelhead populations do not appear to be heavily impacted by water diversions, habitat alteration, *etc*.

In general, the apparent losses or extirpations were inferred from spot checks and involve a certain amount of error. At the level of individual spot checks, the estimated probability of detection failure was 0.0175 (Boughton *et al*. 2005). At the basin level, error was estimated from 17 revisits to novel sites in basins already spot-checked, and in all cases the result (detected; not detected) was the same as that of the previous spot check, giving an error probability of 0.00 (95% c.i.: [0.00, 0.162] by the binomial distribution). In addition, the basins classified as "barrier exclusions" in some cases relied on subjective assessment of barrier passability.

Another assumption in this work, and most other work on *O. mykiss* in the study area, is that

subpopulations inhabiting so-called "anadromous waters" are indeed anadromous. Very rarely is this assumption tested, due to the difficulty of monitoring steelhead runs during the winter. The assumption is questionable, however, because anadromous and resident life-history types appear to co-exist in such populations. There is a recently-developed technique—otolith microchemistry (Zimmerman and Reeves 2000) which allows one to determine the anadromy status of juveniles by sampling juveniles, but this technique requires sacrificing the sampled fish. It has not been applied in the study area for that reason.

For a listing of occurrence in each coastal basin, refer to Table 2 (p. 21). For occurrence in sub-basins of the Salinas and Pajaro systems, refer to Table 5 (p. 26).

3.1. Artificially Isolated Populations

Although barriers appear to have played a large role in basin-wide extirpation of the anadromous life-form, in many cases the species continues to persist in the stream systems above the barriers. For example, *O. mykiss* have been recently documented to occur above barriers in at least 17 of 22 basins where they have been lost below the barriers (Boughton *et al.* 2005, Stoecker and CCP 2001, Donohoe and Adams 2005). These above-barrier fish have been the subject of much uncertainty. Various hypotheses of their origins have been proposed: that they are naturalized descendents of hatchery trout; that they are remnant wild trout; that they are land-locked steelhead that may or may not retain the genetic potential to exhibit the anadromous life-cycle under suitable conditions; and finally, that they are the remnants of flexible populations that originally exhibited both anadromous and freshwater-only life history types in a single population.

3.1.1. Recent Evidence about Relationships of the Isolated Populations

In addition to the genetic studies described in §1.4.2. (p. 7), there are new data pertinent to the relationships of artificially isolated populations in the study area. Girman and Garza (2006) recently described tissue samples from a series of popula-

Table 4. Above-barrier sub-populations examined by Girman and Garza (2006)

Stream (Basin)	Location of Subpopulation
S. Antonio R. (Salinas)	above San Antonio Dam
Nacimiento R. (Salinas)	above Nacimiento Dam
Lopez Cr. (Arroyo Grande)	above Lopez Dam
Piru Cr. (Santa Clara)	between Piru/Pyramid Dams
Piru Cr. (Santa Clara)	above Pyramid Dam
Matilija Cr. (Ventura)	above Matilija Dam
Juncal Cr. (Santa Ynez)	above Jameson Dam

tions above and below key barriers in the study area (Table 4). After analyzing 15 microsatellite markers, they made the following conclusions: First, there is no evidence that the southern TRT contains unexpected or unprecedented genetic variation. Rather, steelhead in the study area exhibit lower genetic variation than their northern California counterparts, as might be expected for such small populations.

Second, in general the populations above the barriers were as closely related to populations below barriers as they were to other populations above the barriers. In other words, barriers were not associated with greater genetic distances between populations.

Third, there was no evidence that the above-barrier populations had been overrun by descendents of hatchery fish. In a consensus tree of genetic distances among populations, the hatchery stocks from Fillmore Hatchery clustered in a distinct region of the tree; the above-barrier populations were distributed in other parts of the tree, and tended to be associated with their neighboring below-barrier populations. Assignment tests for individual fish also supported the idea that hatchery fish have had no detectable influence on the genetics of above-barrier populations.

These results indicate that the above-barrier populations listed in Table 4 are not the descendents of hatchery fish. They might be wild trout populations, but if so they are closely related to nearby steelhead populations. They are most likely the land-locked descendents of steelhead populations, since most of these areas have his-

toric accounts of steelhead runs prior to construction of the barriers.

3.1.2. Recent Evidence about Potential for Anadromy

Recent work from Alaska suggests that land-locked steelhead populations can be resilient to decades of selection against anadromy. In 1926 cannery workers from Little Port Walter in southeast Alaska captured *O. mykiss* from a small creek populated by a wild steelhead run (Thrower *et al.* 2004a). They planted these fish in an upstream lake that had been fishless up to that time and separated from the lower creek by two 15m-high waterfalls. More than 70 years later, the upper population still regularly produces smolts despite the fact that none can successfully return to the upper basin to spawn.

Thrower *et al.* (2004b) did a crossing experiment with the land-locked steelhead in the lake and the anadromous steelhead in the creek. Among the families they studied, they discovered a negative genetic correlation between the likelihood of smolting by age 2 and the likelihood of maturing by age 2. This led Thrower *et al.* (2004b) to suggest that even though smolts could not complete their anadromous life cycle in the lake population, their production over 70 years may have been maintained by natural selection on maturation rate. They concluded that "the genetic potential for smolting can lie dormant or be maintained…for decades despite complete selection against the phenotype" (Thrower *et al.* 2004b: 286). Clearly, steelhead populations can exhibit facultative anadromy, and can maintain a dormant form of that capability for decades.

However, Thrower *et al.* (2004a, b) found that marine mortality of smolts from the lake was about double the marine mortality of smolts from the anadromous population in the creek. This suggests that the land-locked population—though retaining the ability to smolt—is gradually losing certain other adaptations to the marine environment.

No such detailed study exists for the land-locked populations in our study area. However, anecdotal data suggests that the Santa Clara River

Table 5. Original and recent occurrence (2002) of steelhead in Pajaro and Salinas sub-basins (Boughton *et al.* 2005).

Historical Occurrence	Current Occurrence	Principle sub-basins
Pajaro River		
X	X	Corralitos Creek
X	X	Pescadero Creek
X	X	Uvas Creek
X	Absent[1]	Llagas Creek
	Absent	San Benito River[2]
X	X	Pacheco Creek
X	-	Tequisquita Slough[3]
Salinas River		
	X	Gabilan Creek
	Dry	El Toro Creek
	Dry	Chualar Creek
X	X	Arroyo Seco River
		Stonewall Creek
	Dry	Chalome Creek
	Dry	San Lorenzo Creek
	Dry	Pancho Rico Creek
X	Barrier	San Antonio River
X	Barrier	Nacimiento River
	Dry	Big Sandy Creek
	Dry	Estrella River
	Dry	San Marcos Creek
	Dry	Huerhuero Creek
X	X	Paso Robles Creek
X	Absent	Graves Creek
X	X	Atascadero Creek
X	X	Santa Margarita Creek

[1] Based on snorkel surveys at two sites during 2003. J.J. Smith reports a "tiny run" in the 1990s.

[2] Seems likely to have had at least occasional steelhead runs historically, but no records exist.

[3] Arroyo Dos Picachos, a tributary, is reported to harbor a resident population of *O. mykiss*

population has retained the potential for anadromy over several decades of strong selection against it. Around the year 1946, the local water district began diverting winter-time discharge from the mainstem Santa Clara into spreading grounds near the town of Saticoy (Kelley 2004). Spreading grounds are large, shallow ponds designed to allow surface water to percolate into the

underground aquifer. After 1954, the fish screen on the diversion appears not to have been maintained (Kelley 2004), and for 40 years, one may presume, most downstream migrants would have ended up in the settling ponds rather than the ocean.

This constitutes a strong selection gradient away from anadromy, and toward the freshwater-resident life-cycle. Only after 1991 was there a fish-ladder and screen operational at the diversion, at which point a monitoring program of up-stream- and downstream migrants began. Immediately this monitoring effort revealed that a small number of smolts (dozens to hundreds) still regularly made a winter run down the Santa Clara toward the ocean. In short, after about 10 generations of likely failure of anadromous steelhead to reproduce, the land-locked steelhead in the system were still producing smolts.

So-called "adfluvial" populations of steelhead have also been reported from the study area, and their existence suggests that some above-barrier populations continue to maintain the potential for anadromy. Adfluvial populations are *O. mykiss* that inhabit lakes or human-made reservoirs (usually above impassable dams). Steelhead-like adults migrate into streams that are tributary to the reservoir, and smolt-like juveniles later migrate back to the reservoir to mature. Presumably this would be likely to maintain some adaptations to anadromy within a land-locked population. Adfluvial populations have been reported from Whale Rock Reservoir on Old Creek, Jameson Reservior on the Santa Ynez River, possibly from San Gabriel Reservoir, and may occur elsewhere as well.

It is sometimes said that rainbow trout can remain as freshwater fish for several years before they smolt and go to sea; and that they can partially smolt and still revert back to life in freshwater habitats (termed "peri-smoltification"). The scientific literature on these claims is not well developed; but the implications for recovery planning are large. Aas-Hansen *et al.* (2005) support the re-smoltification hypothesis in Arctic char. To our knowledge, evidence for its incidence in *O. mykiss* has not been described, though some sort of re-smoltification mechanism seems necessary for kelts that are returning to the ocean after spawning. These phenomena would indicate a very high level of life-history flexibility beyond the question of anadromy vs. residency, and would have important implications for recovery. They would comprise a mechanism by which the one-basin/one-population rule is violated (for example, by uniting the fish in small Big Sur drainages into larger-extent populations). Also, they would likely allow the fish to respond more rapidly and strongly to recovery efforts.

Part 4. Distribution of Potential Steelhead Habitat

Despite the difficulties involved in formally delineating populations and characterizing their ecological recovery potential, we here attempt to do just that. In particular, in this part of the report we describe a practical method for mapping potential habitat of O. mykiss; and in Part 5 we describe a structured analysis that uses these maps to rank the relative recovery potentials of all O. mykiss populations originally present in the study area. We pursued this exercise in the spirit of McElhaney et al. (2000) and Bjorkstedt et al. (2005). However, our effort to provide recommendations revealed numerous uncertainties, and Part 4 and Part 5 can also be thought of as a structured guide to those uncertainties.

4.1. Intrinsic Potential

A basic way to compare the various steelhead populations is via the amount of potential unimpaired habitat that is available to each. Comparison of populations in their unimpaired state may allow us to identify those populations that have the highest potential to meet viability criteria if they were completely restored.

A simple method for making such a comparison is to use the total stream kilometers as an estimate of habitat amount in each basin, but this approach assumes that all stream reaches have about the same suitability for steelhead. This is clearly untrue for certain basins—particularly those that have large hot arid areas unsuitable for the fish. Examples include the Salinas basin and Santa Ana basin. A better basis for comparison than total stream kilometers is a subtotal of stream kilometers that excludes those reaches considered not suitable for the fish. This requires a model of potential habitat applicable to each stream reach in the study area.

An accepted practice in ecology is to infer species distributions using habitat models (recently reviewed in Scott *et al.* 2002). The key assumption is that species tend to occur more-or-less in equilibrium with their habitat (Scott *et al.* 2002). For now we will treat this assumption as a useful ap-

proximation; in the next section we will examine it more closely.

Our purpose here is a little different from the goals of most habitat models, which is to map current conditions. Here we would like to map potential unimpaired conditions (*cf*. §1.1 and §1.2 on p. 2). Burnett *et al.* (2003) considered how one might do this for salmon and steelhead, and proposed the concept of "Intrinsic Potential." In their concept, a stream reach has high Intrinsic Potential (abbrev: IP) if its mean discharge, gradient, and surrounding topography are such that the reach would likely comprise suitable habitat in an unimpaired condition. The proposal was based on the idea that natural processes will tend to spontaneously generate suitable habitat, but only in reaches where discharge, gradient, and topography meet certain criteria.

Burnett *et al.* (2003) parameterized a model of steelhead IP for the Tillamook and Nestucca Basins on the Oregon Coast. Though their general approach seems compatible to our needs, the specific parameterization does not; the southern California situation appears quite distinct. Specifically,

1) In Oregon, steelhead share streams with coho salmon, who have strong habitat preferences and also appear to exert asymmetric competition on steelhead (Young 2004). Where this competition is lacking, as in southern California, the steelhead might expand the range of conditions in which they occur.

2) The Oregon coast is covered with temperate rainforests; our study area is mostly Mediterranean scrub and savannah with deciduous riparian vegetation. Climate, especially suitable summer temperature, is likely to be an additional component of IP in the south.

3) Stream discharge in the study area is highly variable, much more so than in the typical Oregon stream (see Figure 37 on page 95). Low summertime flows, especially, should be considered as a potential limiting factor.

4) The steelhead in Oregon and southern California may have slightly different tolerance limits for a given environmental parameter, due to local adaptation (*e.g.* Spina 2006).

4.2. Reparameterizing IP using Local Data

The kind of re-parameterization that we might consider is constrained by the available steelhead data, namely the occurrence data described in §1.4 of this report. The key limitations of these data from a structural point of view are two: they were not collected via random sampling, and they are censored, in the sense that negative observations of occurrence tended not to be recorded.

The scientific literature describes three methods for fitting habitat models under these constraints. To deal with the lack of negative observations, the methods all must assume that the observers collecting the data were spreading their effort evenly throughout the stream networks. Each of the three methods combines the presence-only data with a set of GIS environmental coverages to generate a map of potential habitat. They differ mostly in their assumptions about the shape of niche functions and their method for characterizing uncertainty.

The three modeling approaches are Environmental Niche Factor Analysis (ENFA; Hirzel *et al.* 2002); the Genetic Algorithm for Ruleset Prediction (GARP; Stockwell and Peters 1999, Anderson *et al.* 2003); and environmental envelopes (*e.g.*, Carpenter *et al.* 1993). We used the latter because it has the simplest, most intuitive interpretation.

An environmental envelope is an interval on an environmental predictor that encompasses all known occurrences of a species. Imagine a map of the locations at which the species has been observed sometime in the past few decades. Now imagine overlaying that map with a relevant environmental variable, such as mean summer air temperature. Using this overlay, each recorded species location can be assigned a particular summer temperature[1]. Of these locations, there is a warmest and a coolest that provide an estimate of the ther-

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[1] Specifically, mean August air temperature from 1961 to 1990.
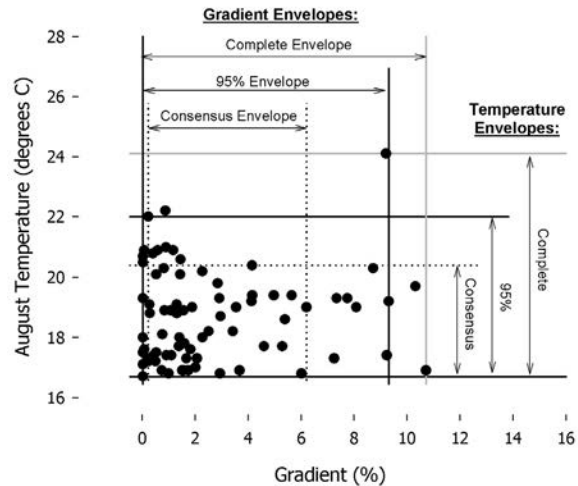
Figure 12. An example of fitted bioclimatic envelopes for two predictors in the south-central California coast study area. The datapoints represent geo-referenced occurrences of *O. mykiss*. The corresponding values of stream gradient and mean August air temperature were obtained from a GIS. 95% and consensus envelopes were generated by resampling the occurrence data 50,000 times. They are defined as the agreement between 95% and between 100% of the envelopes computed for the resamples.

mal tolerance of the species. The environmental envelope is the range of temperatures lying within these tolerance limits (Figure 12). If one has a map of summer temperature, it is then a simple matter to translate it into a map of areas lying within the species' zone of tolerance.

It is important to understand the logic of environmental envelopes because they are an intuitive and useful tool, but they have important limitations. Specifically, there are many mitigating factors that cloud the relationship between the predictor and the fish. For example, using summer air temperature to predict fish distribution makes an implicit assumption that water temperatures closely track air temperatures. This is largely true, but the relationship has scatter. For example, in a comparison of air and water temperatures in the Salt Fork Arkansas River (Kansas), Mohseni and Stefan (1999) found that air temperature was a very good predictor of river temperature, but the relationship had a scatter of ±4° C at all points of the prediction line. One reason for scatter would be reaches that tend to deviate toward coolness

due to local mitigating factors—stream-shading by riparian vegetation or topography; ground-water inputs to streams; and effects of reservoir releases – possibly providing in-stream thermal refugia for the fish. Such thermal refugia would not be identified explicitly by our envelope approach. They might be implicitly identified if the occurrence data include species inhabiting thermal refugia. In this case, however, the model might overpredict for areas without thermal refugia.

In short, the environmental envelope approach is useful if its application is tempered by local knowledge. With these caveats, we proceed.

4.3. Preparation of Models for Potential Habitat

The predictors used in the original formulation of intrinsic potential were stream gradient, valley-width index, and mean annual discharge. Burnett *et al.* (2002) and Bjorkstedt *et al.* (2005) review the evidence for these being valid predictors of potential habitat through their influence on stream geomorphology (see also Montgomery *et al.* 1996, Montgomery and Buffington 1997, and Dvorsky 2000). Here, we use juvenile occurrence data from the study area to fit bioclimatic envelopes to stream gradient and valley-width index. We substituted an estimate of low summer discharge for mean annual discharge (See Boughton and Goslin 2006 for details). In addition, we fit envelopes to two additional temperature-related predictors that we believed were important (due to Douglas 1995, Matthews and Berg 1997, Spina 2006). These are 1) mean annual temperature based on PRISM data (Daly *et al.* 1994), and 2) August mean temperature, also based on PRISM data. The time period for which the coverages were produced was 1961 – 1990. The predictors are described in Table 6, and more fully in Boughton and Goslin (2005).

The occurrence data used to fit the envelopes were of varying quality with regard to location. Some accounts gave latitude and longitude, which was optimal. Others gave descriptions in terms of landmarks, road miles, and so forth. To meet the model assumptions of widely-dispersed sampling effort, we used these poorer-quality data when we

Table 6. Environmental variables used to estimate potential steelhead habitat.

Stream gradient

The slope in percent of the stream channel along the axis of flow. Estimated using a 30m DEM.

Valley-width index

The ratio of the valley width to the active channel width. Estimated after methods described by Bjorkstedt *et al.* (2005).

Low summer discharge (Aug – Sept)

The flow rate of water moving through a particular channel during Aug – Sept. Yearly means averaged for the period 1961 – 1990. Methods in Boughton and Goslin (2006).

Mean annual air temperature

Mean annual air temperature for the period 1961 – 1990. PRISM data, *cf* Daly *et al.* (1994)

August mean air temperature

Mean August air temperature for the period 1961 – 1990. PRISM data, *cf* Daley *et al.* (1994). Datasets are illustrated in Plate I (SCCC study area), Plate II (NOLA) and Plate III (SOLA).

Limiting Accessibility Gradient

The maximum stream gradient downstream of a given reach, assumed to be 12% after Lindley *et al.* (2006).

could sufficiently match the description to a location on a USGS topographic map. Error would be necessarily introduced in the process, particularly for fine-grained predictors such as stream gradient and valley-width index.

To minimize the effect of these errors, we resampled the occurrence data before computing the envelopes (Figure 12). In particular, we created 50,000 resampled datasets (resampled with replacement; each resample having a sample size equal to the original dataset) and fit envelopes to each one, and then constructed a "consensus envelope" for each predictor. A consensus envelope is the interval on the predictor that is common to all 50,000 models (the way in which the 50,000 models "agree" with one another). Similarly, we con-

Table 7. Bioclimatic envelopes used to assess potential steelhead habitat.

Predictor	Consensus Envelopes		95% Envelopes	
	Min	Max	Min	Max
So.-Central California				
Coast Steelhead ESU				
Gradient (%)	0.23	6.2	0.03	9.31
Valley width index	5.84	26.28	3.44	37.53
Mean ann. discharge (cfs)	2.12	58.6	1.06	87.9
Low summer discharge (cfs)	0.24	3.64	0.08	10.61
Mean annual temp. (° C)	-	15.0	-	15.2
Mean August temp. (° C)	-	20.4	-	22.0
Southern California				
Coast Steelhead ESU				
Gradient (%)	0.51	8.26	0.03	10.57
Valley width index	3.76	18.68	2.69	29.56
Mean ann. discharge (cfs)	1.06	56.2	0.35	78.8
Low summer discharge (cfs)	0.09	3.87	0.03	6.06
Mean annual temp. (° C)	-	16.2	-	17.4
Mean August temp. (° C)	-	23.5	-	24.1

Notes: Envelopes for mean annual and mean August temperatures were assumed to have no lower limit. Mean annual discharge used only for sensitivity analyses (see next section).

structed "95% envelopes," defined as the agreement between the 95% of the models that were the least deviant. Envelopes were fit separately for the two steelhead ESUs in the study area. The final values for the envelopes are in Table 7.

When fitting envelopes, we used observations of both resident and anadromous *O. mykiss*, assuming that the two forms have similar freshwater niches. However, when using the envelopes to prepare maps, etc., we wished to screen out areas lying above natural barriers to anadromy. Since we required a method that could be consistently applied across multiple basins, we assumed that reaches upstream of naturally-occurring 12% gradients (as computed from the DEM) were inaccessible to steelhead (Lindley *et al.* 2006, Engle 2002).

4.4. Potential Habitat in the SCCC Section

Maps of potential unimpaired habitat for this study area are depicted in Figure 13 - Figure 15 on the following pages. For reference, we used the information in Table 2 (p. 21) to indicate on the maps the basins with historical or current evidence of steelhead use.

There appear to be two principal differences between the habitat maps and occupancy status. First, the Pacheco Creek subbasin in the north-east corner of the Pajaro system is currently occupied, but is not predicted to contain any potential habitat. There is a reasonable explanation for this: The reservoir on the North Fork Pacheco may keep stream temperatures unnaturally low and stream flow unnaturally high during the summer.

The second principal difference consists of the numerous small patches of habitat on minor tributaries of the Salinas Valley and San Benito Valley. It is not clear whether this difference is a failing of the habitat model or a failing of the historical record. On the one hand, all these patches lie in a hot, extremely dry area, and it is not surprising that such areas have no record of *O. mykiss*. And yet, two similar sub-basins *do* have records of steelhead occurrence, as seen on the map: they are Gabilan Creek (directly east of central Monterey Bay) and Tequisquita Slough (actually, Arroyo Dos Picachos, between Gabilan Creek and Pacheco Creek).

Arroyo Dos Picachos and Gabilan Creek exhibit specific characteristics beneficial for steelhead. Both are relatively well shaded by riparian vegetation. Dos Picachos has consistent summer flows, probably due to volcanic geology; and Gabilan Creek probably has significant influence from coastal weather (i.e. cool fog in the summer). Most of the other streams in the San Benito and east-side Salinas watersheds are in arid areas with low streamflows and little stream shading (savannah and chaparral). Even some of the higher-elevation tributaries, such as Clear Creek in the upper San Benito, are "hot," with asbestos geology, sparse vegetation, and no stream shading.

Possibly the small west-side tributaries near Hollister would have had steelhead runs historically.

Perhaps it is more useful to note the points on which the historical occupancy data and the habitat maps agree. These are:

1) Under unimpaired conditions, the steelhead population in the Pajaro would probably tend to be focused on the southern Santa Cruz Mountains; these are the redwood forests drained by Corralitos, Uvas, Llagas, and Pescadero Creeks.

2) The Carmel River and Arroyo Seco each have extensive areas of potential habitat, in accord with their reputations as steelhead streams.

3) The Nacimiento and San Antonio Rivers, major tributaries of the Salinas, have high potential as steelhead streams; the map suggests that the potential habitat is concentrated in the far upper reaches of each sub-basin.

4) The Big Sur Coast has the potential for numerous extremely small populations of *O. mykiss*. The basins with the most extensive potential appear to be the Big Sur and/or Little Sur basins, although the Big Sur is known to have a natural migration barrier that restricts access to habitat upstream of the state park boundary.

5) A set of more extensive, though still small, populations could potentially occur in coastal San Luis Obispo County (San Corpoforo Creek to Arroyo Grande Creek). The fish in the Arroyo Grande system may have been the most extensive of these populations.
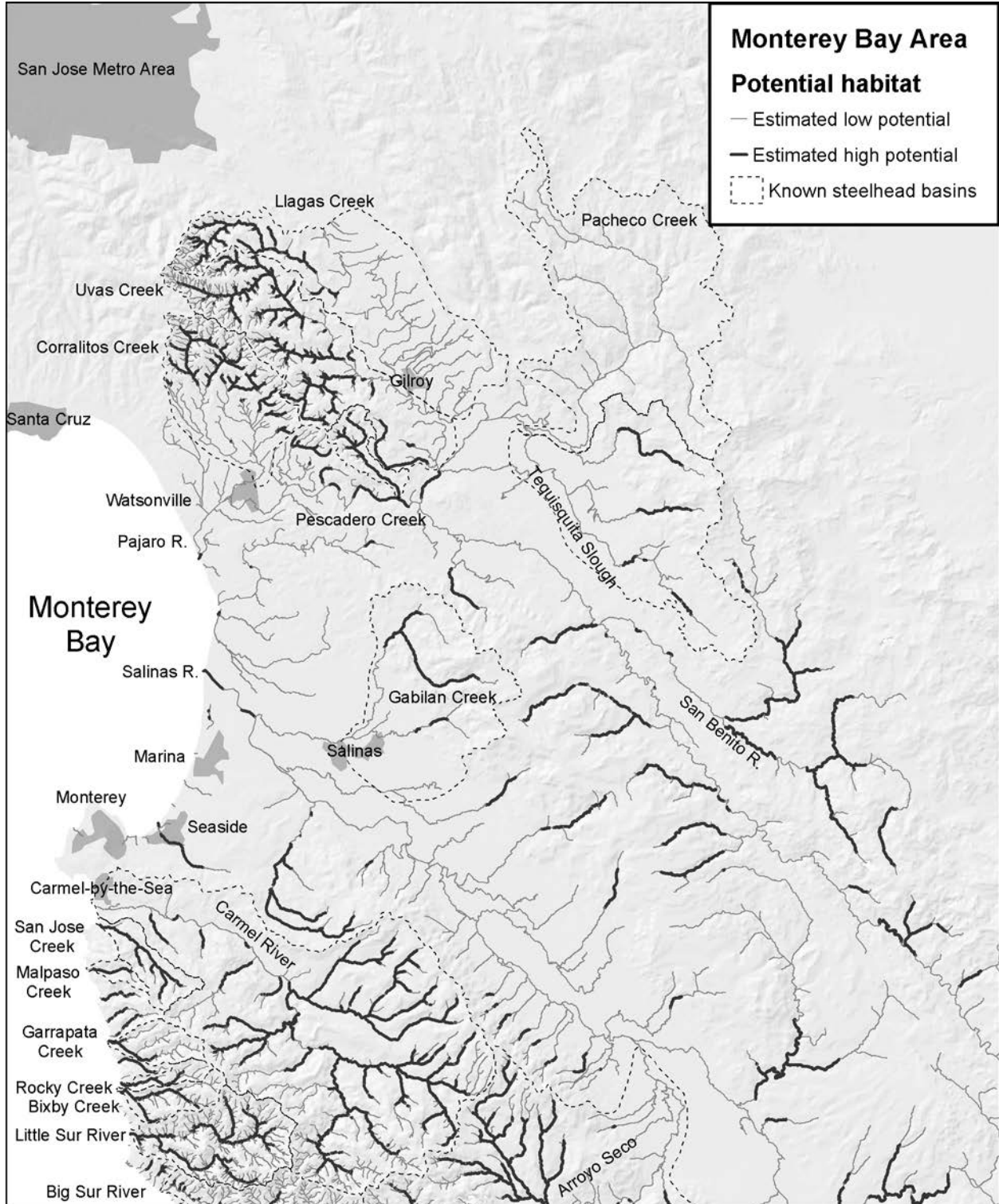
Figure 13. Potential oversumming habitat in the Monterey Bay Area, from Boughton and Goslin (2006).
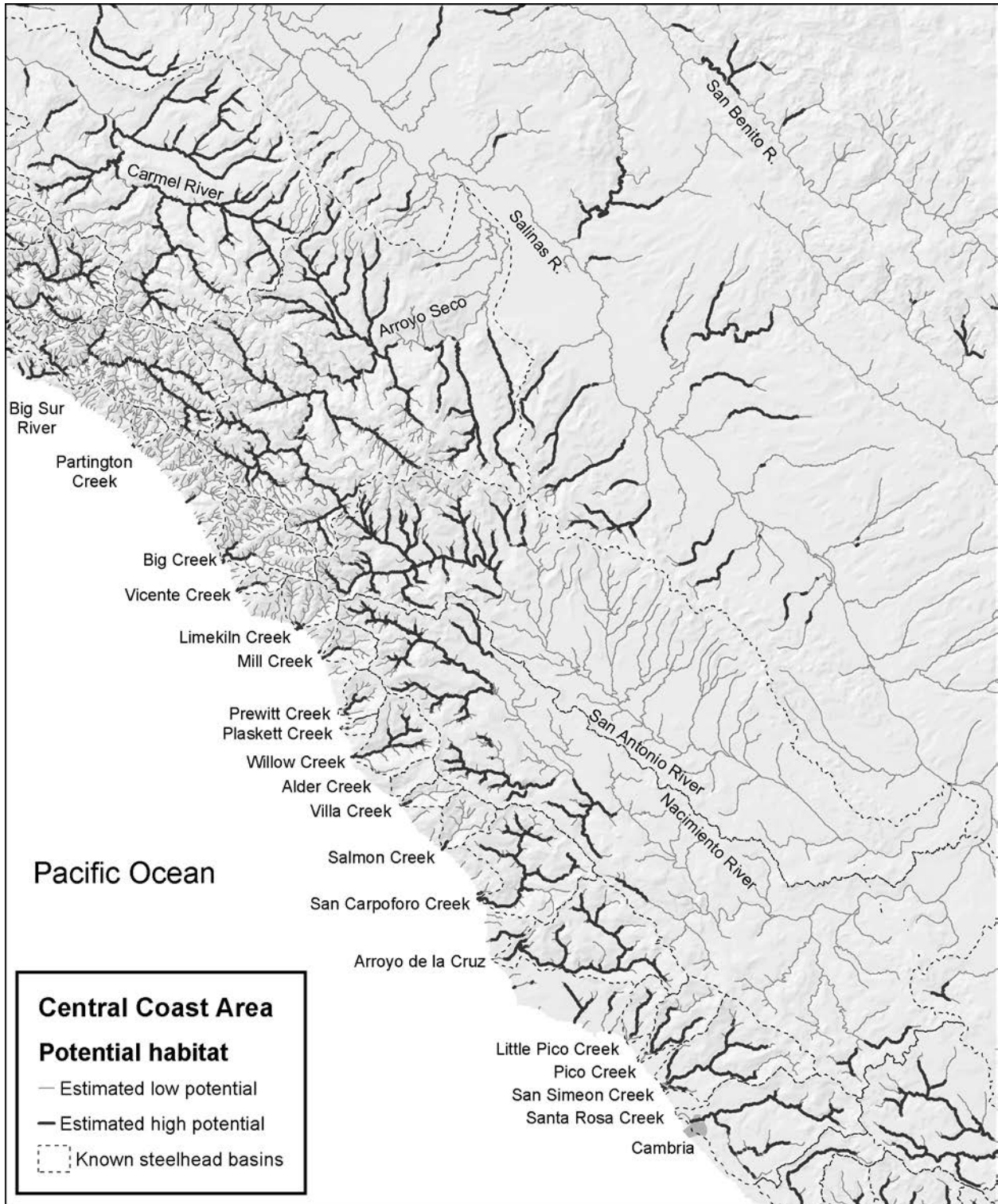
Figure 14. Potential over-summering habitat in the Central Coast Area, from Boughton and Goslin (2006).
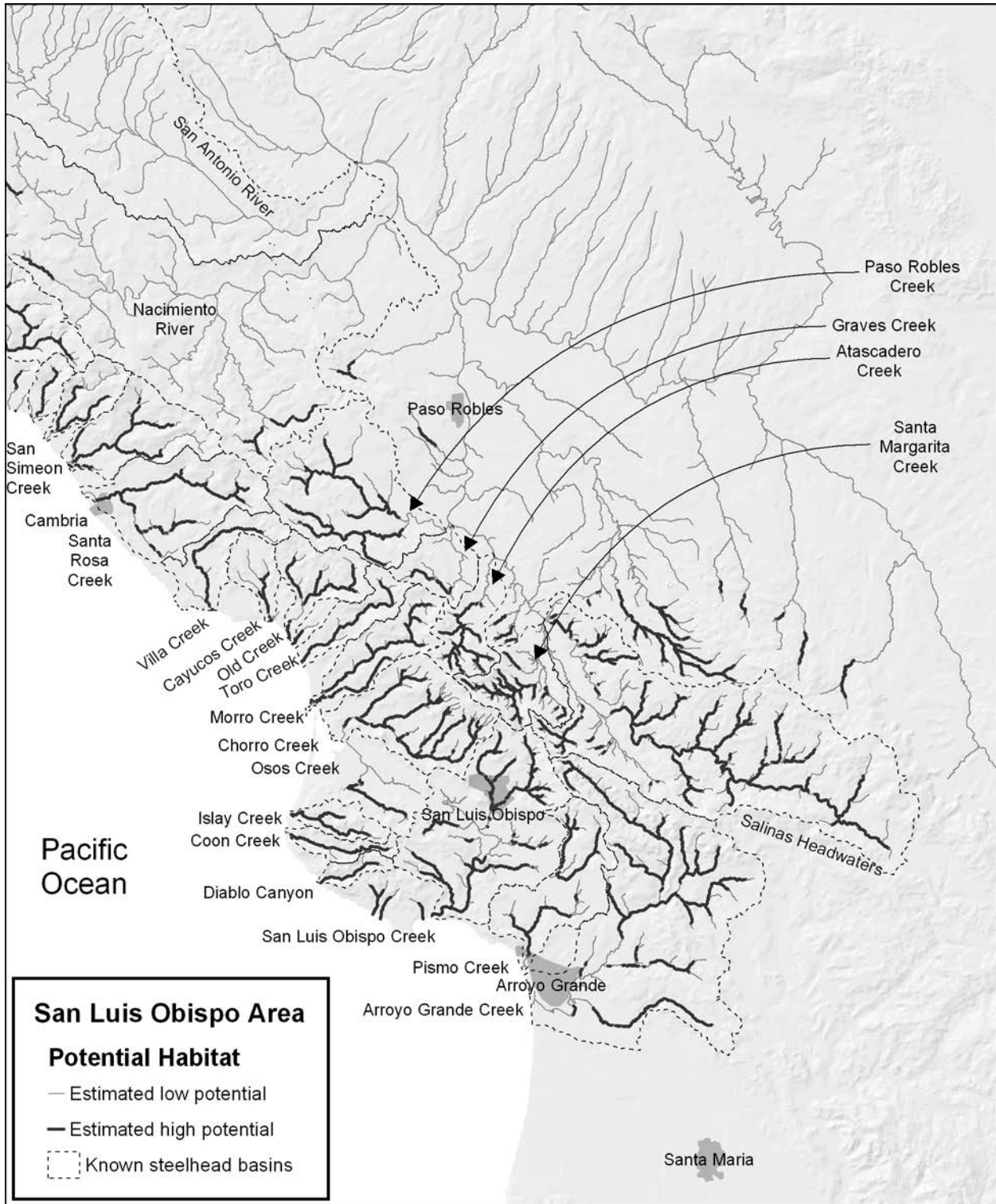
Figure 15. Potential over-summering habitat in the San Luis Obispo Area, from Boughton and Goslin (2006).

4.5. Potential Habitat in the NOLA Section

Maps of potential habitat for this section are depicted in Figure 16 - Figure 18 on the following pages. For reference, we used the information in Table 2 (p. 21) to indicate on the maps the basins with historical or current evidence of steelhead use.

The maps clearly depict that the most extensive area of potential habitat occurs in a wide swath from the headwaters of Huasna and Alamo Creek (north of Twitchell Reservoir in the Santa Maria Basin), southeast through the San Rafael Wilderness (Sisquoc River watershed), the eastern Santa Ynez basin, and finally to the Sespe and Piru watersheds, each major tributaries of the Santa Clara River. This result largely conforms to expectations based on the historical record—that this area is the most important steelhead area in the entire NOLA + SOLA areas.

Specifically, here are a number of points suggested by inspection of the maps:

1) Potential habitat in the Santa Maria, Santa Ynez, and Santa Clara is notably more extensive than in any other basins.

2) Most of the potential habitat in the Santa Maria system occurs in the Sisquoc River basin and in the lower part of the Cuyama River basin.

3) Most of the potential habitat in the Santa Ynez system occurs in the east (upper) half of the basin; however, the model predicts a distinct patch in Salsipuedes Creek (southwest basin) and the adjoining mainstem of the Santa Ynez River

4) The Santa Clara has large areas of potential habitat in basins of Sespe Creek and Piru Creek; most is concentrated in the western headwaters.

5) The model predicts a distinct patch of potential habitat in the far eastern end of the Santa Clara basin. This area appears to be in the rain shadow of the San Gabriel Mountains, and probably does not contain habitat.

6) A significant amount of potential habitat occurs in the numerous small coastal basins lying along the Santa Barbara coast and, to a lesser extent, along the Malibu coast. This is a model result that conforms to expectations based on the historical record and anecdotal observation.

7) Some model predictions do not conform to widely-held expectations. For example, the model suggests potential unimpaired habitat in the Ventura River system occurs in Canada Larga (lower basin) but not much in the headwaters of Coyote Creek, both contrary to expectations and anecdotal observation. One prediction that does conform to expectations is the potential habitat in Matilija Creek and tributaries.

8) Also contrary to expectation were the lowest tributaries in the Santa Clara system. These numerous small drainages immediately north of the towns of Ventura and Saticoy were not expected to comprise potential habitat.

9) Finally, the model predicted a surprisingly modest amount of potential habitat in the Malibu Creek system. It did not include Cold Creek, a tributary thought to currently comprise good over-summering habitat for *O. mykiss*.

Anyone with an interest in steelhead occurrence in this area is similarly going to be able to identify numerous additional discrepancies between the model and their expectations. Given the numerous factors controlling habitat suitability, site-specific information when available is likely to provide a more refined picture than the model predictions summarized above.
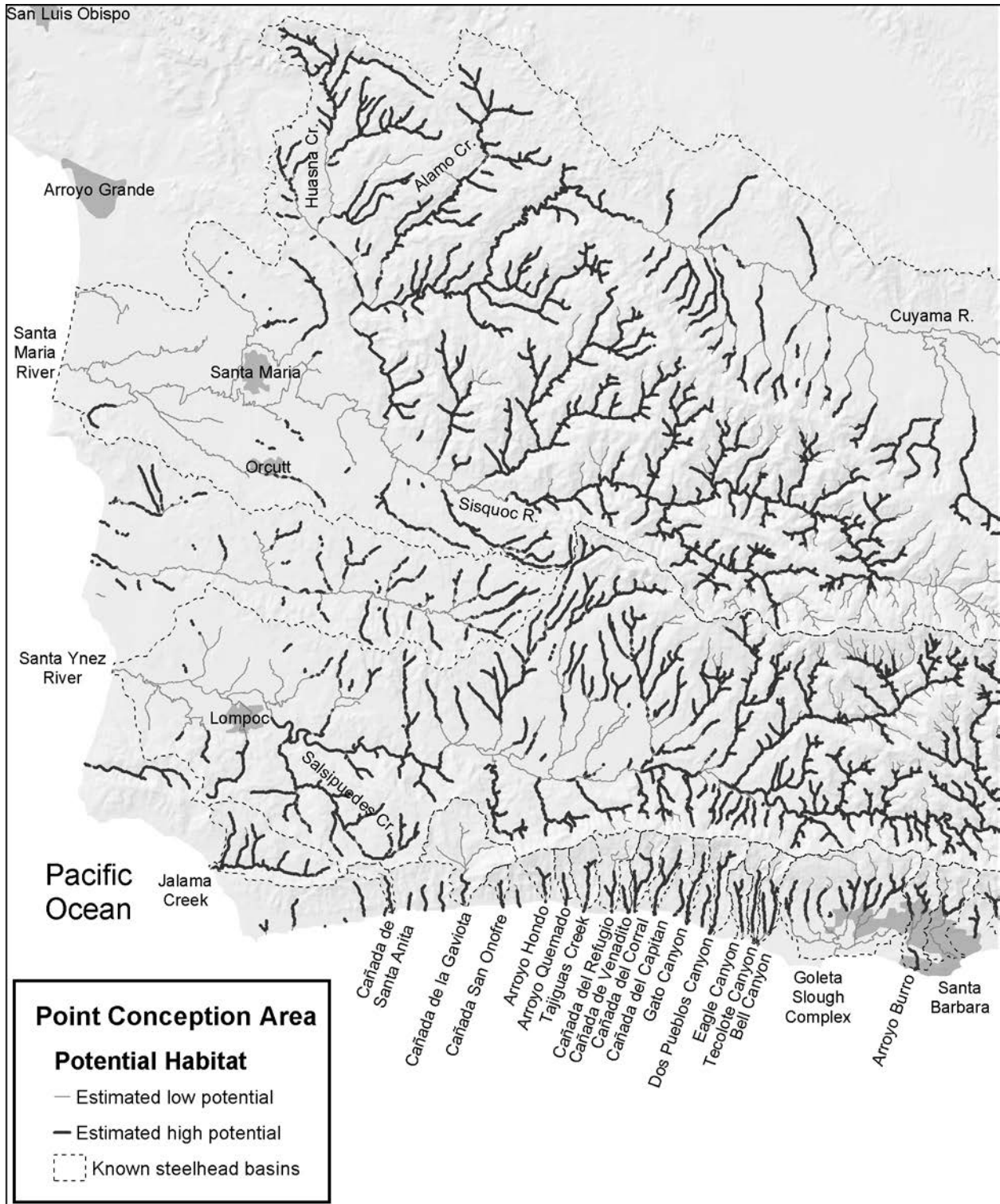
Figure 16. Potential over-summering habitat in the Point Conception Area, from Boughton and Goslin (2006).
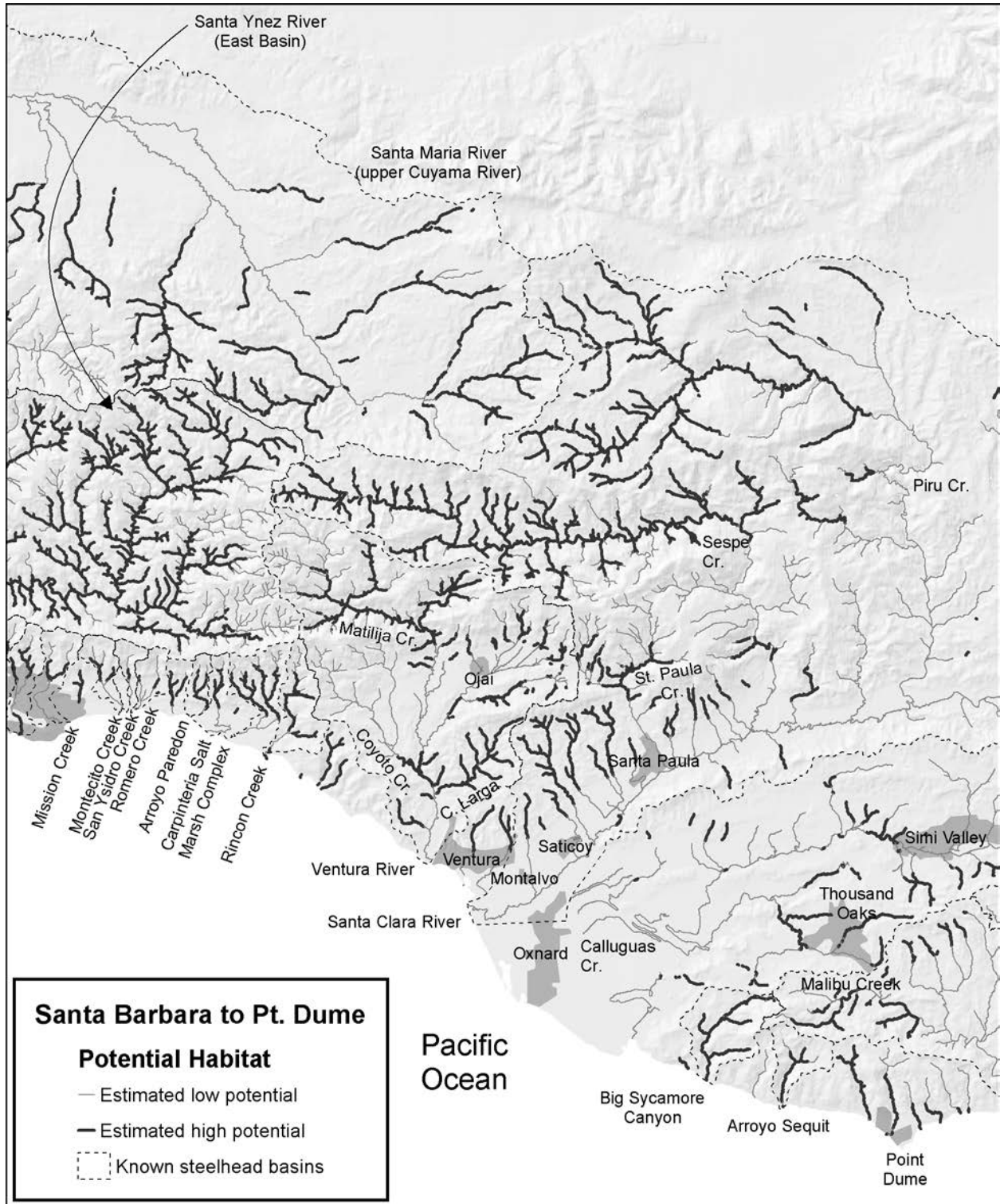
Figure 17. Potential over-summering habitat, Santa Barbara to Point Dume, from Boughton and Goslin (2006).
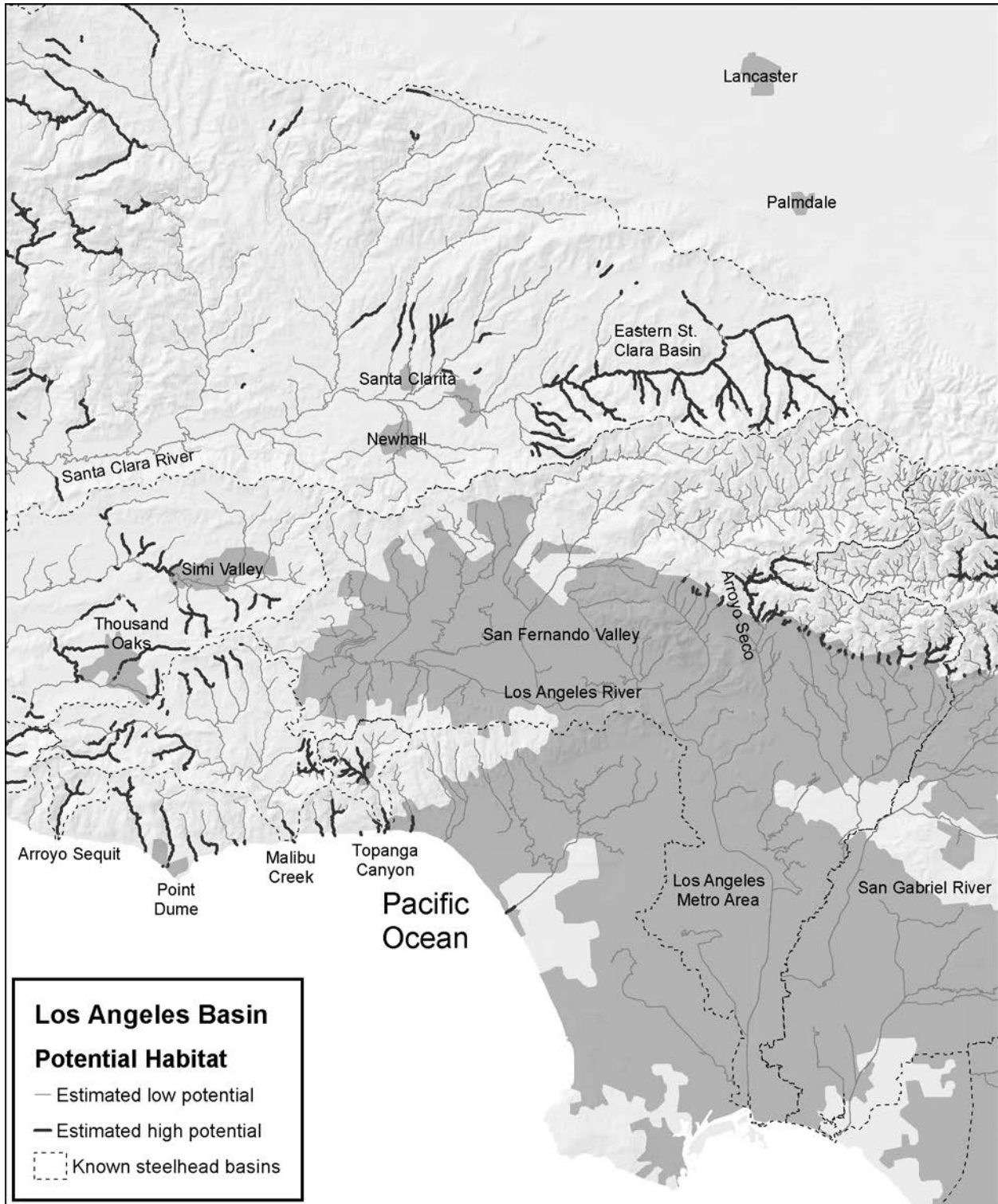
Figure 18. Potential over-summering habitat in the Santa Monica Mountains and Los Angeles Basin, from Boughton and Goslin (2006).

4.6. Potential Habitat in the SOLA Section

Maps of potential habitat are in Figure 19 - Figure 22 on the following pages; also in Figure 18 on the preceding page. It is difficult to compare the model results to expectations for the SOLA study area, because we do not have any firm expectations for the area. The historical record is very sparse (Titus *et al.* 2003). Thus it seems safer to view the model predictions as interesting hypotheses. Some of the more notable are:

1) The Los Angeles River system contains almost no potential unimpaired habitat, with the possible exception of the headwaters of Arroyo Seco and Big Tujunga Creek.

2) The San Gabriel River system appears to have several significant patches of potential habitat in its northern headwaters.

3) Small patches of potential habitat are scattered throughout three headwaters areas of the large Santa Ana basin. The most extensive of these appears to be the area between the Cucamonga Wilderness and Cajon Summit, but Bear Creek and Mill Creek in the mountains above Redlands are also noteworthy. The final of these three areas is in the far headwaters of the San Jacinto River, which infrequently discharges into the Santa Ana via Lake Elsinore. This last patch is very isolated indeed.

4) A noteworthy patch of potential habitat appears to occur in Santiago Creek and tributaries, in the hills southeast of Anaheim. This is the only patch of potential habitat in the Santa Ana River system that is near the ocean.

5) The moderate-sized coastal basins of San Juan Creek, San Mateo Creek, and San Onofre Creek—clustered around the Orange-San Diego County Line—appear to have significant patches of potential habitat.

6) The Santa Margarita basin has two clusters of estimated potential habitat—one in the upper part of Camp Pendleton and the reach between Fallbrook and Temecula; and a second in the headwater region in San Diego County.

7) South of Camp Pendleton, the model suggests numerous small patches of potential habitat, none particularly large. The most extensive appear to be Keys Creek, a tributary of the San Luis Rey River; the mainstem San Luis Rey itself in the canyon below Lake Henshaw; Escondido Creek and San Dieguito River just southwest of the town of Escondido; the headwaters of the San Dieguito River northeast of Ramona; the headwaters of San Vicente Creek just south of Ramona; and headwaters of the San Diego River and Conejos Creek above current-day El Capitan Reservoir. In the extreme far south, both the Sweetwater River and Cottonwood Creek (a tributary of Tijuana River) appear to have surprisingly extensive networks of potential habitat in the upper reaches.

Figure 19. Potential over-summering habitat in the San Gabriel Basin and Orange County, from Boughton and Goslin (2006).

Figure 20. Potential over-summering habitat in the Santa Ana River basin, from Boughton and Goslin (2006).

Figure 21. Potential over-summering habitat in North San Diego County, from Boughton and Goslin (2006).

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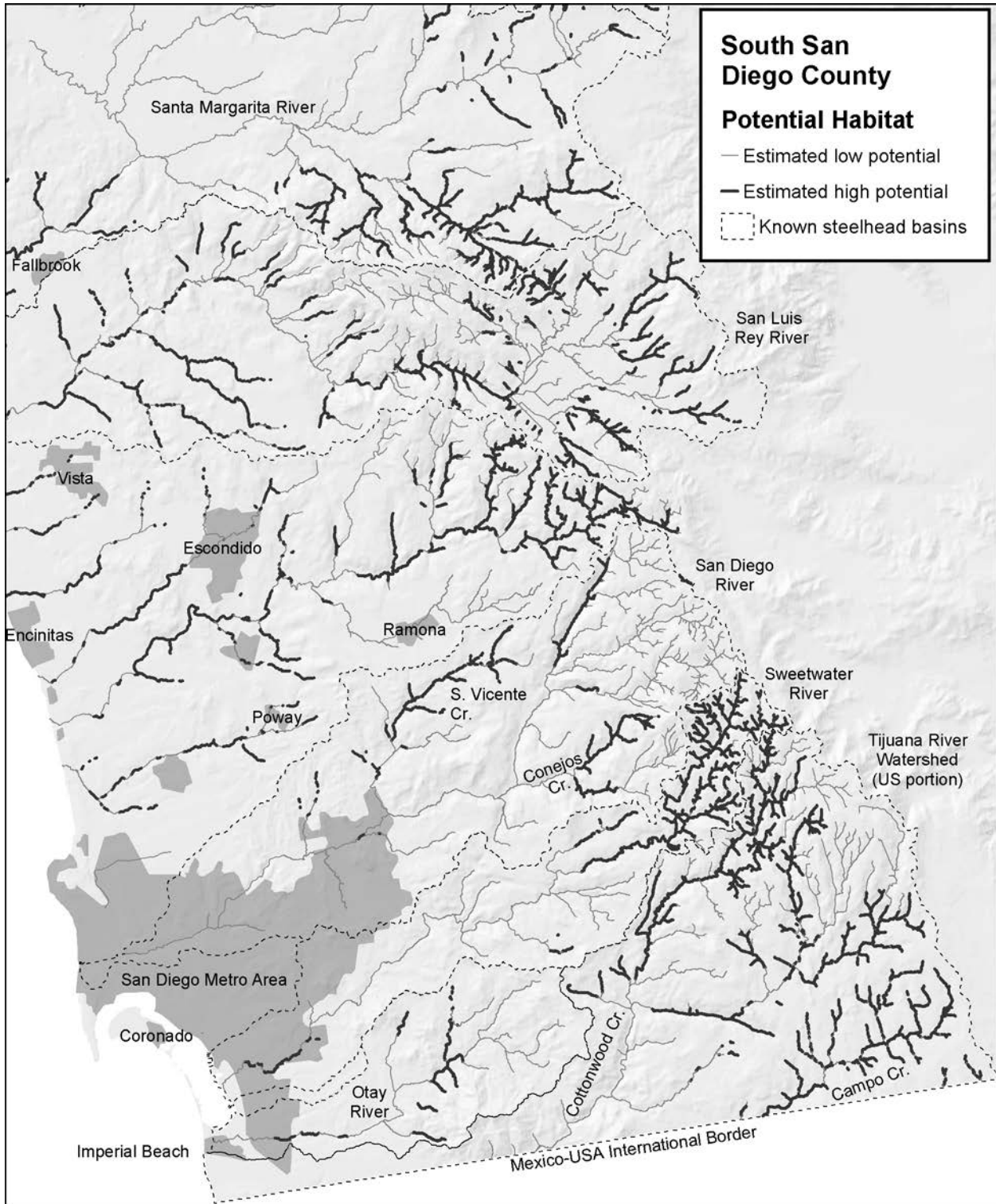
Figure 22. Potential over-summering habitat in South San Diego County, from Boughton and Goslin (2006).
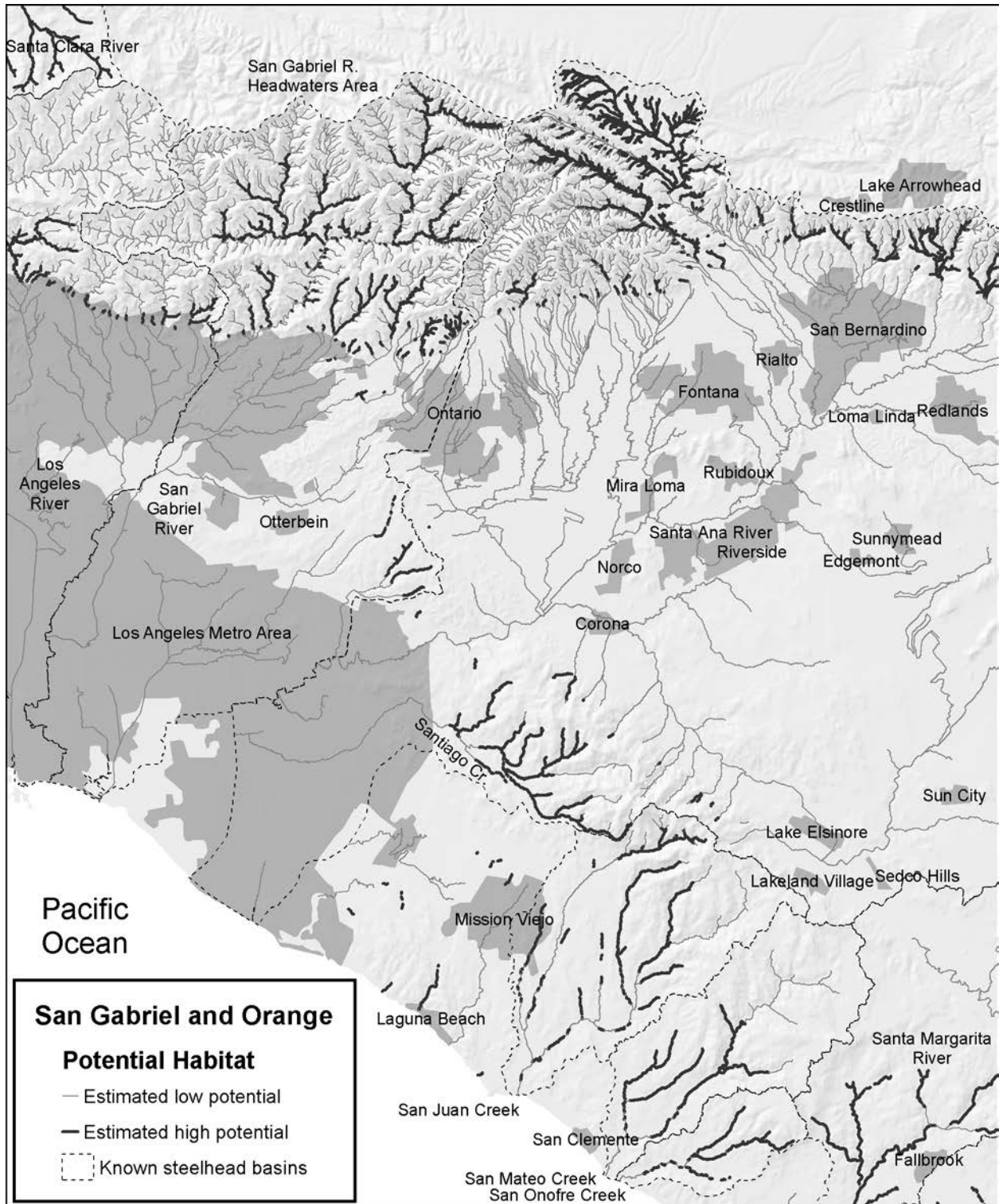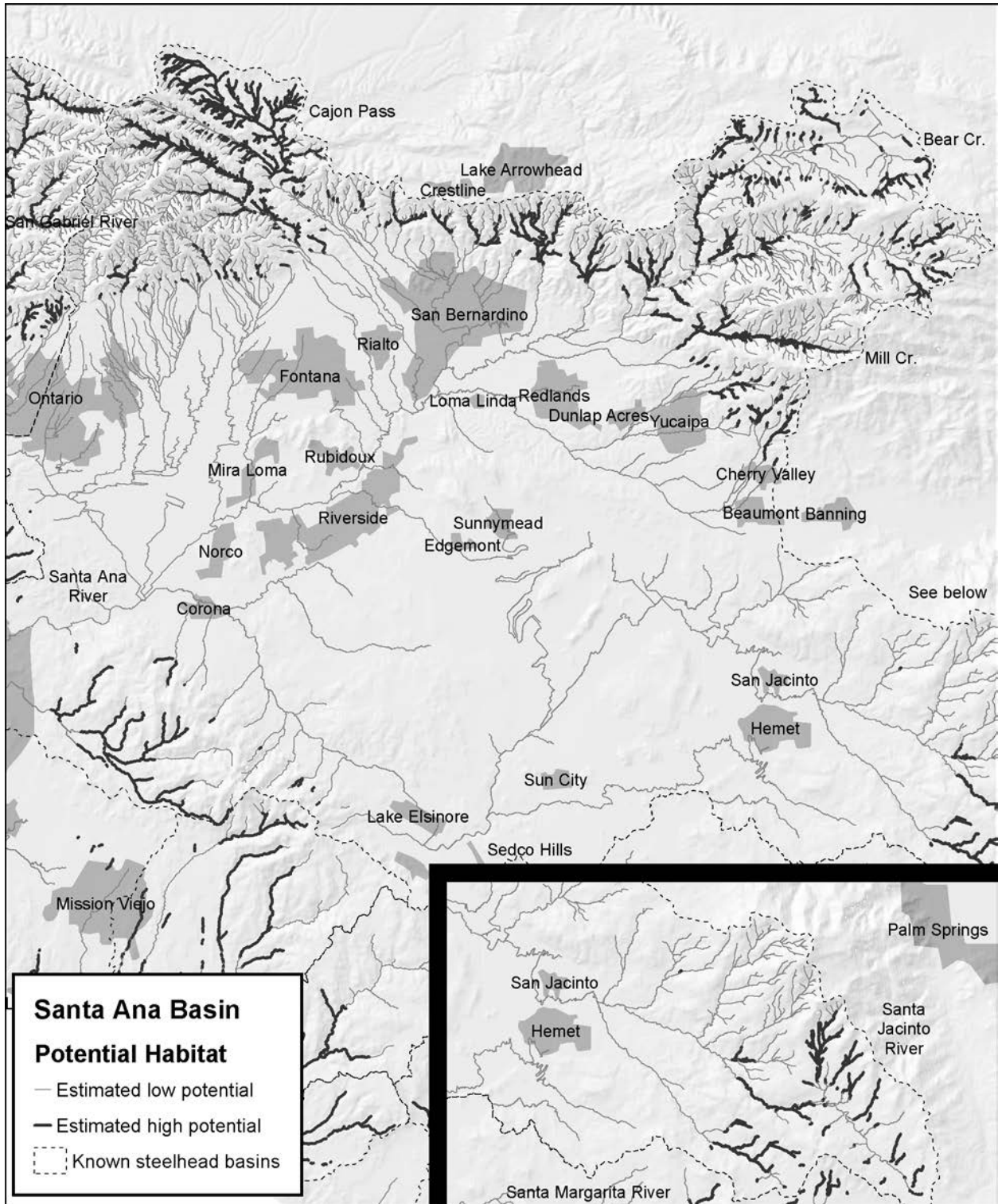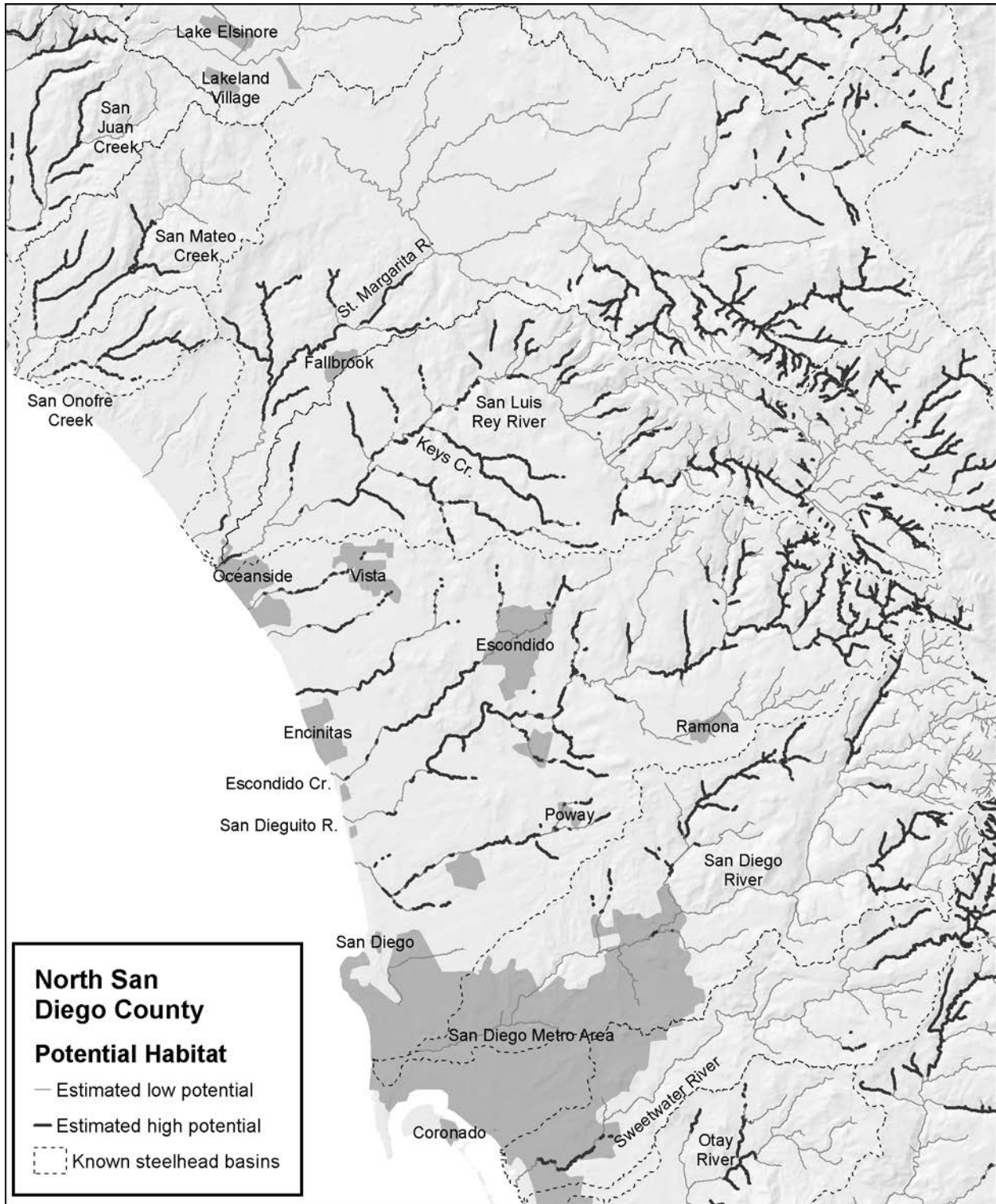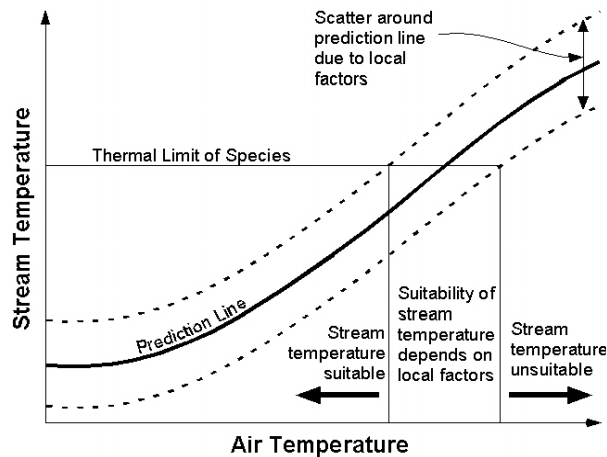
Figure 23. A conceptual model of the relationship between air and stream temperatures, adapted from Mohseni and Stefan (1999). Our habitat model used air temperature to predict steelhead habitat, and would be expected to underpredict in areas where the air temperature is near the thermal limit of the species but local factors create cool thermal refugia.

4.7. Discussion: Key Assumptions and Issues of Interpretation

We wish to direct attention to some key simplifying assumptions of the habitat model that affect interpretation of the assessments described in Part 5 and Part 6 of this report. These assessments used the results from the potential habitat model as input.

The first key assumption is that all potential habitat has about the same potential quality. Quality is generally measured as the productivity of habitat—for example, the average number of smolts produced per kilometer of habitat—or as the "standing crop" that the habitat can support at equilibrium—for example, the mean juvenile density over many generations of fish. Habitat quality can sometimes also mean the stability of the above quantities—that is, habitat that is reliably productive is considered high quality.

There is the possibility that for a given basin, a few small pockets of high-quality habitat would generate most of the fish or provide the most reliable habitat for years with poor climatic conditions; or that high-productivity areas are not con-

sistent year-to-year (Cooper *et al.* 1986). At present we do not have sufficient data to evaluate this hypothesis systematically across the entire study area.

A second key assumption concerns summer temperature. As mentioned earlier, using August air temperature to predict steelhead habitat makes an implicit assumption that monthly air and water temperatures are closely related. Though the two have a direct relationship (Mohseni and Stefan 1999), there is probably scatter around the prediction line caused by local factors such as groundwater inputs, hill-shading, local evapotranspiration of plants, *etc.* (Story *et al.* 2003, Wehrly *et al.* 1997).

Of notable importance is pool depth. We have occasionally observed distinct summer thermoclines in pools deeper than 2 m, in places such as San Mateo Creek (San Diego Co.), the Santa Margarita River between Fallbrook and Temecula, and in Topanga Creek. In each case the colder bottom water appeared to provide refuge for steelhead and also deter predatory warm-water exotics such as largemouth bass. A similar pattern has also been documented by Matthews and Berg (1997) in Sespe Creek, who examined two pools and found only one to maintain suitable temperatures for salmonids. It should be noted that near the study site of Matthews and Berg (1997) are two tributaries of Sespe Creek (Lion Creek and Piedras Blancas Creek) that appear to comprise thermal refugia in their entirety, not just in a small subset of pools. Douglas (1995) described a not-unsimilar pattern in the Santa Ynez River system nearby. We have no quantitative understanding of the underlying factors for such creek-level heterogeneity, though again it ultimately has to do with local factors such as groundwater fluxes, riparian- and hill-shading, and so forth.

Our model would not be expected to identify thermal refugia created by the above-mentioned fine-resolution factors. Moreover, we expect these sorts of refugia to be proportionately more important in the warmer areas where air temperature is near the thermal tolerance of the species (Figure 23). Thus, our model is prone to systematic error in the SOLA area.

Similarly, our model of mean summer discharge ignores the potentially important influence of local factors. It is generally recognized that many streams in the study area are spatially intermittent: some reaches have perennial surface flow and abundant fish, whereas a short distance away the summer discharge is totally underground (Spina *et al.* 2005). Geological substrate and geomorphic structure of the stream channel probably play a large role in determining patterns of groundwater flux and intermittency (Harrison *et al.* 2005; see also Figure 3 concerning Arroyo Seco). Hydraulic conductivity of the soil and depth to bedrock probably influence the retention of winter rains for summer discharge (Beighley *et al.* 2005). Losses to evapotranspiration in riparian plants may also be important. Summer flows are so low and so critical that even small sources of water flux are likely to be important. Also important are instream and riparian cover (Douglas 1995, Carpanzano 1996) and stream depth (Spina 2003).

We believe that these local factors are too complex to model at the broad scale addressed by this memorandum. It is difficult, for example, to make generalizations about the influence of geology on summer discharge that hold true across the entire study area. However, more focused work is likely to be tractable and useful. An example of a more focused analysis is the work of Harrison *et al.* (2005) on hydrologic patterns in the Santa Monica Mountains. They found that the streams with the most persistent summer baseflow were associated with the Santa Monica thrust fault and the Malibu Coast fault. The results led them to suggest that the eastern portion of the Santa Monica Mountains was likely to offer higher potential for summer baseflows due to favorable geology. The work in the Santa Monica mountains strongly suggests a need to better understand geologic and geomorphic controls on habitat and water conditions—particularly summer pool habitat.

Titus *et al.* (2003) identified four historical steelhead basins in the Santa Monica mountains (Table 8), and if we were to rank them via our model of potential unimpaired habitat then the basin with the most over-summering habitat would be Malibu Creek followed by Big Sycamore Canyon.

Table 8. Potential over-summering habitat in four basins of the Santa Monica Mountains

Basin (West to East)	Potential unimpaired habitat[1]	Favorable Geology?[2]
Big Sycamore Canyon.	26.1 km	No
Arroyo Sequit	9.3 km	No
Malibu Creek	57.4 km	Yes
Topanga Creek	19.1 km	Yes

[1] As predicted by the model described here.
[2] *cf* Harrison *et al.* (2005)

However, if one were to take geology into account then the second-ranked basin should probably be Topanga Creek[1]. Indeed, Harrison *et al.* (2005) found that of the 13km of Big Sycamore channels that they surveyed, only 2% had surface flow during summer.

Another issue of interpretation is as follows. Inspection of the bioclimatic envelopes in Table 7 suggests that the two ESUs had similar tolerance limits for most of the predictors, but with notable exceptions. For example, in the 95% envelopes, the lower limit for summer discharge was 2½ times smaller in the southern ESU as compared to the south-central ESU. Similarly, the upper limit for temperature (both mean annual and mean August) was about 2° C higher in the southern ESU compared to the south-central ESU.

One possible explanation for the differences is that steelhead of the Southern California Coast ESU are locally adapted to hotter, drier conditions. Another is that the habitat used by steelhead in the southern-most ESU is not actually hotter or drier, but rather has a different relationship with the predictors we used (mean air temperature and inferred mean summer discharge).

The data are far from sufficient to distinguish between the local-adaptation hypotheses and the different-relationship hypothesis, but for a variety of reasons we tend to favor the latter. So far, researchers have not found local genetic adaptation in the thermal tolerances of *O. mykiss* (Myrick and Cech 2004, but see Spina 2006). On the other hand,

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[1] Malibu and Topanga Creeks are the two basins of the four that currently harbor steelhead populations

researchers have indeed found fine-scale variation in stream temperatures, and have also found that salmonids routinely exploit this variation by retreating to the cold-water patches during the hottest period of the day (Torgerson *et al.* 1999, Ebersole *et al.* 2004, Matthews and Berg 1997). In the southern area, one would expect a larger proportion of steelhead to occur in these refugia, and this would tend to give them the appearance of greater tolerance when in fact the real pattern is that they are more likely to be found in thermal refugia (that is, thermal refugia are proportionately more important to the populations further south). More fish in thermal refugia means a greater difference between mean air temperature and the water temperature of occupied habitat, which in turn gives the (false) impression of higher temperature limits for the fish. A similar argument could be made for mean summer discharge and its relationship to the stream segments with enough depth and flow to actually be used by the fish.

If true, the implication of the different-relationship hypothesis is that the predictions of the habitat model have a greater propensity for false positives in the southern California coast ESU than for false positives in the south-central California coast ESU. These false positives would tend to occur at a finer resolution than addressed by the model.

Another limitation is that we assume the predictors to have no interaction effects—that is, the zone of tolerance on one predictor does not depend on the level of another predictor. One possible violation of this assumption is a positive interaction between water temperature and stream flow. High stream flow is thought to increase the food supply of the fish, which might make them more tolerant of warm water (which boosts basal metabolic rate and thus energy consumption). High stream flow also tends to reduce diurnal fluctuations in temperature—that is, it would tend to decrease the maximum daily temperature for a stream even though it probably would have negligible effect on the mean daily temperature (Sinokrot and Gulliver 2000). Thus, the envelope model may underpredict with respect to the suitability of large, warm streams. See Boughton and Goslin (2006) for more detail about model assumptions.

A final point concerns the model-fitting process. To fit the habitat models, one must assume the species to currently occupy the full range of conditions that it did so originally. In short there must be extant examples of the full range of suitable habitats for the model to avoid underprediction. One possible violation of this assumption concerns large mainstem rivers in alluvial valleys. These have all been impacted by human activities, namely the clearing of riparian vegetation and the alteration of hydrologic cycles. There is historic evidence that these large mainstem rivers once had a very different character than they do now, and they were quite possibly suitable habitat under these original conditions. The interested reader is referred to the appendix (§10.2 on p. 98), which describes historical accounts of baseline conditions, and later accounts of extensive clearing of riparian vegetation, downcutting of channels, and loss of perennial flow in some of the larger streams in the study area.

Part 5. Assessing Potential Viability of Unimpaired Populations

In this part of the report we continue our structured assessment of recovery potential, focusing on 1) a detailed description of the uncertain assumptions necessary for the assessment, and 2) the assessment itself, in the form of a ranking system for recovery potential. This assessment is intended to address, so far as is possible, a fundamental question about recovery:

Which of the original populations of steelhead in the study area would have the highest likelihood of being viable if restored to an unimpaired state?

Here, "viability" means an acceptably low extinction risk within a specified time horizon; the convention in the scientific literature has been to set "acceptably low" as < 5%, and the time horizon as 100 yrs. However, these numbers are somewhat irrelevant to our purposes here, because we lack the data to judge viability at this level of precision. Typically, with even the simplest quantitative models one would need to have at hand estimates of annual abundance for 30 yr or more (Lindley 2003, Lotts *et al.* 2004).

Thus, a more qualitative approach is necessary. Before developing such an approach, however, it is useful to review some key elements of the theory of population viability.

5.1. Key Concepts in Viability Theory

Population viability is based on a few core concepts. The first is simply that, for a population to persist indefinitely, on average each adult fish in a population must give rise to at least one adult fish in the next generation. This number is known as the net reproductive rate (or basic reproduction ratio). If this number is less than 1.0, the population declines to extinction (although if the number is 0.999, it can take a very long time). If the number is greater than 1.0, the population increases to carrying capacity, at which point the net reproductive rate equilibrates at 1.0 and the population stabilizes. It is useful to think of the above conditions as the "deterministic criterion" for viability.

More recent concepts of viability emphasize stochastic elements of viability. "Stochastic" simply means processes with a random component—*i.e.*, processes with a component that can be predicted not with certainty but via statements of probability. Real populations are faced with a large array of stochastic perturbations, and fluctuate randomly. A population can have a long-term upward trend (average net reproductive rate greater than 1.0 over multiple generations), but be fluctuating up and down with respect to this overall trend (*i.e.*, some years have net reproductive rate much greater than the mean, some much lower than the mean). If the fluctuations are large enough, the population is likely to fluctuate to zero animals even though the overall trend is upward. A branch of population viability theory therefore asks: what traits of a population reduce its probability of being driven extinct by random events? Much of the discussion in McElhany *et al.* (2000) focuses on this question.

One thing is clear: The importance of the number of independent, parallel vital events in a population. Vital events are of three kinds: birth, death (or lack thereof), and mating. For a given kind of event (say deaths), the larger the population, the lower the probability that randomness in deaths will cause a large deviation from the expectation (*i.e.* the mean mortality rate). If the expectation is for low death rate and high birth rate (*i.e.*, the first core concept), then this favors persistence. This is the second core concept of population viability. To see how it works, consider a population of fish in which the expectation for mortality is 10% per year. If the population consists of two fish, the probability of them both dying (that is, of extinction) is 10% times 10%, which is 1%. Three fish is 0.1%, four fish is 0.01%, *etc*.

The math shows that the probability of extinction becomes very small very fast as the number of fish increases but their deaths or births remain independent. Thus, the second core concept can be rephrased as: The larger the population, the less likely it is to go extinct. The same type of reason-

ing applies to matings: the larger the population, the larger the number of potential mates and the lower the probability that an animal will fail to find a mate. The larger the population, the lower the probability that all individuals will simultaneously fail to produce eggs. The larger the population, the lower the probability that a given gene will be randomly lost from the population. Large population size is the single most important trait for protecting a population from being driven extinct by random events.

This statement is so important it is worth repeating: Large population size is the single most important trait for protecting a population from being driven extinct by random events. We therefore expect that large populations will form the backbone of any effective recovery strategy. Even under unimpaired conditions, small populations are expected to eventually fluctuate to extinction due to natural events such as droughts, forest fires, or a succession of poor water years.

How large must a population be to qualify as "viable?" One can get very sophisticated about modeling various random events and estimating the minimum viable population size required to withstand them 95% of the time. However, the unifying idea of such exercises is relatively simple: when vital events are correlated (not independent), population size must be larger to avoid extinction.

To explain this, it is first useful to recall that in the "10% mortality" example described a few paragraphs ago, the math we used crucially assumed that each death was an independent event. Now consider a 10% mortality rate that is caused by drought drying up a stream in 1 out of 10 years. In this case, the same event (drought) is posing the risk to all fish simultaneously. There is no independence here; there is simply a 10% chance that drought will kill all the fish. Increasing the number of fish does not decrease the risk of extinction, because the deaths are perfectly correlated across the population. The third core concept of population viability is that positive correlation (non-independence) of vital events (births, deaths, matings) increases extinction risk, sometimes dramatically.

Table 9. 3 key concepts of population viability[1]

One
For a population to persist indefinitely, on average each adult fish in a population has to give rise to at least one adult fish in the next generation (net reproductive rate greater than 1.0)

Two
All populations experience random events, and random events increase extinction risk. Large population size is the single most important trait for protecting a population from being driven extinct by random events.

Three
The more correlated that births or deaths tend to be across the population, the larger the population has to be to protect it from extinction (Environmental stochasticity increases the population size necessary for persistence).

[1] A population is a group of fish and their progeny that share a reasonable expectation of co-occurrence in a stream segment at some point in their freshwater life cycle. See §2.4 (p.17).

In general, most correlations are less than perfect. What this means is that the risk is higher than if the births/deaths were independent across the population, but lower than if the births/deaths were perfectly correlated. In our example of 4 fish under a 10% mortality risk, a less-than-perfect correlation would entail a risk somewhere between 0.01% and 10%. This span of values is very imprecise, and it only gets more so with larger numbers of fish. It is therefore highly beneficial to have at least a rough estimate of the level of correlation, to have a more meaningful estimate of risk.

A different way of stating the third core concept is that the more correlated that births or deaths tend to be across the population, the larger the population must be to protect it from extinction. The technical term for this sort of risk (correlated births or deaths) is environmental stochasticity, because such correlations tend to be caused by environmental fluctuations, such as droughts, fires, floods, *etc*.

For convenience, we have summarized the three core concepts in Table 9. Here is a statement that we think virtually all population biologists would agree with: All else being equal, higher environmental stochasticity causes larger fluctua-

tions in population size, which requires a larger mean population size to maintain low extinction risk.

However, there are exceptions to the above statement. Imagine a situation where environmental stochasticity takes the following form: in most years conditions are slightly bad for the species, but every 10 years or so is a very good year in which conditions are nearly ideal and the members of the population experience enormous reproductive success, with little or no competition from other species. This is a scenario in which environmental stochasticity can, in a sense, prevent an extinction. Although it seems like a contrived example, it appears to be important in desert annual plants, marine reef fish, and plants with seed masting (*e.g.* Higgins *et al.* 2000).

5.2. Expectations for the Study Area

Based on population theory, we have an expectation that the largest populations in the ESU will form the backbone of an effective recovery strategy, because they are likely to have the highest viability if restored to an unimpaired state. This expectation must be qualified by the statement "all else being equal," since extinction risk is sensitive to other traits of a population besides mean size. One of the most important such traits is environmental stochasticity, expressed as the variability of the population growth rate.

We expect environmental stochasticity to be higher for steelhead in the study area than for more northerly populations. Since environmental stochasticity increases the risk of extinction, these southern populations would therefore need to have a larger mean size to compensate for the higher stochasticity, if they are to achieve the same level of safety as populations north of the study area. This statement assumes "all else being equal" which may not be the case, particularly if the southern populations have specific adaptations that enhance their resilience to environmental variability. One such possible adaptation is extreme life-history plasticity; another is an expanded level of tolerance to extreme environments, though we have no conclusive evidence for either type of adaptation.

The potential sources of environmental stochasticity in the study area are many: drought years, hot years, years when sandbar barriers at the mouths of rivers fail to be breached, *etc*. Whatever accentuates the among-year variability in survival or reproduction may be a component of environmental stochasticity. How much larger do populations need to be to compensate? To answer that question we need quantitative estimates of environmental stochasticity, and for that we need 30 yr or more of data on run size (Lindley 2003). In the next section we expand upon this issue a bit.

Finally, we expect that environmental stochasticity will be strongly influenced by the two primary climatic gradients in the study area. One gradient is the north-south trend in temperature and precipitation. The other is the coastal-inland gradient in temperature, precipitation, and seasonality; and the tendency for inland populations to have alluvial mainstems that may comprise less reliable habitat for the fish.

The north-south gradient is well known, but the coastal-inland gradient may actually be more important with regard to steelhead viability. The coastal climate appears to be cooler and to have a more restricted range of temperatures (see Plate VII). Both of these factors would lead us to expect that environmental stochasticity is weaker in coastal populations of steelhead. However, this coastal climatic zone is rather narrow (see Plate VII, especially the bottom map). Only populations in small coastal basins would likely benefit from it.

5.3. A Qualitative Ranking System

To review: For a recovery plan, we would like to identify the populations with the highest ecological potential for restoration to viability. Unfortunately, we are lacking data on some key parameters to which viability is very sensitive. Below we outline an approach based on a parameter we do have some indirect information about—namely, mean population size in an unimpaired state. We assume that the quantity of potential habitat in each basin—estimated in the previous section-- is a reasonable index of this population size, and can form the basis for a ranking system.
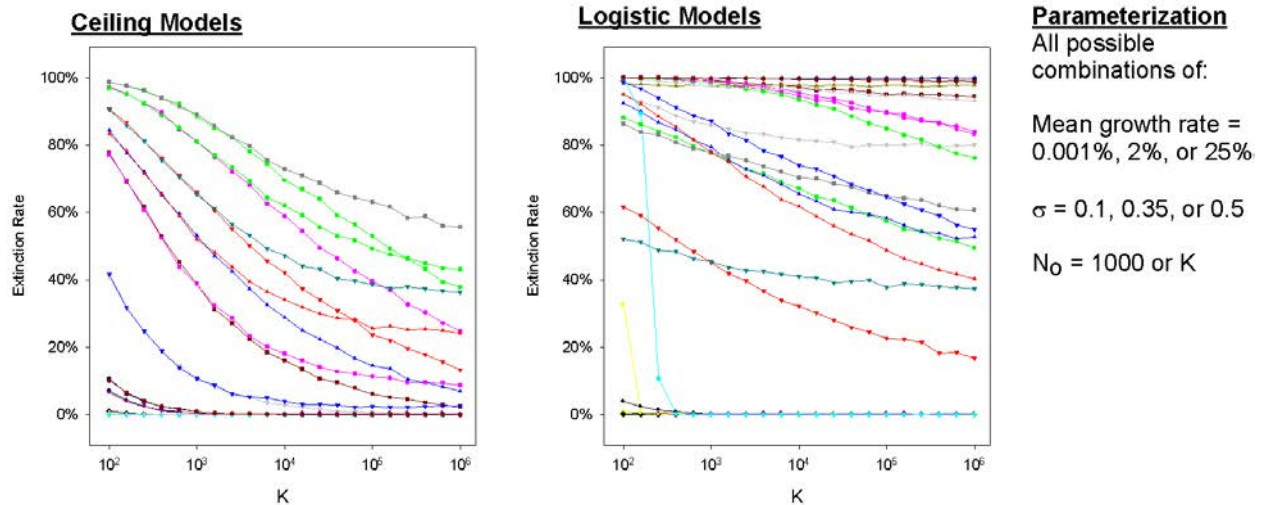
Figure 24. Robustness of the monotonic relationship of K and extinction rate. Shown are the results of 36 population models spanning a range of parameterizations. Each model was run for 100 generations, replicated 10,000 times, with the extinction rate computed from the outcomes. Mean growth rate is the average percent increase in population size each generation; sigma (σ) is a measure of variation in this growth rate among generations [$\sigma = \sqrt{Var(\ln(1 + \text{growth rate}))}$]. Typical estimates of sigma for *Oncorhynchus* populations in other parts of California range from 0.1 to 0.4 (S. Lindley, pers. comm.). The parameter N_o is the starting size for each replicate population at the start of the simulation. Density-dependence was specified as either logistic or ceiling type (The logistic model is the discrete version of the familiar logistic growth curve; the ceiling model has exponential growth up to a maximum of K, beyond which the population cannot grow).

Although this approach appears reasonable, it rests on numerous assumptions that may not always be realistic. The four over-arching assumptions that must hold true for most populations most of the time are as follows:

The Population-Size Assumption
Viability is an increasing function of mean population size, which is an increasing function of carrying capacity.

The Habitat-Quantity Assumption
Carrying capacity is an increasing function of habitat quantity

The Disturbance-Regime Assumption
Under normal ecosystem dynamics, the ratio of available habitat amount to potential habitat amount is effectively the same for the populations being compared.

The IP-Estimation Assumption
The model prediction for potential habitat has acceptably small estimation error.

When the above four assumptions hold, a ranking of IP quantity maps directly to a ranking of viability. Below we evaluate the support for, and likely exceptions to, each of these assumptions.

5.3.1. The Population-Size Assumption

> *Viability is an increasing function of mean population size, which is an increasing function of carrying capacity.*

A large scientific literature supports the idea that in general, carrying capacity (K) and viability have an order-preserving relationship. Perhaps the point is most easily illustrated with some simple population simulations designed to span the realm of possibilities for *Oncorhynchus* itself (Figure 24). The simulations summarized in the figure illustrate mainly the interplay of K, mean growth rate, and variance of mean growth rate (*i.e.*, environmental stochasticity). Each parameterization shows a monotonic, or order-preserving, relationship between viability and K,

necessary for our ranking scheme. Although we omitted certain other factors that affect extinction risk in real populations (genetic variation, demographic stochasticity), the literature suggests that they also have effects that exhibit order-preserving relationships.

The curves for the various parameterizations lie above and below each other in Figure 24, and sometimes cross. This implies the order-preserving relationship only holds in real populations if K is the only parameter that varies significantly among populations. For example, if populations with larger K tended to have more variable growth, the relationship might not hold—the risk-increasing effects of the variability might counter the risk-reduction of increased K.

In general, there is no particular reason to expect an inverse relationship between K and environmental stochasticity of the type just described. However, in the particular case of our study area there is perhaps a reason to expect it: The larger basins penetrate further inland, away from the moderating influence of the marine climate. Their larger size gives an expectation of large carrying capacity (relative to small coastal basins). However, their penetration inland gives an expectation of an unreliable climate and thus greater environmental stochasticity (relative to small coastal basins). Below we examine further evidence for this possibility, which we name "the size-stability trade-off."

Evidence for the South-Central California Coast Steelhead ESU

The temperature maps in Plate VII suggest a possible size-stability trade-off in the south-central California coast study area. The only part of the study area that has both a low mean temperature and a low range of temperature is the coast. Another bit of evidence comes from the recent survey of *O. mykiss* summarized in Table 2 on page 21. Note that in the survey, *every one* of the historical steelhead basins along the Big Sur coast was occupied by the fish.

Some of these stream systems are quite small— consisting of a few hundred to a few thousand meters of habitat that are accessible to migrating steelhead. Presumably they have a corre-
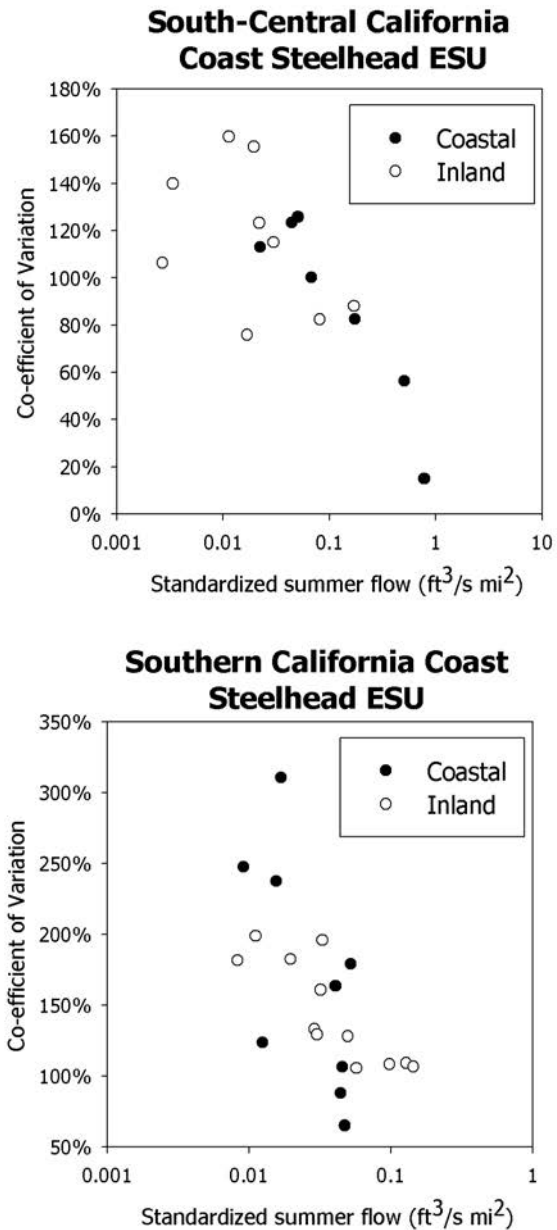
Figure 25. **Variability in summer discharge for coastal and inland creeks inhabited by the two ESUs. Standardized summer discharge is the mean discharge from June – Sept. (inclusive), divided by the drainage area above the gauge. Coefficient of variation applies to among-year variation in summer discharge. Data from USGS gauges as noted in §10.5 (p. 105).**

spondingly small carrying capacity and thus contain small populations. All else being equal, these very small populations should be highly vulnerable to chance extinctions caused by environmental stochasticity. However, if this were the case then at any given time some populations

would be extinct (awaiting recolonization from neighboring populations), and thus some vacant basins should have been observed during the survey (particularly since the observation were made in a dry year). Since vacancies were not observed, we conclude that most likely, all else was not equal. This suggests that some trait of the Big Sur Coast confers resilience to very small populations of steelhead, or perhaps the habitat is so productive that the populations are larger than the small amount of habitat would suggest. Either of these possibilities argues that Big Sur *O. mykiss* populations are unexpectedly resilient to population-level extinctions.

A number of USGS gauges are in the region, and provide discharge data by which to judge the stability of stream-flow during the summer (Figure 25 top), likely to be an important cause of variability in population growth. The data in the top panel of Figure 25 suggest that coastal basins have higher mean flow and less between-year variability than the inland basins. However, the difference is not statistically significant ($p = 0.33$ by a t-test on the principal component of the data from Figure 25, top)[1]. The fact that the datapoints appear to lie in the lower-right quadrant of the graph suggests that they tend to have higher summer discharge per unit area of watershed. Since it almost never rains in the summer in this area, the result hints that the coastal basins have a greater ability to store water from winter rains. Other reasons that coastal basins might have greater summer flows are a greater tendency for alluvial gravels in the lowlands, less transpiration (via riparian vegetation) near the cooler coastal areas, and actual dry-season "rainfall" in the form of fog condensing onto trees and bushes.

In summary, we have some limited evidence that coastal populations are relatively stable, based on climate maps, fish-occurrence data in very small basins, summer discharge, and stream morphology; but the evidence is not conclusive. This indicates that recovery planning would likely benefit from a better understanding of the popula-

tion dynamics and resilience in these small coastal systems.

Evidence for the Southern California Coast Steelhead ESU

Is there evidence for coastal stability further south? According to the temperature maps in Plate VII (end of document), the coastal areas have a relatively low annual range, but are not particularly cool. The areas that have both a low annual mean and a low annual range in temperature occur inland. One such area encompasses the highlands of upper Sespe and Upper Piru Creeks. Just to the west, the mean temperature is also cool in the headwaters of the Santa Ynez and Sisquoc Rivers, but the annual range is somewhat greater. Two other inland areas with both low mean and low range are the San Gabriel Mountains and a small patch in the extreme headwaters of the mainstem Santa Ana River (Plate VII).

As for occurrence-data, many of the small coastal basins on the southern Santa Barbara coast still contain *O. mykiss*; but the data in Table 2 (p. 21) suggest that as many as 5 have lost their populations for reasons other than barrier-exclusion. Some of this loss may be related to development along the Santa Barbara coast. However, a regression analysis by Boughton *et al.* (2005) found climate (mean annual air temperature) to be a significant correlate of loss (agricultural/urban development was not a statistically significant predictor of loss in this analysis). Thus, environmental stochasticity may be a significant risk in the coastal basins.

The USGS gauges data do not suggest that coastal streams are more stable than inland streams in this part of the study area. Figure 25 (bottom) shows data for a series of coastal creeks between the towns of Lompoc and Ventura, compared to inland tributaries of the Sisquoc, Santa Ynez, Ventura, and Santa Clara systems. The coastal creeks do not appear to be more stable; in fact three of them are less stable than any of the inland creeks depicted in Figure 25. Overall, in the NOLA section there is little evidence for a coast-inland tradeoff between the size and stability of populations.

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[1] This test assumes that USGS are sited randomly, when in fact practical considerations often dictate siting of gauges.
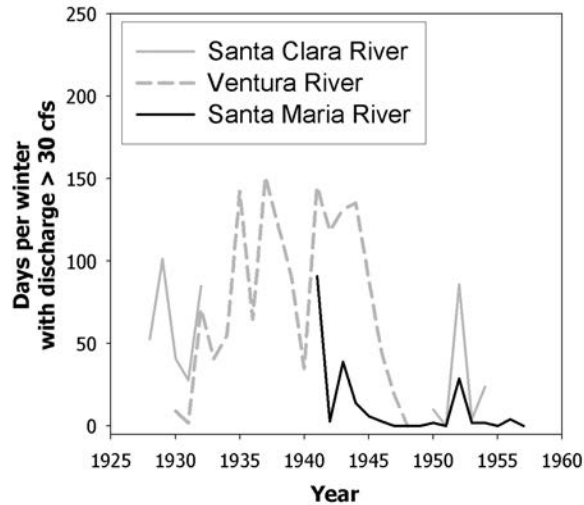
Figure 26. Days per winter (Jan. – May) in which mean discharge exceeded 30 cfs under a natural flow regime, near the river mouths of three major systems in the NOLA study area. If these data are taken as an index for the reliability of steelhead migration access to each of the three systems, the Santa Maria appears to provide lower reliability. Data are for discharge prior to the construction of large dams (Santa Clara: USGS gauge 11114000; Ventura: USGS 11118500; Santa Maria: USGS 11141000).

We do note however that the evidence suggests other significant patterns in environmental stochasticity. In particular, the wintertime discharge of streams appears to be much less reliable in the SOLA section than in the NOLA section; this was discussed on page 14 (see especially Figure 6 and Figure 9). Unreliable flows during the migration period would in our estimation be a very significant form of environmental stochasticity that increases extinction risk. There is also reason to believe that within the NOLA section itself, the Santa Maria River tends to have less reliable winter flows than other large systems in the area (Figure 26).

A Theoretical Model of the Size-Stability Trade-Off

Since a size-stability trade-off is a possible concern for one of the steelhead ESUs, it is useful to evaluate more closely the sensitivity of viability to environmental stochasticity. A diffusion-approximation model described by Foley (1994) is a mathematical distillation of this issue and provides some useful insight. The model is very sim-

ple. It envisions population size as constrained between two fundamental limits: extinction (zero size, an "absorbing boundary"), and carrying capacity (K, a "reflecting boundary"). It is sometimes called the ceiling model, since the population stops growing when it hits the ceiling K. Within these bounds the population changes size stochastically. Specifically, its growth rate is assumed to be adequately described by a mean and a standard deviation. The latter is known as sigma, and represents environmental stochasticity in the model (see the caption of Figure 24 for a precise definition of sigma). Simply put, the larger the value of sigma, the greater the chance of large year-to-year fluctuations in population size, both up and down.

In Figure 27, we have used Foley's (1994) model to plot isoclines for extinction risk as a function of K and sigma. Notice that the y-axis is logarithmic: K must increase exponentially to compensate for a small increase in environmental stochasticity. What does this imply?

It is informative to work through a thought-experiment comparing the Nacimiento/Upper Salinas population to the Big Sur River population. According to the habitat model developed in the last section, the Nacimiento/Upper Salinas system has about 16 times more kilometers of potential stream habitat than the Big Sur system (776 km vs. 48 km). For the sake of argument let us assume that K for the Nacimiento/Upper Salinas is 16 times greater than K for the Big Sur and that migration barriers within these systems have been somehow removed. Let us also assume that the populations can on average grow at 10% per generation when below carrying capacity.

If the environmental stochasticity for the Big Sur population is 0.25, then inspection of Figure 27 indicates it must have a K of at least 650 fish to be viable. Suppose that sigma for the Nacimiento population is larger, say 0.35; its required K would be about 40,000 fish, about 61 times larger than the required K for the Big Sur[2]. In this thought-

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[2] To make this more concrete, for the example a sigma of 0.25 means that population growth is between –40% and 65% most of the time, and a sigma of 0.35 means that growth is between –50% and 100% most of the time. Here, "most" is defined as
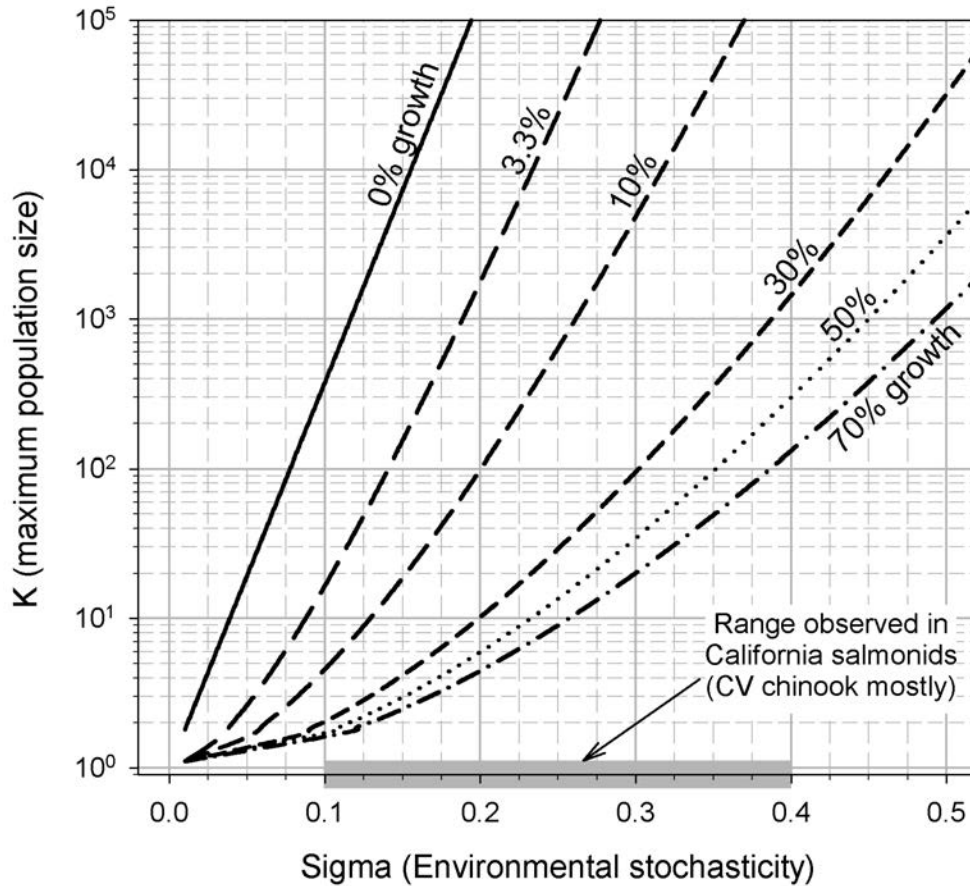
Figure 27. Risk isoclines for K and sigma (defined in the caption of Figure 24). The isoclines are for a 5% risk of extinction in 34 generations (c. 100 yr for steelhead with a 3-yr generation time). Isoclines are computed using Foley's (1994) diffusion-approximation model with ceiling K.

experiment, the increased risk due to environmental stochasticity more than outweighs the advantage of larger carrying capacity in the inland population.

The effect of environmental stochasticity is weaker if populations have a high mean growth rate. This is consistent with intuition because high growth rate implies faster recovery after a downward fluctuation. The recent upward trend in the Carmel steelhead population suggests that mean growth rate may well be on the order of 30% to 70% per generation[3]. If so, then in the above scenario of the Big Sur and Nacimiento, the difference would not be so stark. Under 30% growth the Big Sur would require a carrying capacity of just 30

fish, vs. 400 in the Nacimiento/Upper Salinas. (these two K's differ by a factor of 13).[4]

Of course, this example is only relevant if the Foley model (1994) is a reasonably useful approximation for the actual steelhead populations. In recent years environmental stochasticity has emerged as a key factor for extinction risk in general, because of the large predicted impacts implied by Figure 27, and because highly-variable growth rates are observed to be the norm in natural populations. Based on first principles, we would expect environmental stochasticity to have special importance at the margins of a species' geographic range. At the margin, the species is presumably at the limits of its environmental tolerances, and small changes in the climate translate

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about 95% of the generations. The model assumes that logarithm of lambda (growth-rate + 1) is normally-distributed.
[3] It should be noted that the apparent upward trend observed in the Carmel River in recent years is based on partial counts.

[4] At such low capacities, other considerations not covered by the Foley model would come into play. Namely, loss of genetic variation and risk due to demographic stochasticity.

to exaggerated fluctuations in population growth. Because it incorporates environmental stochasticity, Foley's (1994) model is probably the simplest population model that could be responsibly used to gain insight about the steelhead populations in our study area. Even so, it omits many important features of steelhead populations, such as age structure, low-density depensation, demographic stochasticity, and stochastic variation in carrying capacity.

Getting back to the point of this section, we are interested in establishing an order-preserving relationship between expected population size and viability. Clearly the generality of this relationship is very sensitive to environmental stochasticity. Even a slight tendency toward greater stochasticity in the larger populations would rapidly erode the benefit of being large, and the order-preserving relationship might break down. This situation appears to be plausible for the South-Central California Coast Steelhead ESU—there is suggestive evidence that the small coastal populations are more stable.

Are they more viable? To make a valid comparison one would need to achieve fairly precise estimates of sigma, due to the exponential isoclines depicted in Figure 27. This would require run-size data for perhaps two decades (Lindley 2003). Also, the ceiling-model omits or vastly simplifies many potentially important details about salmonid population dynamics, such as the form of density-dependence (Barrowman and Myers 2000, Barrowman *et al*. 2003).

There is no escaping the fact that an unmeasured parameter (sigma) has great consequence to the ranking scheme. This suggests that the recovery plan should incorporate a "bet-hedging" strategy. By bet-hedging, we mean a strategy that will be successful if coastal populations turn out to be more resilient because of their stability, but will also be successful if inland populations turn out to be more stable because of their large potential size.

Freshwater Residents

One important uncertainty not yet discussed is the role of freshwater residents (trout) in the population dynamics and viability of anadromous fish (steelhead). In some basins there appear to be

at least as many adult resident trout as there are anadromous adults, although we have no hard data on the subject (Titus *et al*. 2003). In some California ESUs there appears also to be some level of interchange between the two types—steelhead having non-anadromous progeny and vice-versa (C. Donohoe, personal communication). To the degree that trout are numerous and that they can give rise to anadromous fish, the viability of the steelhead population may be enhanced: by contributions to abundance and productivity, and by allowing the population to persist through multi-year droughts that interfere with steelhead migration from the ocean. However, trout restricted to freshwater will not be able to enhance the connectivity of populations across basins. Given the large implications but lack of specific information about the role of trout in viability of steelhead populations, the standard recommendation in the conservation biology literature would be to take a precautionary approach—that is, to assume viability enhancement is negligible until further information becomes available. In our opinion, studies that decisively clarify this issue should be given high priority.

5.3.2. The Habitat-Quantity Assumption

Carrying capacity is an increasing function of habitat quantity.

The idea here is that K is proportional to the amount of habitat in a basin. For this assumption to hold true, a number of conditions must be met:

1) The mean productivity per unit length of stream habitat must be about the same among different basins. "About the same" means variation among basins is small relative to variation in basin size.
2) There is no tight coupling of fish populations with a prey species, a predator or a disease, causing population cycles, chaos, *etc*. This might lead to attractors that are not expressible as a single point value K, and our rationale for setting priorities might break down.

There is a complication about the first condition: steelhead do not just occupy one type of habitat; they occupy a series of habitats through

the course of their life cycle. So how to evaluate the condition? A reasonable way is to identify what is thought to be the most limiting habitat, as this is what would determine the population ceiling for each basin. For steelhead in our domain we hypothesize that the most limiting habitat in terms of amount is over-summering habitat. This seems intuitive, given the aridity of summer in much of the region, but is by no means an established scientific finding. Indeed, alternative scenarios are possible—for example, in some watersheds the most limiting habitat may be spawning gravels of suitable size; or perhaps there is no single habitat that is most limiting in the sense of controlling the overall productivity of a watershed. The concerned reader should read the brief summary of the issues provided in §10.6.

Another complication in the link between carrying capacity and habitat quantity is variability in the quality of habitat, both spatially and temporally (Cooper *et al*. 1986). Besides variation in the quality of freshwater habitat, it has recently become clear that the seasonal lagoons at the mouths of stream systems also provide over-summering habitat, and very high quality habitat at that. For example, Smith (1990) described lagoon use by yearling steelhead in three out of the four creeks he studied between Santa Cruz and San Francisco. His data suggest that lagoons, though only a small part of the total stream network, play a disproportionately large role in the survival and rapid growth of juvenile steelhead. For example,

> At Pescadero Creek, November 1986 estimates of stream densities of steelhead at two representative sites…averaged 2368 fish per mile. It would take 8 miles of stream to equal the numerical production of steelhead in Pescadero lagoon in 1986. When fish size is taken into account the value of the lagoon is even greater. In the stream there were only an estimated 467 fish per mile that were longer than 100mm SL. The entire 25 miles of accessible streams in the watershed would probably be able to produce only two-thirds as many large fish as the lagoon, and those fish would still be smaller than most of the fish reared in the lagoon (Smith 1990: 29)

More recently, Bond (2006) has made a thorough case for lagoons serving as key nursery habitat for steelhead, based on a case study he conducted in Scott Creek, northern Santa Cruz County. Bond (2006) showed that:

1) Juveniles rearing in lagoons have a much faster growth rate than juveniles rearing in freshwater streams, doubling in length over the course of a single summer;
2) Size at ocean entry is larger for lagoon-reared juveniles vs. freshwater-reared juveniles; and
3) Returning adult steelhead show evidence for size-selective mortality during the ocean phase.

Consequently, Bond (2006) concluded that because lagoon-reared juveniles enter the ocean at a larger size than freshwater juveniles, they survive better in the ocean and are disproportionately represented in the adult spawning run. Bond (2006:vii) states "based upon tagged recaptures and scale samples, estuary-reared steelhead showed a large survival advantage and comprised 85% of the returning adult population, despite being between 8% and 48% of the juvenile population."

Thus, in comparing the potential viability of populations in the study area, it may be more relevant to compare the productivity of lagoons than the quantity of freshwater habitat. Unfortunately, we are aware of no established methods for a rapid comparative assessment of the lagoon productivity. Productivity probably depends in part on lagoon size, which is readily measured, but it also depends on primary productivity of the lagoon ecosystem itself, and key driving variables such as the degree of mixing between salt- and freshwater during the summer[5].

There may be other habitats that produce smolts with large size at ocean entry. For example, in a small tributary in northern California, Harvey *et al*. (2005) observed generally low summer growth rates for *O. mykiss*, but in 15% of their 59 sites there was rapid growth by fish smaller than 20 g. Observations in our study area suggest small

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[5] Mixing prevents development of hypoxia or extreme heating in the heavier saltwater lens, both detrimental to fish life; a similar result can be obtained by complete conversion of the lagoon to freshwater by sufficient summer stream flow.

freshwater ponds and impoundments may sometimes support rapid summer growth of juveniles.

Another concern is the potential role of large mainstem rivers in providing summer habitat. These mainstems may have originally been more suitable for steelhead than they are presently, a hypothesis discussed at length in the appendix (§10.2, p. 98). By about 1900 they were by and large unsuitable, likely due to various land management practices. They are omitted from our habitat model, though in principle they might be viewed as potential habitat, perhaps even high-quality habitat. For example, Moore (1980b) describes high summertime growth rates of *O. mykiss* in a spring-fed portion of the mainstem Ventura River.

Thus, the validity of the "Habitat-Quantity" assumption rests on two underlying assumptions: 1) the amount of over-summering habitat is the key limiting factor for steelhead, 2) the role of lagoons and potential role of low-gradient mainstems as over-summering habitat is not confounding to the ranking scheme. Assumption (2) is clearly not true even approximately, and therefore a high research priority is broad-extent studies on unimpaired lagoons and low-gradient mainstems.

As for the population-cycling scenario raised on the previous page: The fish are generalists and quite unlikely to specialize on a single prey species that might lead to cycles. Likewise, we cannot think of a predator that might have a tightly coupled specialist relationship with steelhead. Cannibalism between age classes has been described as a cause of complex population cycles in cod (Bjornstad *et al.* 1999), but there is no evidence for this in *O. mykiss*. Biro *et al.* (2003) have provided evidence that cannibalism between size classes in lake populations can impose significant mortality on the smaller *O. mykiss*, but some of the same authors in an earlier report suggested that size-class interactions would tend to produce stable compensatory population dynamics, not chaotic dynamics (Post *et al.* 1999).

Contagious disease would be the most likely candidate for tight-coupling, but we are not aware of any evidence for this phenomenon in the study area. Competitors may also prevent *O. mykiss* populations from fully occupying potential habi-

tat, particularly in the form of native and exotic fish species that co-occur with *O. mykiss*. In most of the drainages, native competitors might include stickleback, sculpin and lampreys, with the Pajaro, Salinas, and Los Angeles basins also harboring a native fauna of minnows and suckers. Some of these natives have colonized the Santa Clara system and so are exotic there. In addition, populations of true exotics are scattered around the study area, and may function both as competitors and predators. These species include brown trout, channel catfishes, green sunfish, among others. Tight-coupling of population dynamics among these fish and *O. mykiss* seems unlikely due to the diversity of their shared prey base and their associations with different temperature regimes.

A final point is that two pre-historic predators are now missing or much reduced in the study area: grizzly bears and native Americans. It is difficult to imagine they did not impact steelhead. Keeley (2002b) discusses archaeological evidence that population densities of native Americans in the study area were among the highest densities anywhere in North America. Smallpox and other European diseases reached the region before European settlers, reducing population densities by 50% – 90% and thus releasing hunting pressure on many species. The first European explorers may have thus encountered abnormally abundant populations of steelhead.

5.3.3. The Disturbance-Regime Assumption

Under normal ecosystem dynamics, the ratio of available habitat amount to potential habitat amount is effectively the same for the populations being compared.

The above assumption implies an order-preserving relationship between habitat and potential habitat, necessary for our ranking scheme. The key question is: what happens during the normal course of natural disturbances, including the wildfires, floods, droughts, and landslides characteristic of the study area? Does the disturbance regime disrupt what seems like an obvious mapping between the amount of actual habitat and potential habitat in a basin?

Most natural disturbances have effects that are temporary, though "temporary" in this context

can mean anything from a year to multiple decades. Due to such disturbance processes, across the basin as a whole there would be a shifting mosaic of habitat patches, with ongoing destruction of some habitat patches simultaneous with recovery of others[6]. Thus it would be useful to consider how the patch-dynamics of this shifting mosaic might support or invalidate the disturbance-regime assumption.

A simple way to think about patch dynamics is to think of habitat patches as having a mean birth rate (B), a mean lifetime (S), and a mean size (A) (Boughton and Malvadkar 2002). One can then develop a simple equation for describing changes in the amount of habitat over time:

$$dH\!\!\big/\!\!dt = AB(L_{IP+} - H) - H\!\!\big/\!\!S$$

where H is the amount of actual habitat, L_{IP+} is the total stream kilometers of potential habitat, and B is in units of patch-births per unit length of stream. If A, B, L_{IP+}, and S are constant, the amount of habitat converges toward a stable equilibrium:

$$H^* = L_{IP+}\left(\frac{BSA}{1 + BSA}\right)$$

According to this simple model, if the product BSA is constant across basins (or if it is much larger than 1.0), then the amount of actual habitat would tend to be directly proportional to the amount of potential habitat. The relationship of the two quantities would be order-preserving, at least in the long term. Only in the case where the product BSA is both close to 1.0 and is smaller in the larger basins, might the order-preserving relationship not hold true. This is a deterministic criterion for the disturbance-regime assumption.

There is also a stochastic criterion for the disturbance-regime assumption. Recall our earlier

concern, discussed at length above, that environmental stochasticity can disrupt the mapping between mean population size and viability. A similar concern applies to "populations" of habitat patches. In particular, in the shifting-mosaic of habitat caused by disturbance processes, the total amount of habitat is expected to fluctuate around the mean amount. If patches of habitat are independently created and destroyed by ecosystem dynamics, this fluctuation is not expected to amount to too much. Often, however, patch creation or destruction is not independent across a stream network. Rather, it is occasioned by some broad-scale environmental event such as a catastrophic wildfire or a flood. When such is the case, there is increased chance that the total number of patches in a basin will fluctuate to zero, causing extirpation of the local fish population. Although eventually the habitat network may recover spontaneously due to ecosystem dynamics, for the fish population to recover there must be recolonization from elsewhere. This form of risk has been called "landscape stochasticity" (Boughton and Malvadkar 2002).

It appears to us that there are three disturbance processes that are especially relevant for the study area: floods, wildfire, and droughts.

Floods

The recent flood regime appears to have been less erratic then in preceding centuries. Tree-ring data indicate that precipitation in the study area during the last 100 yr has been higher and less variable than the preceding 300 yr (Haston and Michaelsen 1997). In fact, the middle years of the 19th Century (*circa* 1820 – 1870), when the historical record of the region mostly began, marks an unusual time climatically: "Apparently, there was not only high variability in the magnitude of precipitation from year to year during this time, but also a high degree of north-south contrast" (Haston and Michaelsen 1997:1845).

Even so, the flood regime of the "less variable" 20th Century has been highly episodic. Inman and Jenkin (1999) documented streamflow and sediment flux for the 20 largest streams in the study area, and found a dry period from 1944 to about 1968, and a wet climate from 1969 to the

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[6] It is widely recognized that disturbance events may pose short-term problems for a species, but also long-term benefits. For example, floods may cause immediate "redd scour" (destruction of steelhead egg deposits), but in the long run they are responsible for such beneficial effects as recruiting spawning gravels to the stream and scouring out sediment-filled pools.

present. Sediment flux of rivers at their mouths was 5 times higher during the wet period; in fact the abrupt transition from dry climate to wet in the year 1969 brought an amount of sediment to the Santa Barbara channel that was greater than the total for the preceding 25 years. Clearly there is great potential for the flood regime to cause landscape-level stochasticity in the habitat dynamics of *O. mykiss*, even during the relatively stable period of the 20th Century.

Floods are, probably with landslides, important in delivering and sorting gravel, producing and cleaning pools and enhancing spawning areas; they may also wash away spawning areas or fill pools with sediment in some circumstances. Thus, they are generally expected to both destroy and create spawning or rearing habitats in different parts of a basin—that is, flood frequency affects both *B* and *S* in the simple model given earlier. Whether this leads to a net loss or net gain of habitat depends on many factors governing erosive and depositional processes. At present we have only the beginnings of an understanding of the geomorphic controls on these processes.

Large roughness elements, such as boulders and rock outcrops in the stream channel, may be key modulators between flood regimes and the shifting mosaic of summer pool habitat. Moreover, the flood regime itself—particularly the seasonal timing of high-flow events-- likely has direct effects on the ability of *O. mykiss* populations to persist (Fausch *et al.* 2001). Superimposed on the natural regime are anthropogenic effects of water management practices, such as shorter higher flood peaks.

At present we do not know if any of these factors potentially governing flood regimes would differ systematically across basins and perhaps invalidate the ranking system.

Wildfires

Wildfires are a normal occurrence in the study area, both in historic and prehistoric times (Keeley 2002a and b). Wildfires have numerous documented effects on stream habitat—directly (by burning riparian vegetation) and indirectly (by changing the sediment flux and run-off patterns from the surrounding watershed after the fire re-
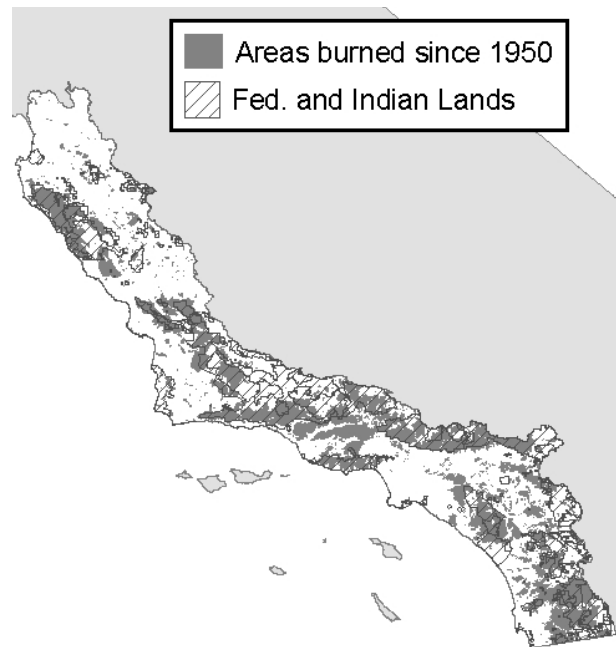
Figure 28. Area burned by one or more large fires since 1950 (>50 acres in CDF dataset; >300 acres in USFS dataset. Note that the data probably have a reporting bias for public lands.

moves the vegetation; see references below). These effects influence what fraction of potential habitat is suitable at any given time, and thus are relevant to the disturbance-regime assumption described at the beginning of this section.

The fire regime.—The fire regime is the long term pattern of wildfire occurrence for a particular type of ecosystem. It is conveniently characterized in terms of three descriptors (Agee 1993): mean fire size; mean fire return time (the mean time between burnings at a particular point in the landscape); and fire intensity.

Fire intensity is typically high in our study area, with wildfires burning the shrubland "canopy" as well as the ground vegetation (grasses and forbs). The shrubs are often highly flammable and burn very hot, removing most of the live vegetation. However, most of the plant species are fire-adapted and resprout or produce seedlings within a year or two after a fire. Some are indeed fire-dependent.

As for the other two descriptors, there appears to be a certain amount of disagreement about the underlying controls for fire size and return time in

our study area. Throughout much of the western United States, fuel accumulation (in the form of living and dead plant biomass) is viewed as a key component of wildfire risk, and Minnich (1983; 1995; see also references in Keeley 2002a) argued that this paradigm applies in our study area as well. However, Keeley (2002a and b; Keeley *et al.* 1999) has argued extensively that ignition rate, rather than fuel accumulation, is the primary control on the wildfire regime. The distinction is important because the two controls imply different management strategies—one focusing on where and how fuels accumulate; the other on where and how ignition occurs. One possibility is that the ignition-rate model applies to areas subject to extreme Santa Ana winds, whereas the fuel-accumulation model applies elsewhere. The shrubland fire regime and attendant controversy are reviewed by Keeley (2002a and b); other useful references are Minnich (1988) and Minnich and Howard (1984).

Effects on stream habitat.—Much work has been done on the effect of wildfire on terrestrial plant communities and habitats in our study area; less work exists on effects on stream habitats (Keller *et al.* 1997). The two primary effects identified thus far are increases in the water yields of streams, and changes to sediment dynamics of streams. Effects on biota also occur, but are more uncertain (S. Cooper, personal communication)

Effects on hydrology.—Wildfire has been observed to increase the water yield of basins in southern California; brief reviews of the small literature on this phenomenon are in Keeley (2002b) and Loaiciga *et al.* (2001). The phenomenon appears to be inconsistent: wildfire increases the average annual discharge in some examples but not others (Loaiciga *et al.* 2001); the number of case-studies is small.

Of particular relevance to *O. mykiss* are effects of wildfire on stream discharge during the summers following the wildfire. In a paired-watershed study, Hoyt and Troxell (1934) observed a 475% increase in summer flow in Fish Creek (San Gabriel Mountains) after a wildfire in its watershed. However, the summer discharge diminished back to pre-fire levels in about 4 years (Hoyt and Troxell 1934, cited in Keeley 2002b and Loaiciga *et*

al. 2001). Keeley (2002b) suggested that a regular cycle of burning, by preventing reversion of grassland back to shrubland, can sometimes convert an ephemeral stream into a perennial stream. He argued that Native Americans may have once burned the watersheds to this end, stating "There is every likelihood that many contemporary seasonal streams [in southern California] were capable of perennial flow under different fire management by Native Americans." It is a compelling hypothesis with large implications for the potential distribution of *O. mykiss* in our study area.

Effects on stream morphology.—Terrestrial vegetation impedes the erosion of sediment from hillsides into stream channels. Wildfire, by removing much of that vegetation, can have a large effect on the sediment dynamics and sediment budgets of streams, and thus on overall stream morphology.

Winter storms can be a major driver of sediment entering stream channels after a fire (Spittler 1995); however in some areas dry ravel (the downhill-movement of sediment due to gravity) can be prevalent (Florsheim *et al.* 1991). The increase in sediment transport to the channel may be as short-lived as one or two years after the fire (Florsheim *et al.* 1991, Keller *et al.* 1997), due to rapid recovery of terrestrial vegetation.

Once the sediment is in the channel, winter storms play a large role in transporting it. Keller *et al.* (1997) drew distinctions between three types of fluvial transport: normal sediment transport, sediment flushing events, and debris flows. Normal sediment transport occurs nearly every year, mainly during winter storms. Sediment-flushing occurs when exceptionally large winter storms follow a wildfire by one or two years. These events transport several times the average sediment discharge, but have insufficient power to transport coarse debris such as large boulders. Finally, debris flows are very large and infrequent events that transport enormous amounts of debris of all sizes. Keller *et al.* (1997) hypothesize that such events usually require not just a wildfire followed a year or two later by a large storm; they require a pre-existing geomorphic instability, caused by the buildup of several centuries worth of coarse debris that is too large to be transported by normal processes.

Implications.—For *O. mykiss*, the transport processes described above probably impose a shifting mosaic of suitable and unsuitable habitat patches. Spawning gravels can be buried or scoured by sediment transport (Spina and Tormey 2000), and fine sediments may render summer habitat less favorable by raising embeddedness (Suttle *et al*. 2004). Yet new spawning gravels and summer habitat may be created by sediment sorting and deposition (*e.g.* Collins and Dunne 1989). Pools—used for over-summering—may get filled in by sediment; but new pools scoured out elsewhere. Likewise, if the perenniality of streams depends on the recent fire history as suggested by Keeley (2002b), this mechanism would also impose a shifting mosaic of suitable summer habitat.

A quantitative description of the shifting mosaic—the "birth" rates and lifetimes of suitable habitat within a matrix of potential habitat (Boughton and Malvadkar 2002)—has not yet been estimated for steelhead habitat in the region, much less compared across different ecotypes. Thus it is difficult to evaluate the validity of the disturbance-regime assumption described at the beginning of this section. One obvious hypothesis is that the inland basins would have more frequent fires and greater areas burned, due to the hotter and drier climate.

According to data on historic wildfire occurrence, this is not obviously the case. In Figure 28 we have mapped data from a database compiled by the California Department of Forestry (CDF), describing wildfires since 1950. These data are records of fires reported by the CDF and the USFS, and there is no clear signal that inland areas are more likely to be burned. The data may suffer from various reporting biases based on population density and public access, so it makes sense to standardize the dataset with respect to these potential biases. One way to do so is to restrict the analysis to Federal lands.

Since 1950, the number of years with 0% burning has been larger in coastal areas vs. inland areas, at least on Federal lands (Figure 29). This supports the general hypothesis that inland areas are more fire prone. The difference is not very great, however—most of the extra fires in the inland basins were small, cumulatively burning
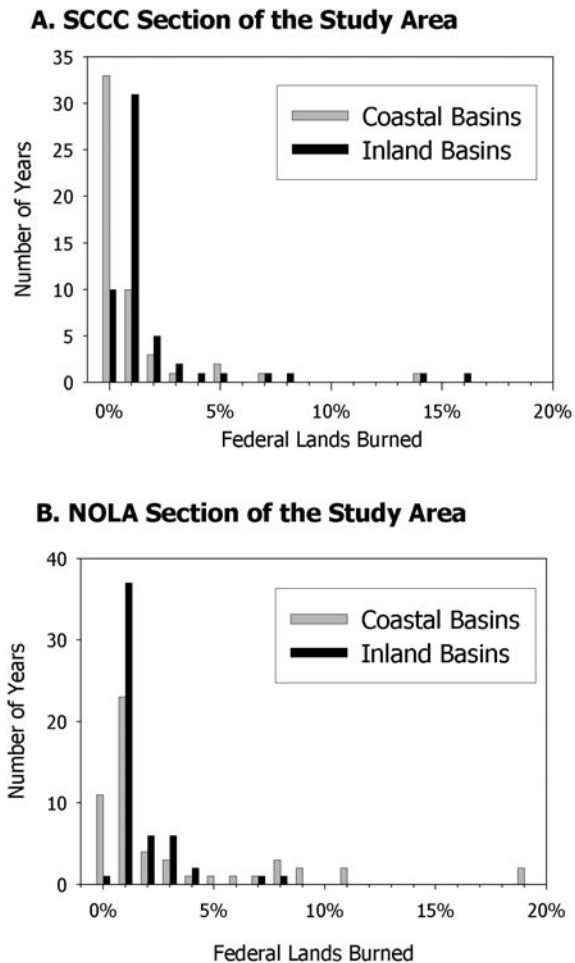
Figure 29. Histograms of burned area per year for coastal areas and inland areas. Only data for Federal lands are depicted, under the assumption that these data are more representative of the unimpaired fire regime than is the entire dataset depicted in Figure 28. Area burned was rounded up to the nearest 1%.

less than 1% of the inland area per year. While this pattern of burning may have significant local effects, it does not clearly illustrate the large-scale systematic effects that we are interested in here, suggesting that the disturbance-regime assumption is reasonable until proven otherwise. The topic of fire regimes clearly deserves more sophisticated analysis. In particular, we expect that wildfires are a key component of landscape stochasticity and habitat dynamics of the fish; and we expect that they are sensitive to ongoing changes in climate (Westerling *et al*. 2006).

Droughts

The climate in the study area is classified as Mediterranean, characterized by a distinct short wet winter/spring season and a prolonged dry summer/fall season. However, inter-annual precipitation is highly irregular and can vary as much as 400% from the long term average annual rainfall. Within-year patterns can also vary considerably, with precipitation being concentrated in a few short duration events at the beginning or towards the end of the normal rainfall season, thus greatly influencing run-off patterns in rivers and streams. Useful references on the southern California climate are Bailey (1966) and Felton (1968).

The distribution of yearly-rainfall is left-skewed, with many years of low rainfall and relatively few of high (i.e. median rainfall is lower than mean rainfall). Periodic extended droughts over multiple years or decades can curtail the available steelhead habitat by reducing both direct run-off during the winter, and recharge of groundwater basins that sustain baseflows during the summer and fall. These prolonged dry periods can strongly influence migration and spawning opportunities for adult steelhead, and survival and growth of juveniles and outmigrating smolts.

Droughts appear to have broad spatial extent, larger than the size of the study area. Lindley *et al.* (2006) suggested that the "correlation distance" of droughts was 640 km in California, based on an analysis of a 2000-year drought record constructed from tree-ring data by Cook *et al.* (2004). Correlation distance is the distance at which the correlation in drought conditions reaches zero—that is, it is the average distance that one must travel to be assured of escaping a drought-stricken area.

Since the scale of droughts tends to be larger than the geographic ranges of entire ESUs, the pertinent question for the fish is not which populations tend to experience droughts most frequently, but rather in which places is habitat quality most resilient to drought. In short, where are the drought refugia? Currently the answer is not clear.

5.3.4. The Estimation Assumption

The model prediction for potential habitat has acceptably small estimation error.

In other words, the error is small relative to differences among basins. If this condition holds, true amount and estimated amount have an order-preserving relationship. Note that for the purposes of ranking it does not matter if the model of potential habitat over-predicts, as long as it overpredicts by a consistent amount across basins, since this would still be order-preserving. What is of primary interest is whether the ranking system is robust to various uncertainties in the estimate.

One way to evaluate the robustness of the estimation assumption is to vary the assumptions of the habitat model, and then determine whether the rankings are changed as a result. This procedure is known as a sensitivity analysis, because it allows one to determine the sensitivity of one's conclusions to the assumptions one has made during an analysis. The rankings that are robust to alterations in model assumptions are assumed to be the ones with greater support.

In the case of the model of potential habitat that we developed earlier, there are a number of key assumptions that are particularly uncertain. These are listed in Table 10, along with "end-points" that bound the range of uncertainty for each assumption. For our sensitivity analysis, we looked at all possible combinations of these endpoints, a total of 48 habitat models for each ESU. Specifically, for each of the 48 variants of the habitat model, we worked through these steps:

1) The specified variant was fit to the data.
2) Using the variant model, each reach in the GIS was classified as either potential habitat or not (reaches are generally 100 – 1000m in length).
3) For each basin, the lengths of reaches classified as potential habitat were summed, giving each basin a total score.
4) The basins were sorted and ranked by their habitat score.

Then, for each basin we computed its mean, minimum, and maximum rank according to the 48 variant models. Core assumptions are in Table 11.

Table 10. Endpoints considered in a sensitivity-analysis of potential unimpaired habitat. All possible combinations of the endpoints produce a set of 48 variants of the habitat model.

Type of Sensitivity Evaluated	Endpoints considered
Type of occurrence data	1) All observations of *O. mykiss* 2) juvenile observations only
Cut-off gradient assumed to render up-stream habitat inaccessible to spawners	1) 12% gradient 2) 20% gradient
Bootstrapping method for fitting envelopes to observational data	1) Simple envelope 2) Envelope spanning 95% of 50,000 bootstrap resamples 3) Consensus envelope of 50,000 bootstrap resamples
Geological substrate assumption	1) All substrates 2) Alluvial sections masked off
Flow Assumption	1) Mean annual flow (MAQ) 2) Mean flow during August – September (Q89).

Table 11. Core assumptions underlying the ranking scheme.

Core Assumptions & Weaknesses	Applicable ESU[1]		Recommendation
	SOCEN	SOCA	
Population-Size Assumption			
Environmental stochasticity may be higher in the larger, inland popula-tions.	Suggestive Evidence	No Evidence	Bet-hedging strategy in the recov-ery plan for SOCEN.
Non-anadromous fish have unknown effect on viability	Relevant	Highly relevant	Research on the pattern of inter-change and its effects on viability.
Habitat-Quantity Assumption			
Over-summering habitat may not be the most limiting habitat type.	Plausible	Plausible	Full life-cycle research in repre-sentative basins.
Lagoon habitat is important, but is omitted from the habitat model.	Highly relevant	Highly relevant	Regional assessment of lagoon productivity.
Disturbance-Regime Assumption			
Different basins may have distinct wildfire regimes, with implications for habitat dynamics, carrying capac-ity, and viability	Highly relevant	Highly relevant	Research on the historic fire re-gime and effects on stream habi-tat dynamics.
Estimation Assumption			
Mainstems may have originally been suitable over-summering habitat.	Relevant	Highly relevant	Test the hypothesis empirically.

[1] SOCEN = South-Central California Coast steelhead ESU. SOCA = Southern California Coast steelhead ESU.

5.4. Potential Viability in the South-Central California Coast Steelhead ESU

When populations in this study area are assigned mean ranks from the 48 habitat models, the top-ranked populations are the Nacimiento, the Pajaro, Arroyo Seco, and the Carmel population, in that order. The sensitivity analysis indicates ranks of these four populations are sensitive to model assumptions (Figure 30, top). However, their collective status as the top four is insensitive (note the error bars in Figure 30: none of these four ever sink below rank 4; and none of the other populations ever rise above rank 5).

Except for the Carmel River, these top four are inland populations; and the Carmel itself is somewhat inland in character, having an alluvial mainstem and portions lying outside the direct influence of the marine climate. Earlier we argued that a size-stability tradeoff in the study area may negate the benefits of large population size for viability. We do not know if this is the case, so we rank the inland and coastal populations separately.

Within the set of coastal populations, ranks were sensitive to model assumptions, indicated by the wide overlap of error bars in Figure 30. There are two ways to take this sensitivity into account. One is a risk-neutral approach, in which one uses the mean rank. This risk-neutral approach suggests the following top 10 coastal populations:

Risk-neutral ranking
1 Carmel River
2 Arroyo Grande Creek
3 San Luis Obispo Creek
4 Chorro Creek
5 Arroyo de la Cruz
6 Big Sur River
7 Little Sur River
8 Santa Rosa Creek
9 Gabilan Creek
10 San Carpoforo Creek

The rankings fit our intuition, with the exception of San Carpoforo Creek at the bottom of the list. Both Chorro and Gabilan Creeks are considerably smaller and do not seem to possess as complex an array of habitats as San Carpoforo Creek.

Another way to take into account the sensitivity is a risk-averse approach, in which one strives to avoid populations that are possibly low-ranked. A risk-averse ranking can be done using the minimax algorithm. Minimax is a method in game theory for minimizing the expected maximum loss In the present context this means sorting the populations according to the minimum values of the maximum possible ranks of each population. This risk-averse approach suggests the following top 10 coastal populations:

Risk-averse ranking
1 Carmel River
2   San Luis Obispo Creek
3   Chorro Creek
4 Arroyo de la Cruz
5 Santa Rosa Creek
6 San Simeon Creek
   San Corpoforo Creek (tied)
8 Pismo Creek
   Morro Creek (tied)
10 Big Sur River

The risk-averse ranking seems closer to intuition than the risk-neutral ranking, except for the placement of the Big Sur River at the bottom of the list.

Figure 30. Basin-ranking in the South-Central California Coast Steelhead ESU. The ranking is based on the amount of potential habitat as in indicator for potential viability. Circles show the rank based on the single habitat model that is preferred on *a priori* biological grounds (as in Figure 13 through Figure 15). Error bars show the range of ranks (minimum and maximum) for 48 variant models.

A final way to rank is to choose the single one of the 48 models judged to have the most biologically realistic assumptions. This would be the model described earlier in this report, and mapped in Figure 13 through Figure 15 (pp. 33 - 35). This model assumes that only juvenile data should be used to fit the model; that steelhead can migrate up any stream gradient less than 12%; that mean summer discharge is a more appropriate predictor than mean annual discharge; that alluvial valleys do not generally comprise potential habitat; and that the 95% envelope is the most appropriate habitat model to predict potential habitat. A ranking based on this habitat model is as follows (data not shown in the figure):

Rank according to biological plausibility
1   Carmel River
2   Arroyo Grande Creek
3   San Luis Obispo Creek
4   Chorro Creek
5   Little Sur River
6   Big Sur River
7   Arroyo de la Cruz
8   San Carpoforo Creek
9   Santa Rosa Creek
10   Morro Creek

Slight differences in environmental stochasticity between these basins could easily disrupt the validity of the ranking scheme. So could an important environmental predictor that we omitted from our model, such as a geologic substrate that promotes summertime discharge, or that is especially conducive to pool formation. In addition, this ranking method omits lagoon habitat, and has other problematic assumptions as described in the preceding sections.

5.5. Potential Viability in the Southern California Coast Steelhead ESU

When populations in this study area are assigned mean ranks from the 48 habitat models, the top-ranked populations are the Santa Maria, Santa Clara, Santa Ynez, and Santa Ana populations, in that order (Figure 31). As before, the sensitivity analysis indicates that the relative rank of these four populations is sensitive to model assumptions, but their collective status as the top four is not (again, note the gap in error bars between the Santa Ana and San Luis Rey populations).

There is a key feature that is overlooked in this ranking scheme, however. We believe that certain basins have more reliable winter flows, and hence more reliable migration access (See §2.3, p. 14). In interpreting the rankings depicted in Figure 31, we suggest the following rule-of-thumb: All the large basins in the SOLA region, and the Santa Maria basin in the NOLA region, probably have unreliable winter flows, even in an unimpaired state, which would introduce an unquantified risk factor. We rank them separately, as "Category 2" basins.

In addition, we expect our model to make its biggest errors in the SOLA region. To put it simply, the habitat maps for this region are best thought of as extrapolations, whereas in the NOLA region they are more reasonably described as interpolations. In general, extrapolations are subject to more kinds of errors than interpolations.

Taking into account the above rule-of-thumb, a risk-neutral ranking method is to use mean rank from the 48 models. This approach produces the following top 10 populations in Category 1:

Risk-neutral ranking
1   Santa Clara River
2   Santa Ynez River
3   Ventura River
4   Goleta Slough complex
5   Jalama Creek
6   Rincon Creek
7   Big Sycamore Canyon
8   Dos Pueblos Canyon
9   Arroyo Burro
10 Malibu Creek

This ranking generally matches intuition, with the exception of Malibu Creek at the bottom. Malibu Creek is often considered to have high restoration potential, due in part to its status as the largest stream network draining the Santa Monica Mountains.

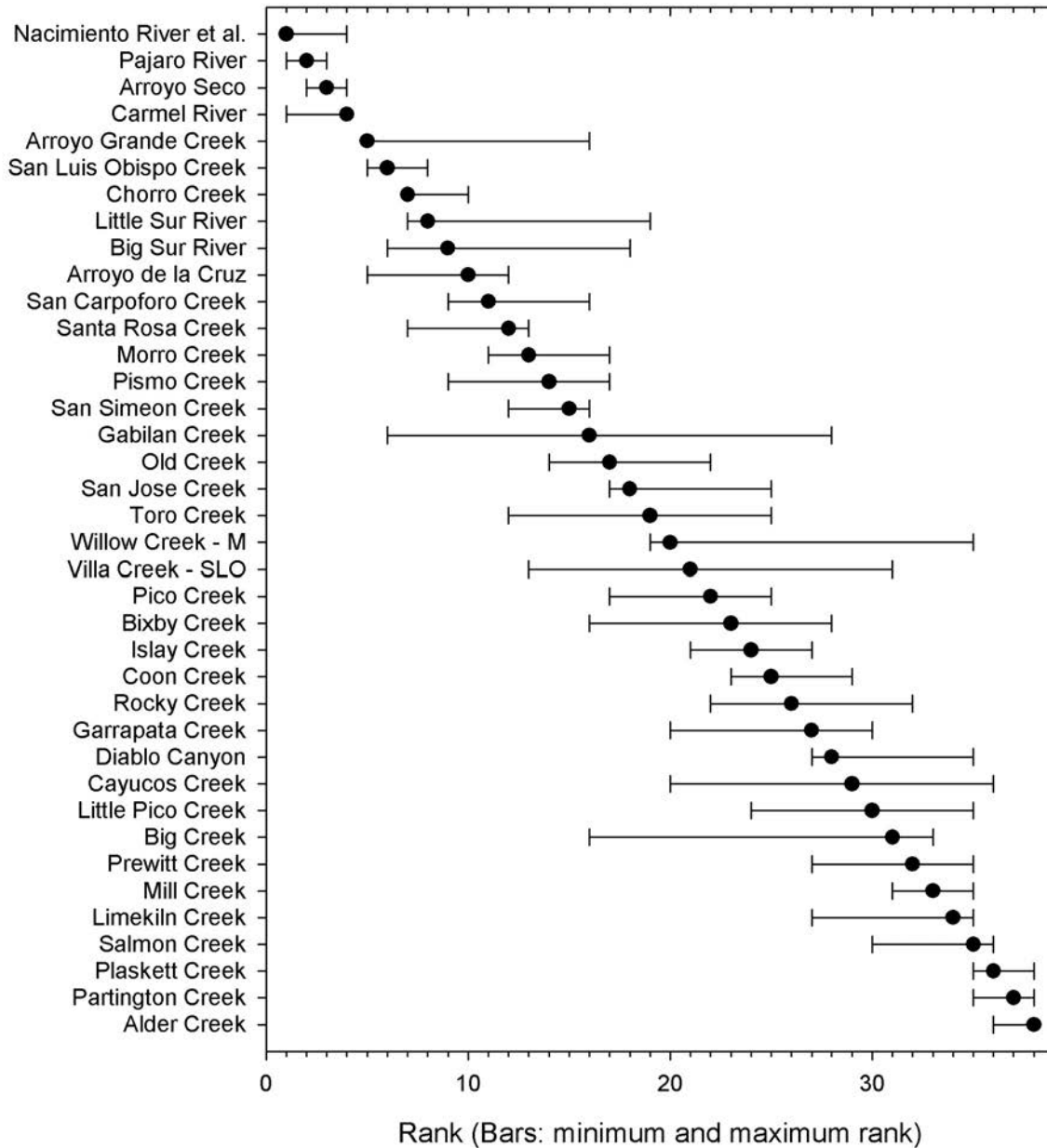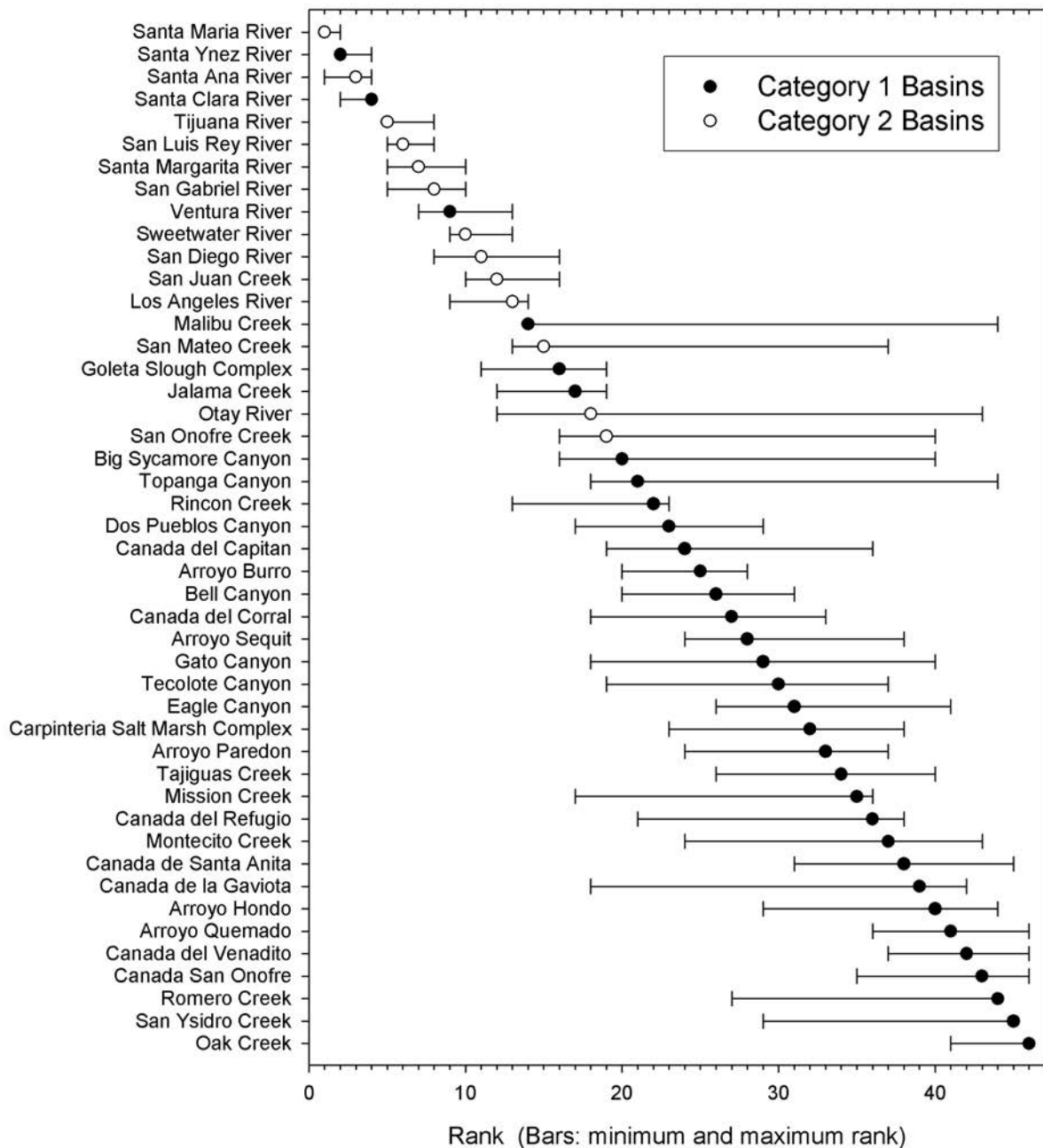**Figure 31. Basin-ranking in the Southern California Coast Steelhead ESU. The ranking is based on the amount of potential habitat as in indicator for potential viability. Circles show the rank based on the single habitat model that is preferred on *a priori* biological grounds (as in Figure 16 through Figure 22). Error bars show the range of ranks (minimum and maximum) for 48 variant models. Category 2 basins are those thought to have particularly unreliable migration flows.**

As noted in the previous section, a risk-averse ranking scheme uses the minimax algorithm. This leads to the following top 10 populations in Category 1:

Risk-averse ranking
1   Santa Clara River
    Santa Ynez River (tied)
3   Ventura River
4   Goleta Slough complex
    Jalama Creek (tied)
6   Rincon Creek
7   Arroyo Burro
8   Dos Pueblos Canyon
9   Bell Canyon
10 Canada del Corral

Finally, there is a ranking based on the single model that is most realistic biologically (as in the previous section). This ranking is as follows for Category 1:

Rank according to biological plausibility
1.   Santa Ynez
2.   Santa Clara
3.   Ventura
4.   Malibu
5.   Goleta Slough complex
6.   Jalama
7.   Big Sycamore Canyon
8.   Topanga Canyon
9.   Rincon Creek
10. Dos Pueblos Canyon

We provide a separate ranking for Category 2 populations, believed to inhabit basins with unreliable migration opportunities. Using the biologically-preferred model, the top-ranked populations in Category 2 are:

Rank according to biological plausibility, Category 2 basins
1.   Santa Maria River
2.   Santa Ana River
3.   Tijuana River
4.   San Luis Rey River

5.   Santa Margarita River
6.   San Gabriel River
7.   Sweetwater River
8.   San Diego River
9.   San Juan Creek
10. Los Angles River

In terms of viability, these last two lists probably overlap (i.e., interdigitate), so that for example the Santa Maria population should be ranked over the population in Dos Pueblo Canyon. But without knowing the amount of additional extinction risk caused by the unreliable flows, there appears to be no objective method to determine the pattern of interdigitation.

5.6. Using the Ranks for Recovery Planning

The ranking schemes described above represent an informed guess. Even if we had much more data than we do, assessing the potential viability of each population would embody substantial uncertainty; in our case the uncertainty is higher yet. A particular recovery strategy—in which some populations are targeted for restoration to viability at the expense of attention to others—is a bet, and the successful recovery of particular steelhead populations is far less certain than death and/or taxes.

That said, clearly our analysis suggests the chances of successful restoration to viability are greatest in the high-ranked populations. The more a recovery strategy is based on low-ranked populations, the less likely it is to succeed.

To avoid waste of time and money, it is paramount that the recovery strategy include provisions for monitoring the populations, and for learning more about them. This allows the bet-in-progress to be periodically re-assessed, and the recovery strategy to be improved over time. We recommend that the strategy explicitly assume that many mistakes will be made during the long-term process of recovery, and be structured so as to learn from those mistakes and thereby improve the chances of success as time passes.

Part 6. Assessing Potential Independence of Unimpaired Populations

Dispersal occurs when a migrating adult steelhead returns to a basin different than the one in which it originally hatched. This sort of movement, if common, has the potential to cause the dynamics of populations in different basins to become interdependent. Earlier in this report we made the simplifying assumption of one basin/one population, which treats dispersal as rare enough to be negligible. We are now in a position to re-evaluate certain aspects of that assumption.

Dispersal can have both a positive and a negative aspect. The positive aspect is that a modicum of dispersing fish can rescue a population that is on the verge of extinction due to environmental stochasticity (Hanski *et al.* 1995). Dispersing fish can also reverse an extinction once it has happened by re-colonizing the empty habitat[1]. We will defer an analysis of the positive aspects of dispersal to a future report on ESU-level viability, and here focus on the negative aspect.

The negative aspect of dispersing fish is this: though a population may depend on the rescue effect, the dependency is difficult to detect. Thus, a population maintained by immigrants can easily be mistaken as viable if the immigrants are not taken into account.

One scenario in which some populations maintain others via dispersal is known as a "source-sink system" (Pulliam 1988, Harrison 1991). In a sink, the habitat is of such poor quality that fish on average do not produce sufficient offspring to replace themselves. Yet if enough immigrants continue to enter the basin (from the source population), the population has the superficial appearance of being stable and viable. Since dispersing fish are difficult to count, and habitat pro-

ductivity is difficult to measure, the detection of sink populations is not easy.

Another version of the above scenario is sometimes called an "island-mainland system," after MacArthur and Wilson (1967). In this case, "islands" are small habitat patches that may have highly suitable habitat, but are so small that the resident population is vulnerable to stochastic extinction. In order for the species to maintain a long-term presence in the island patches, there must be a "mainland" patch that is sufficiently large to support a viable population, and sufficiently close to supply colonists to the islands (Harrison *et al.* 1988, Harrison 1991).

We wish to determine which of the hypothetical unimpaired populations described in the last section are the least likely to be dependent on immigrant fish from other basins. As elsewhere in this report, to do this task we must make some simplifying assumptions.

6.1. Assumptions and Analysis

One reasonable assumption is that larger populations should generally produce more dispersers. Assume the average number of dispersers to be proportional to mean population size. It follows that the emigrants from a large population will have a much bigger effect on a neighboring small population than vice-versa. To make this example concrete, assume a population of 10,000 adults, another population of 500 adults, and a dispersal rate of 5%. The large population will contribute 5% of 10,000 adults to the small—that is, 500 immigrants will enter a population of 500. In contrast, the small population will provide 25 fish to the large population (an immigration fraction of 0.25%). This is an illustration of source-sink dynamics being driven by differences in habitat amount rather than habitat quality. It is not an unrealistic scenario for the study area.

If the above thought experiment is expanded to include multiple populations, then the dispersing fish must somehow allocate themselves across

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[1] Using "extinction" to mean temporary absence of a population may seem odd usage, but is standard in the scientific literature. A site at which the population is absent for more than one generation before being recolonized from elsewhere is commonly called a "population extinction," to be distinguished from species extinction, in which *all* populations comprising the species are lost, and recolonization is therefore impossible.

the basins. Do all dispersers go to neighboring basins? Disperse randomly? What do they do?

Steelhead, like other anadromous salmonids, have a pronounced homing ability. This involves an early imprinting process on olfactory cues in their natal stream, and an ability to identify these cues to re-locate their natal stream years later during the spawning migration (reviewed by Dittman and Quinn 1996). Most of what is known about the homing ability of salmonids is based on studies of their movement behavior once they have entered freshwater. Much less is known about the underlying mechanisms for homing behavior in the ocean, mostly because of the difficulty of studying migration behavior on the high seas (Dittman and Quinn 1996). Still less is known about the spatial pattern of dispersal for those fish that do not home (Quinn 2005, chapter 5).

Genetic data for coastal steelhead in California indicate a pattern of isolation-by-distance (Garza *et al.* 2004), with most populations showing a high degree of genetic differentiation, attributed mostly to genetic drift rather than divergent selection (Aguilar and Garza 2006). The high degree of differentiation suggests that dispersal is infrequent (i.e. homing ability is strong), although this conclusion is confounded with other causes of drift such as small population size and past bottlenecks. Indeed, there is genetic evidence of recent bottlenecks in population size for most of the coastal steelhead populations in California that have been studied (Garza *et al*. 2004).

The pattern of genetic isolation-by-distance suggests that dispersal events are spatially structured. Garza *et al.* (2004: 2) state "there is a strong signal that migration [dispersal] is dependent on distance,…with geographic distance alone explaining about 20% of the genetic variation in the samples." This suggests that short-distance dispersal events are more common than long-distance dispersal events. In other words, most dispersers end up spawning in basins relatively close to their natal stream.

Yet we have at least one notable example of a significant number of fish simultaneously exhibiting a long-distance dispersal pattern. According to Hovey (2004), at least 4 steelhead colonized San Mateo Creek in San Diego County during the mid 1990s[2]. If long-distance dispersal events are truly rare, the simultaneous colonization of this basin by 4 fish is highly improbable. The mouth of the creek— in northern San Diego County—is fully 120 km south of the nearest potential source of colonists, Topanga Creek (measured as the fish swims). Topanga Creek is a relatively small watershed; the nearest potential source population of any size is in the Santa Clara River system, the mouth of which is 310 km from San Mateo Creek. We do not know the current run size of the Santa Clara River population, but at the very most it is a few hundred fish; more likely a few dozen.

Although this is a single anecdote about the colonization abilities of steelhead, it suggests that long-distance dispersal events are frequent enough to be ecologically important. Indeed, colonization of distant non-natal streams is well within the capability of the species, which can migrate thousands of miles while in the ocean.

6.2. An Index of Dispersal Pressure

The mathematical construct used to think about dispersal is the "dispersal kernel," a matrix of probabilities or rates describing the distribution of movement distances of propagules (Kot *et al*. 1996). As described previously, we are nowhere near even a first approximation for the dispersal kernel of steelhead in our domain. Moreover, because of the unreliable migration flows in southern California, there is reason to believe that steelhead have a qualitatively different dispersal kernel here than in the wetter parts of their geographic range. Finally, the colonization of San Mateo Creek and Topanga Creek suggest that dispersing fish move in groups. The degree to which they do so has enormous implications for their recolonization abilities.

To deal with all this uncertainty, we take an analytic approach comparable to the one taken in the last section on potential viability: We do a sensitivity analysis and apply the minimax algorithm to the results. The sensitivity analysis uses three variant models of the dispersal kernel.

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[2] Sporadic immigrants (all dead) have also been found in San Juan Creek and the Santa Ana River in recent years.

The first variant is the "homogenous dispersal pool", in which each population is assumed to receive an equal fraction of the total number of dispersers generated by the ESU. The second variant is the "nearest neighbor model," in which half the dispersers from each basin immigrate to the next population south, and the other half to the next population north. Note that these two variants describe the opposite ends of a continuum: from long-distance dispersal being common to long-distance dispersal being negligibly rare.

In a third variant we assume that dispersal is structured not by the spatial separation of river mouths, but rather by the reliability of migration flows in those mouths. In particular, as a first approximation we assume that immigration rate to a population is proportional to mean annual flow at the river mouth. All three of our variant models assume that emigration from populations is proportional to their long-term mean abundance.

Unfortunately, we do not know the basic dispersal rate—that is, the fraction of a run that disperses in the first place. We believe the fraction lies somewhere between 1% and 15%, based on estimates of 2% - 3% from an intensive field study by Shapovalov and Taft (1954) and our general recognition that other basins are likely to vary somewhat. However, it could be considerably higher as a result of adaptation to unreliable migration flows or perhaps to small basin size.

Rather than focusing on the basic dispersal rate, which is not known, we can focus on relative rates. In other words, we can simply rank our populations. A simple (perhaps simplistic) metric for doing so would be the number of immigrants relative to the number of natal adults in each population (i.e. the long-term average of i_x / n_x, where i_x is the number of immigrants and n_x is number of natal adults per generation in population x). Our limited data constrains us to use an indirect index of this quantity, derived as follows:

$$\frac{i_x}{n_x} = \frac{\alpha_x I}{\beta h_x} = k \frac{\alpha_x}{h_x}$$

where I is the total number of dispersers per generation for the entire ESU, α_x is the proportion that immigrate to population x, h_x is the amount of potential habitat in the stream system used by population x, and β is a constant describing the mean per-unit productivity of the potential habitat, in units of adult spawners. All these quantities are taken to be long-term means. The ratio I/β is an unknown that is taken as constant across populations; for an index of relative values it can be disregarded, leaving the ratio α_x/h_x as a relative index of dispersal "pressure" on a population:

Index of dispersal pressure on population x =
The fraction of dispersing fish generated by the ESU that immigrate to population x, divided by amount of potential habitat in population x.

In short, potential habitat is taken to be an index of mean population size, so that the dispersal pressure is a relative measure of immigrants per capita in any given population. Units are per-cent dispersers per km of potential habitat. The index is computed for the ESU in the unimpaired state, and is considered to be a long-term average.

In the index, the value of α_x depends on the dispersal model being used. In the dispersal-pool model, all populations have the same α_x, equal to the reciprocal of the number of populations comprising the ESU. In the nearest-neighbor model, the total amount of potential habitat in the ESU is rescaled to equal 1.0, and α_x is the sum of the rescaled values for the two neighbors of population x (i.e. the next steelhead basin north, and the next steelhead basin south). This formulation assumes that number of dispersers produced by a population over the long term is proportional to the amount of potential habitat. Finally, in the reliable-flow model, mean annual discharge is rescaled so that its sum for all river mouths inhabited by the ESU is equal to 1.0, and α_x is then the rescaled value for the basin inhabited by population x.
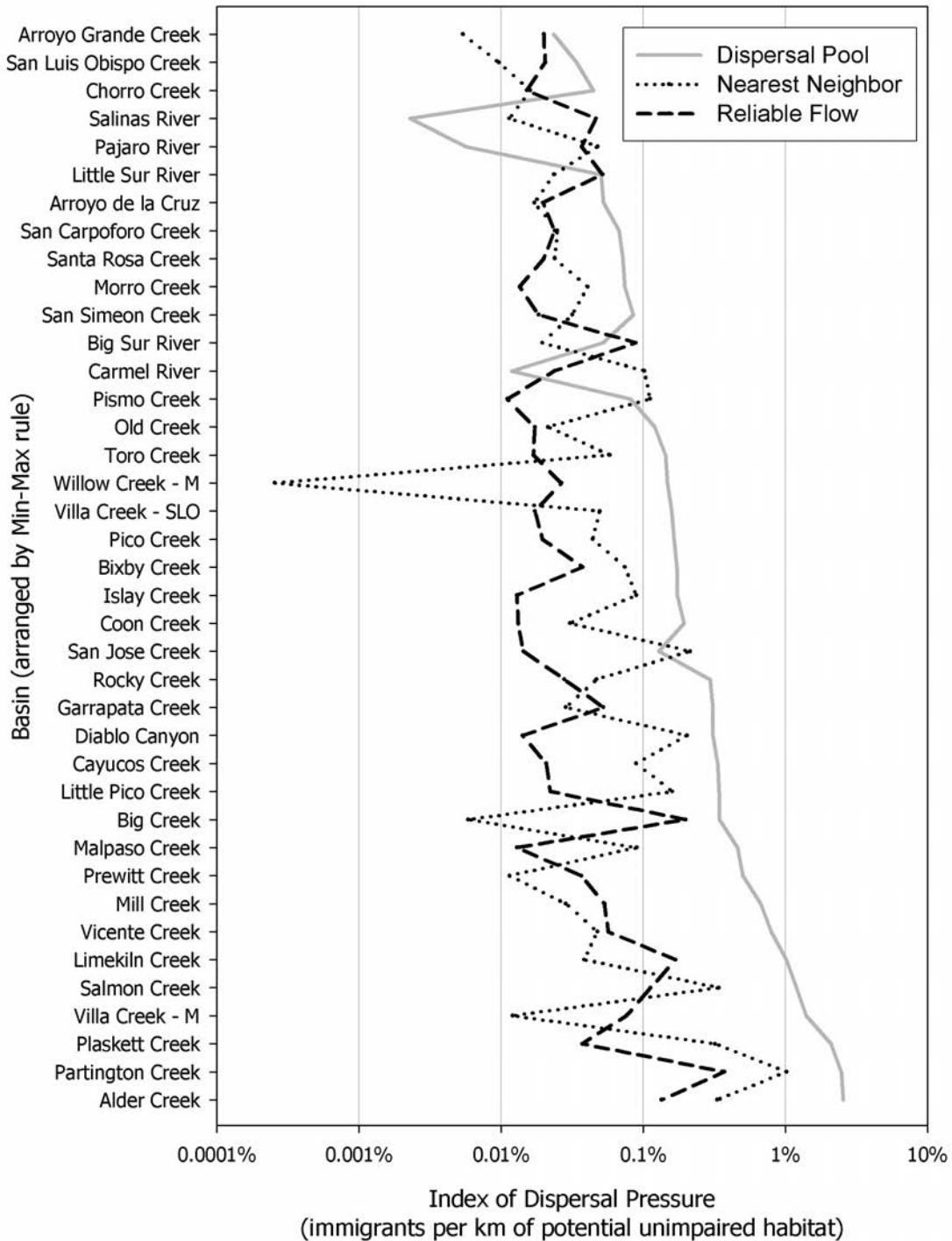
Figure 32. Index of dispersal pressure for each of three dispersal kernels in the South-Central California Coast Steelhead ESU. The populations are arranged using the minimax rule. The top-ranked populations have the greatest assurance of being independent, provided the assumptions of the analysis (described in the text) turn out to be reasonably accurate. The three dispersal kernels—homogeneous dispersal pool, nearest neighbor model, and reliable-flow model—are described in the text. Note that for most of the basins the Dispersal Pool model provided the maximum index of dispersal pressure.

6.3. Dispersal Pressure in the South-Central California Coast Steelhead ESU

The index of dispersal pressure for the ESU in the south-central California coast is depicted in Figure 32. For a given basin, the three variant models sometimes differ in their index by one or two orders of magnitude. Once again it is appropriate to rank the basins using the minimax rule; this can be interpreted as a ranking of one's assurance that the population is relatively unaffected by immigration.

The top-ranked populations—those most assured to have population dynamics unaffected by immigration—are dispersed throughout the south-central study area. The top two are the populations in Arroyo Grande Creek and San Luis Obispo Creek, both at the south end of the study area. Ranks four and five are the Pajaro and Salinas populations (Arroyo Seco and Nacimiento populations are lumped in this analysis). The remaining top 10 are dispersed between Morro Bay and the Little Sur River. This wide-dispersion could be an important element in the recovery of the ESU. A surprise was that the population in the Carmel River did not occur in the top 10; nor did the population in the Big Sur River.

Under the minimax rule, the dispersal-pool model ended up being the model used to rank most of the populations (however, the dispersal-pool model is probably the least plausible of the three models under consideration). A casual inspection of Figure 32 indicates that a ranking based on one of the other variant models would be quite different. This represents the cost of uncertainty about the dispersal kernel. The minimax rule is a way to minimize the risk of being wrong, but an even better way to minimize the risk of being wrong would be to learn more about the actual dispersal kernel.

6.4. Dispersal Pressure in the Southern California Coast Steelhead ESU

The index of dispersal pressure for this ESU is depicted in Figure 33. The three top-ranked populations inhabit the three largest basins of the NOLA section of the study area: Santa Maria River, Santa Ynez River, and Santa Clara River. The next 6 are all large systems in the SOLA section. Then, at rank 10 and 11 are the populations in the Ventura River and Malibu Creek, respectively.

An interesting difference between this ESU and the other is the fact that only two of these basins received their top-ranked status based on the dispersal-pool model. Most achieved their status based on the reliable-flow model, or by close agreement between it and the nearest neighbor-model. With this in mind, it is important to realized that our simple model did not take into account year-to-year variability of flow. Thus it seems prudent to retain from the last section our system of Category 1 and Category 2 basins (more reliable and less reliable flow, respectively). The top-ranked basins in Category 1 (more reliable flow) are:

1. Santa Ynez
2. Santa Clara
3. Ventura
4. Malibu
5. Goleta Slough complex
6. Topanga Canyon
7. Rincon
8. Dos Pueblos Canyon
9. Canada del Capitan
10. Arroyo Burro

Most of the small basins along the southern coast of Santa Barbara County received a low rank that was based on the dispersal-pool model. If this model were to be ruled out we would have greater certainty that immigration to these populations is very low. This has important implications, not just for our purposes here, but also for the positive aspects of dispersal mentioned earlier—namely, the rescue effect and recolonization dynamics.
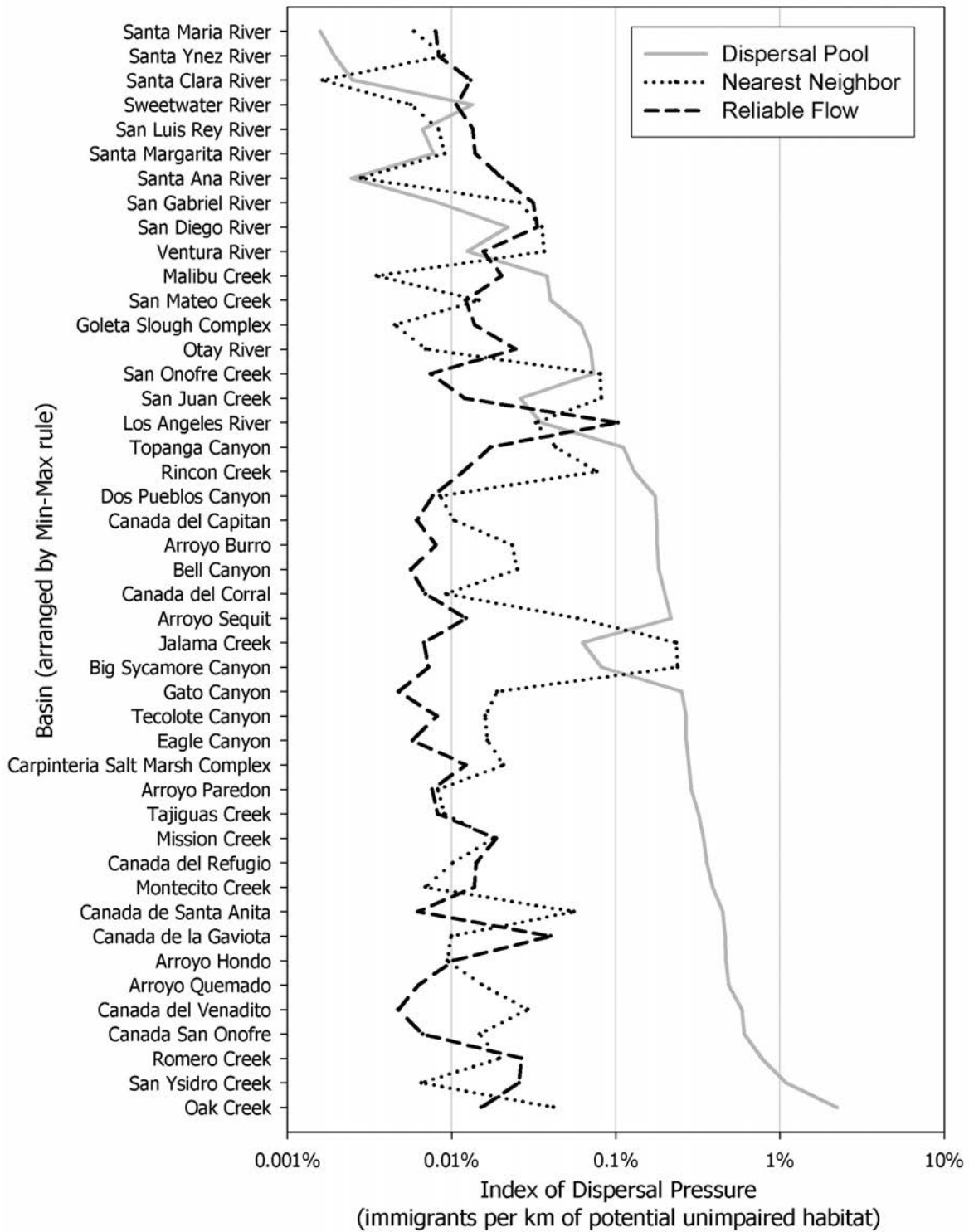
Figure 33. Index of dispersal pressure for the Southern California Coast steelhead ESU. Otherwise as in Figure 32. The three dispersal kernals—homogeneous dispersal pool, nearest neighbor model, and reliable-flow model—are described in the text.

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We expect recolonization and the rescue effect to be important forces because these coastal basins probably have small carrying capacity. If the dispersal pool is the most realistic model of dispersal, then it supports a flexible approach to recovering these small coastal populations, because their spatial position relative to one another is not terribly important. If the nearest-neighbor model or reliable-flow model is the more accurate description, it is more likely to impose additional constraints on the recovery strategy along this section of coast, because connectivity would depend on recovery of basins that are neighbors, or that have reliable flow.

The top-ranked basins in Category 2 (less reliable flow) are:

1. Santa Maria
2. Sweetwater
3. San Luis Rey
4. Santa Margarita
5. Santa Ana
6. San Gabriel
7. San Diego
8. San Mateo
9. Otay
10. San Onofre

It is difficult to know how seriously to take the ranking for Category 2 streams, based on the fact that we expect variability of flow to play a large role in limiting the entry of migrants. We have no empirical basis at this point for a comparative assessment of this limit.

6.5. Using the Ranks for Recovery Planning

The first-ranked populations are more likely independent than the low-ranked populations. How is this relevant to recovery planning?

The answer is the last-ranked populations have a higher risk of being exceptions to the "one-basin/one-population" rule described earlier in this document. They are more likely to experience high levels of exchange with subpopulations in neighboring basins, or even be dominated by them, in which case their dynamics would be

heavily influenced by the conditions in neighboring basins. Such a group of steelhead would not constitute a distinct population, but a subpopulation, a component of a larger, basin-spanning steelhead population.

What, specifically, is the problem with being an exception to the "one-basin/one-population" rule? We discuss two scenarios below.

6.5.1. Low-ranked for Both Independence and Potential Viability

Populations that are low-ranked along both axes—that is, small amounts of potential habitat and high dispersal pressure from elsewhere—would seem to merit low priority in a recovery plan. However, if several such populations occur in a geographic cluster, they may jointly comprise a single large basin-spanning population with great potential for viability. This would require significant interchange of individuals between neighboring basins. Thus, to evaluate this possibility one would need to know something about absolute levels of dispersal, not the relative levels that we roughly address here. If between-basin dispersal were common enough, it would cease to be dispersal *per se*, but rather would constitute within-population mixing, sometimes called trivial movement.

We have some very preliminary indications that fish in one area, the Big Sur Coast, may enter the marine environment on a more flexible schedule than the standard view of the steelhead lifecycle. In an ongoing study of the *O. mykiss* population in Big Creek, Williams, Lindley and Rundio report the occurrence of sea-lice on some of the larger inhabitants of the creek, *O. mykiss* of about 35 cm TL (S. Lindley, personal communication). They assessed strontium-calcium ratios in the otoliths of one such fish, and found clear evidence that the fish used the marine environment on a regular basis, perhaps annually. This does not necessarily indicate significant movement among basins—fish may still show high fidelity to their natal stream—but it clearly implies the fish are more flexible than implied by standard views of steelhead life history.

The risk, then, of taking the low ranks at face value is that some significant recovery opportunities might be overlooked. The tell-tale sign would be geographic clusters of low-ranked basins that each have stable occurrence of steelhead. The potential for this situation seems highest along the Big Sur Coast and the stretch of coast between Point Conception and Ventura; these areas may warrant more intensive studies of fish movement to accurately evaluate their population structure and recovery potential.

6.5.2. Low-ranked for Independence, High-ranked for Potential Viability

The principle problem for populations in this category is operational—the response of the population to in-basin recovery actions may be obscured by immigrants from neighboring basins. In the extreme, large neighboring basins might supply so many immigrants that the population is kept perennially above local carrying capacity. If such density-dependence were not taken into account, the habitat might appear to be poor, due to demonstrable low survival, when in fact the survival might be quite high at lower population densities. This phenomenon is sometimes called a pseudosink, because it has the superficial appearance of a population sink (a population in poor habitat whose continued existence depends on continual immigration from more robust populations elsewhere).

The principle risk of a pseudosink is not recognizing it as such, and erroneously writing off a population as not potentially viable. The existence of a pseudosink, however, would require large amounts of immigration. At present we have encountered no evidence, anecdotal or otherwise, for such a phenomenon in the study area. A less extreme, and more plausible, situation would be sufficient immigration to obscure the effects of recovery actions on the endogenous subpopulation of fish.

Thus, a low rank on the independence scale should not be viewed as negating a high rank on the potential-viability scale. Rather, it should be viewed as an indicator of potential complicating factors in the recovery of the population, particularly with regard to monitoring and the interpretation of monitoring data.

Part 7. Summary

7.1. Introduction

1. The purpose of this report is to inform recovery planning for *Oncorhynchus mykiss* populations comprising the South-Central California Coast Steelhead ESU and the Southern California Coast Steelhead ESU. Under the Federal Endangered Species Act, the anadromous component of the former is currently listed threatened, and the anadromous component of the latter is currently listed as endangered.

2. The study area is the set of coastal basins bounded by the Pajaro River Basin in the north and the Tijuana River Basin in the south (inclusive).

3. The report has two fundamental goals. The first goal is to characterize the normal (unimpaired) state of each ESU, as a frame of reference for recovery. The second goal is to identify the complete set of original and extant populations in the study area, and assess the potential viability and independence of each one (§1.1 and §1.2).

7.2. Methods

4. To aid in recovery planning, we assess which of the original steelhead populations have the highest biological potential for restoration to a viable state. Our assessment is based on the concept of unimpaired state, which is the hypothetical present-day structure of the ESU if European settlement had had no significant impact on the species *O. mykiss* (§1.1 on p. 2).

5. Biological potential is assessed in terms of potential viability and potential independence of individual populations under the hypothetical unimpaired state.

6. The ranking scheme for potential viability requires numerous simplifying assumptions, grouped for convenience under four headings: 1) the population-size assumption; 2) the habitat-quantity assumption; 3) the disturbance-regime assumption; and 4) the IP-estimation assumption (Part 5 on p. 48).

7. To assess amount of potential habitat for each population, we assumed that the most limiting habitat is freshwater stream reaches used for over-summering (§5.3.1. on p. 51). Our basis for this assumption is that the arid Mediterranean summers of the study area typically cause reduction in amount and extent of habitat relative to other times of year.

8. The habitat model used to generate the ranking scheme was based on the concept of "environmental envelopes," which is a coarse-grained tool for modeling habitat, and has certain limitations as described below and in the findings (§4.2 on p. 29).

9. The habitat model addressed only stream habitat; it omitted consideration of lagoon habitat, which is highly productive over-summering habitat but is insufficiently understood to be modeled quantitatively.

10. The predictors in the habitat model were chosen based on biological considerations (§4.1 - §4.3 on p. 28). They are: 1) stream gradient; 2) valley constraint; 3) mean annual air temperature; 4) mean discharge of streams during August and September; 5) mean August air temperature; and 6) limiting access gradient. These are all described more fully in Table 6 (p. 30). The latter three predictors merit special attention when interpreting the assessment, for reasons described below.

11. The model of mean summer discharge used in this report is based on a correlation between measured summer discharge and two predictors: mean annual precipitation and contributing watershed area. As such, it omits complicating local factors. These include losses to evapotranspiration and groundwater flux (both influent and effluent) (§4.7).

12. Migrating steelhead were assumed to not ascend stream gradients greater than 12%, though this may not be an absolute limit, depending on stream geomorphology.

13. For the purposes of this report it is useful to determine which of the populations would be least likely to receive immigrants under un-impaired conditions. These populations would probably have the greatest demographic independence from other populations (Part 6 on p. 70).

14. For the study area, very little is known about how often or how far steelhead disperse. We develop three quite different but plausible models as a ranking tool. They are 1) the homogeneous dispersal pool; 2) the nearest neighbor model; and 3) the reliable-flow model (§6.2 on p. 71).

15. Since we do not know which dispersal model is most appropriate, we used the minimax algorithm to interpret their predictions. The minimax algorithm minimizes the maximum expected cost of making a mistake under uncertainty (§6.2 on p. 71).

7.3. Findings

7.3.1. Original and Extant Populations

16. A review of the historical record by Titus *et al.* (2003) and others confirmed that steelhead were once widespread in the study area (Part 2 on p. 11). The list of coastal basins in which they originally occurred is given in Table 2 (p. 21).

17. Various lines of indirect evidence and Occam's Razor suggest that recovery planning be based on the "one basin/one population" rule, unless specific data suggest otherwise. This rule states that each coastal basin listed in Table 2 be regarded as capable of supporting a discrete population of steelhead, some which may be viable or potentially viable (§2.4 on p. 17).

18. The weight of evidence for the Salinas Basin indicates that it should be regarded as capable of supporting three discrete populations of steelhead (§2.6): One in Gabilan Creek; one in Arroyo Seco; and one in the Nacimiento River and nearby streams (San Antonio River and upper Salinas tributaries).

19. The study area has three regions in which numerous small basins line the coast: the Big Sur, the southern Santa Barbara coast, and the Santa Monica Mountains. If adults or juveniles regularly make interbasin transfers in these regions then they would comprise exceptions to the one basin/one population convention. A few observations suggest this possibility.

20. Efforts to document the species' current pattern of occurrence indicate that steelhead are still widespread, though the steelhead components of *O. mykiss* populations appear to have been lost in about a third of the basins. A majority of these are in the southern portion of the Southern California Coast Steelhead ESU (Part 3 on p. 24).

21. About a third of the basin-wide steelhead losses are associated with watersheds having a warm climate. About a third are associated with anthropogenic barriers that currently have *O. mykiss* populations above the barriers. And about a third are associated with anthropogenic barriers for which *O. mykiss* presence above the barrier has not been determined (Part 3 on p. 24).

22. Subpopulations of *O. mykiss* above anthropogenic barriers are not descendents of hatchery fish. In most circumstances, they are as closely related to subpopulations below barriers as they are to other subpopulations above the barriers. In short, barriers were not associated with greater genetic isolation.

23. There is evidence from Alaska that land-locked steelhead populations can retain the potential for anadromy for at least 70 yr, despite strong selection against it. However, there is evidence that the first generation of land-locked fish to be able to migrate to the ocean have lower fitness than fully anadromous populations.

24. The evidence summarized above suggests that the subpopulations currently above barriers were once integral components of the region's steelhead populations, and likely have the potential to be restored to an anadromous state.
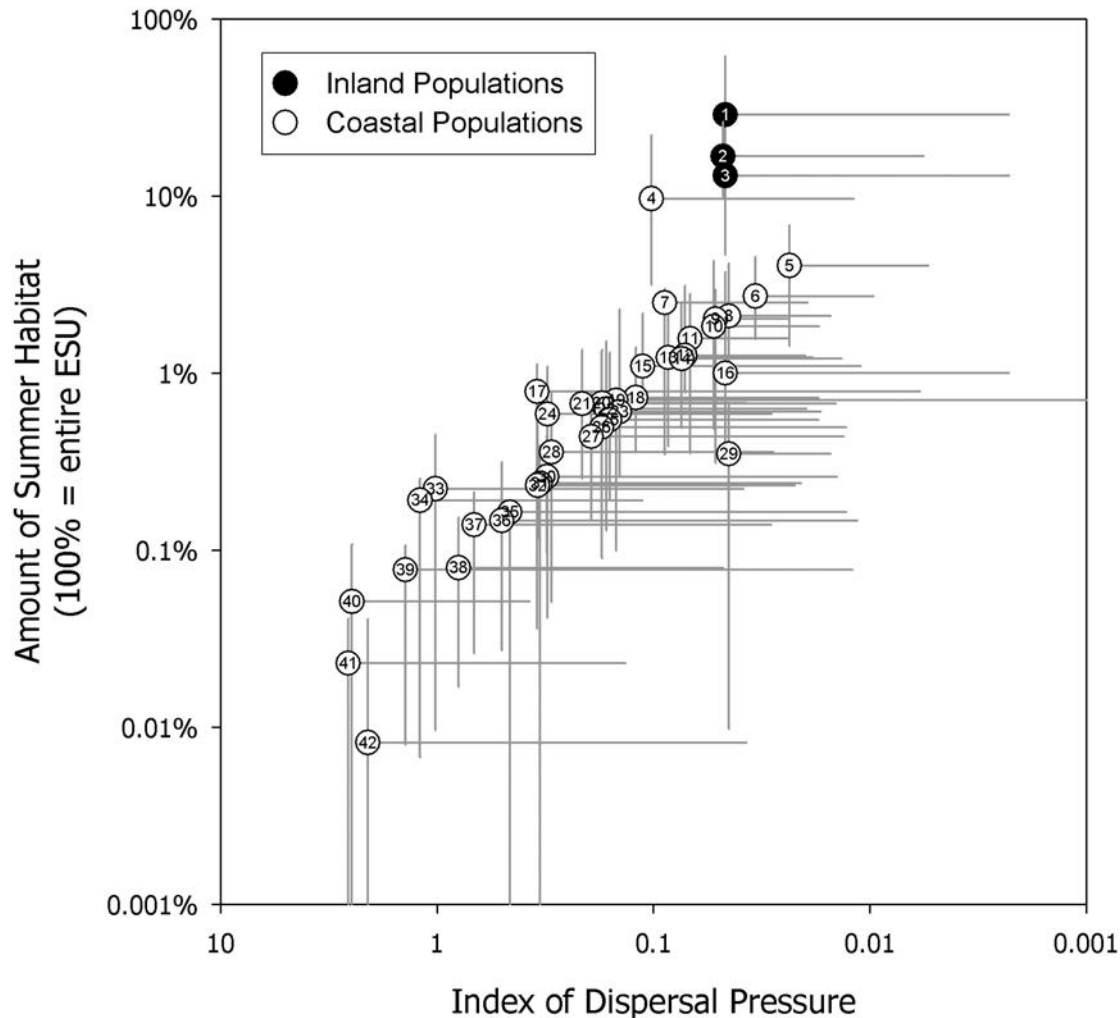
Figure 34. Potential viability and independence of populations comprising the South-Central California Coast Steelhead ESU. Amount of summer habitat is an indicator of potential viability (but see notes in text about unaccounted risks in the inland populations). The index of dispersal pressure is an indicator of independence, with lower values implying greater likelihood of independence. The circled numbers correspond to viability rankings using the biologically-preferred habitat model. Error bars describe the range of possible values from sensitivity analyses (see text).

Key:

1 = Nacimiento *et al.*; 2 = Pajaro River; 3 = Arroyo Seco; 4 = Carmel River; 5 = Arroyo Grande Creek; 6 = San Luis Obispo Creek; 7 = Big Sur River; 8 = Chorro Creek; 9 = Little Sur River; 10 = Arroyo de la Cruz; 11 = San Carpoforo Creek; 12 = Santa Rosa Creek; 13 = San Simeon Creek; 14 = Morro Creek; 15 = Pismo Creek; 16 = Gabilan Creek; 17 = Big Creek; 18 = Old Creek; 19 = Willow Creek – Monterey Co.; 20 = Bixby Creek; 21 = San Jose Creek; 22 = Pico Creek; 23 = Toro Creek; 24 = Garrapata Creek; 25 = Villa Creek – SLO Co.; 26 = Islay Creek; 27 = Coon Creek; 28 = Rocky Creek; 29 = Los Osos Creek; 30 = Diablo Canyon; 31 = Cayucos Creek; 32 = Little Pico Creek; 33 = Limekiln Creek; 34 = Salmon Creek; 35 = Malpaso Creek; 36 = Prewitt Creek; 37 = Mill Creek; 38 = Vicente Creek; 39 = Villa Creek – Monterey Co.; 40 = Partington Creek; 41 = Alder Creek; 42 = Plaskett Creek.

7.3.2. Potential Viability

25. Environmental stochasticity is a form of risk that constrains the interpretation of the viability ranking scheme. There was compelling evidence that the inland populations of the South-Central California Coast steelhead ESU inhabit a less stable environment than the coastal populations. This might increase their extinction risk to such a large degree that it overwhelms the advantage of their larger size. Or it might not (§5.3.1. on p. 51).

26. Given the above considerations, populations of the South-Central California Coast Steelhead ESU can be tentatively ranked in terms of potential viability. The top-ranked inland populations are 1) Nacimiento River *et al.*; 2) Pajaro River; and 3) Arroyo Seco. The top-ranked coastal populations are 1) Carmel River; 2) Arroyo Grande Creek; 3) San Luis Obispo Creek; 4) Chorro Creek; 5) Little Sur River; 6) Big Sur River; 7) Arroyo de la Cruz; 8) San Carpoforo Creek; 9) Santa Rosa Creek; and 10) Morro Creek. A complete ranking is in Figure 34.

27. For the Southern California Coast Steelhead ESU, there was no compelling evidence that coastal populations are more stable than inland populations. However, there is compelling evidence that migration opportunities are less reliable south of Los Angeles and in the Santa Maria River. Before interpreting the ranking scheme, the coastal basins should be sorted into two categories based on reliability of winter discharge.

28. The top-ranked Category 1 populations (in basins having relatively reliable winter discharge) are 1) Santa Ynez River; 2) Santa Clara River; 3) Ventura River; 4) Malibu Creek; 5) Goleta Slough complex; 6) Jalama Creek; 7) Big Sycamore Canyon; 8) Topanga Canyon; 9) Rincon Creek; and 10) Dos Pueblos Canyon. A complete ranking is in Figure 35.

29. The top-ranked Category 2 populations (in basins with unreliable winter discharge) are 1) Santa Maria River; 2) Santa Ana River; 3) Tijuana River; 4) San Luis Rey River; 5) Santa Margarita River; 6) San Gabriel River; 7) Sweetwater River; 8) San Diego River; 9) San Juan Creek; and 10) Los Angles River. A complete ranking is in Figure 35.

30. There is reason to believe that lagoons play an important role in determining the productivity and carrying capacity of coastal basins in the study area. Unfortunately, the science is not sufficiently developed to make even a rudimentary comparative assessment of lagoon habitat across basins. Thus, the assessment of potential viability omits the contribution of lagoons to the carrying capacity of each basin and the stability of steelhead populations, despite the likelihood that lagoons contribute disproportionately to the anadromous component of each population (§5.3.2.).

31. Using August air temperature to predict steelhead habitat involves an important assumption. Namely, that air temperature and stream temperature are closely related. As a result, the habitat model would not be expected to identify thermal refugia caused by factors other than air temperature; for example, hill-shading or groundwater inputs. We expect the importance of these sorts of refugia to be proportionately higher in warmer areas, especially the southern portion of the study area (§4.7 on p. 45).

32. Spatially intermittent streams appear to be extremely common in the study area, but are not predictable using our broad-scale method. This is in part due to the intricate geological structure of the region. Fine-resolution hydrologic studies are necessary to characterize patterns of intermittency (§4.7 on p. 45).

33. The wildfire regime should be expected to have a profound— but as yet poorly characterized—effect on steelhead habitat dynamics. Regional variation in the fire regime— particularly fire return interval, mean fire size, and the statistical distribution of fire sizes— may have important implications for summer stream discharge and sediment dynamics, and probably constrains steelhead population viability in the long run (§5.3.3. on p. 58).

34. Flood and drought regimes have been highly episodic, were even more so in the 19th Century, and may become even more so under future climate patterns. This is a form of stochasticity that may have significant implications for steelhead population viability (§5.3.3. on p. 58).

35. The long-term prospect of the species will probably be constrained by future climate patterns and the above three types of disturbance regimes—flooding, drought, and wildfire.

7.3.3. Potential Independence

36. According to the minimax algorithm, the populations with the highest assurance of being independent in the South-Central California Coast Steelhead ESU are 1) Arroyo Grande Creek; 2) San Luis Obispo Creek; 3) Chorro Creek; 4) Salinas River populations; 5) Pajaro River; 6) Little Sur River; 7) Arroyo de la Cruz; 8) San Carpoforo Creek; 9) Santa Rosa Creek; and 10) Morro Creek. A complete ranking is in Figure 34.

37. The Category 1 populations in the Southern California Coast Steelhead ESU that have the highest assurance of being independent are 1) Santa Ynez; 2) Santa Clara; 3) Ventura; 4) Malibu; 5) Goleta Slough complex; 6) Topanga Canyon; 7) Rincon; 8) Dos Pueblos Canyon; 9) Canada del Capitan; and 10) Arroyo Burro. A complete list is in Figure 35.
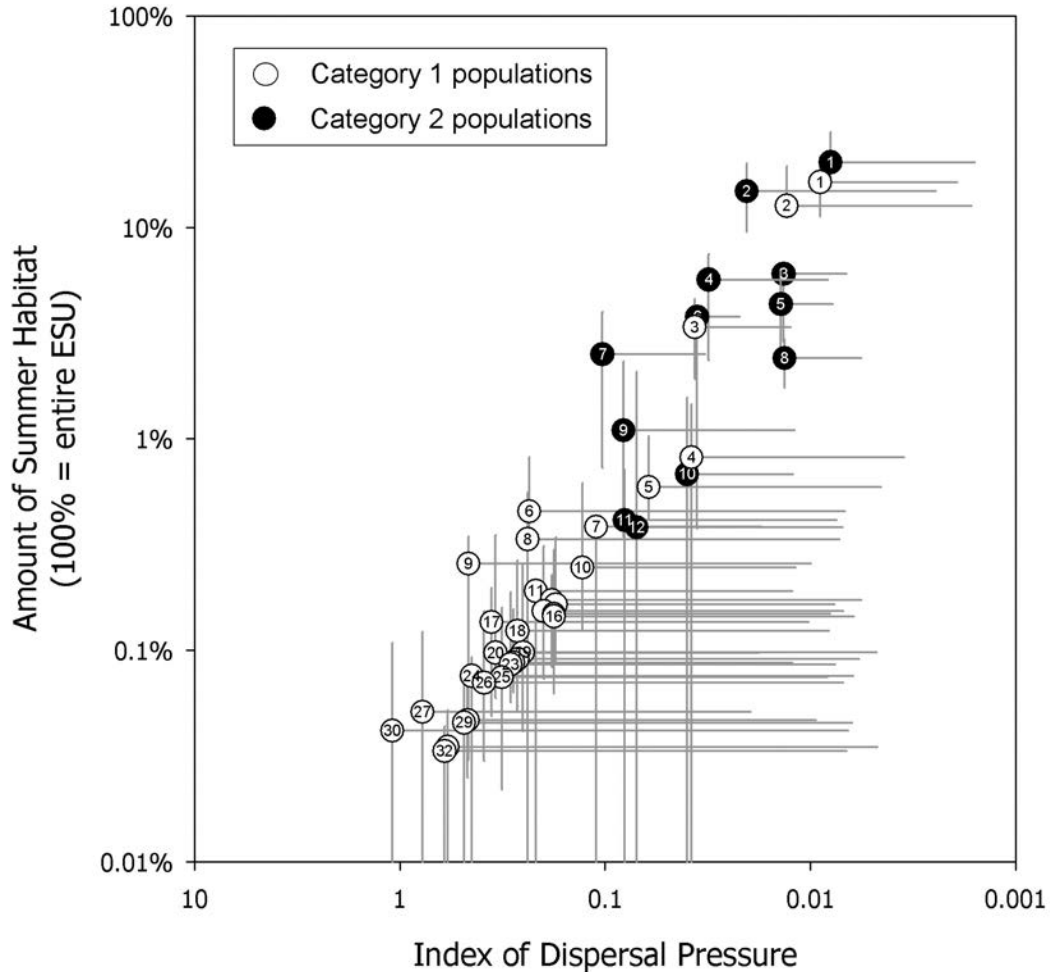
Figure 35. Potential viability and independence of populations comprising the Southern California Coast Steelhead ESU. Amount of summer habitat is an indicator of potential viability (but see notes in text about unreliability of migration access in Category 2 populations). The index of dispersal pressure is an indicator of independence, with lower values implying greater independence. The circled numbers correspond to viability rankings using the biologically-preferred habitat model. Error bars describe the range of possible values from sensitivity analyses (see text). Key:

Category 1 (basins with relatively reliable winter discharge)

1 = Santa Ynez R.; 2 = Santa Clara R.; 3 = Ventura R.; 4 = Malibu Cr.; 5 = Goleta Slough Complex; 6 = Jalama Cr.; 7 = Topanga Canyon; 8 = Big Sycamore Canyon; 9 = Cañada de la Gaviota; 10 = Rincon Cr.; 11 = Arroyo Sequit; 12 = Bell Canyon; 13 = Dos Pueblos Canyon; 14 = Cañada del Corral; 15 = Arroyo Burro; 16 = Cañada del Capitan; 17 = Cañada del Refugio; 18 = Tecolote Canyon; 19 = Gato Canyon; 20 = Mission Cr.; 21 = Eagle Canyon; 22 = Carpinteria Salt Marsh Complex; 23 = Arroyo Paredon; 24 = Cañada de Santa Anita; 25 = Tajiguas Cr.; 26 = Montecito Cr.; 27 = Romero Cr.; 28 = Arroyo Hondo; 29 = Arroyo Quemado; 30 = San Ysidro Cr.; 31 = Cañada del Venadito; 32 = Cañada San Onofre; 33 = Oak Cr.

Category 2 (basins with unreliable winter discharge)

1 = Santa Maria R.; 2 = Santa Ana R.; 3 = San Luis Rey R.; 4 = San Gabriel R.; 5 = Santa Margarita R.; 6 = San Diego R.; 7 = Los Angeles R.; 8 = Sweetwater R.; 9 = San Juan Cr.; 10 = San Mateo Cr.; 11 = San Onofre Cr.; 12 = Otay R.

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Part 9. Glossary

anadromous waters. Stream reaches that are accessible to migrating steelhead.

current population structure. Population structure of the ESU during the period 1970 – 2005.

environmental envelope. An interval on an environmental predictor that encompasses all known occurrences of a species.

environmental stochasticity. Between-generation variation in population growth caused by correlated births, deaths, *etc*.

ESU. Evolutionarily Significant Unit, comprising an important evolutionary component of the species that is substantially reproductively isolated from other such components.

ESU viability. The hypothetical state(s) in which extinction risk of the ESU is negligible and full evolutionary potential is retained.

independent population. A 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.

index of dispersal pressure. The proportion of the mean number of dispersing fish produced in each generation of the ESU that immigrate to a particular basin, divided by the amount of potential unimpaired habitat in that basin.

lagoon. An estuary that becomes closed off from the ocean seasonally. In the study area lagoons close off during the dry season, when wave action creates a sandbar barrier between the stream system and the ocean.

land-locked. A term for persistent steelhead populations prevented from migrating to or from the ocean by anthropogenic barriers such as dams, culverts, or water diversions.

migration season. The time of year when steelhead typically make spawning runs. Assumed in this report to be January through May.

NOLA study area. "North-of-Los-Angeles," the coastal basins north of Ballona Marsh in Los Angeles, up to and including the Santa Maria River system.

original population structure. The population structure of an ESU at the arrival of European settlers (1769 – *c*. 1850).

population structure. For an ESU, the number of populations, their geographic distribution, size distribution, pattern of interaction, etc.

potential unimpaired habitat. Stream reaches that could serve as habitat in the present day if the impacts of modern human settlement were negligible.

residualized. A term for hatchery steelhead that have remained in freshwater rather than migrating to the ocean.

risk-averse. A decision or scheme that gives weight to the cost of being incorrect.

risk-neutral. A decision or scheme based only on expectations, without taking into the account the possibility that expectations are wrong.

sensitivity analysis. A quantitative analysis of a scientific model, in which one assesses the sensitivity of conclusions to model assumptions or uncertainties in the data.

SOLA study area. "South-of-Los-Angeles," Ballona Marsh and all coastal basins with mouths south of it, up to the U.S. border with Mexico.

steelhead. 1) the anadromous form of the fish *Oncorhynchus mykiss*. 2) Operational definition: Fish of the species *O. mykiss* that occur in anadromous waters.

stray. 1) An adult steelhead that runs up, and spawns in, a different stream system than the one in which it originated. The general term for straying is "dispersing."

unimpaired population structure. The hypothetical present-day structure of an ESU if European settlement had never occurred, or had had no significant impact on the fish.

viable population. An independent population of any Pacific salmonid that has a negligible risk of extinction due to threats from demographic variation (random or directional), local environmental variation, and genetic diversity changes (random or directional) over a 100-year time frame.

Part 10. Appendices

10.1. Evidence for Two or More Populations in the Salinas Basin

Section 2.4 (p. 17) suggested that steelhead population structure should be regarded as "one basin contains one population," unless specific information indicates otherwise. In this appendix, we assess specific information for the Salinas Basin.

The Salinas system is so large that the watersheds of some of its larger tributaries dwarf the nearby coastal basins in the Big Sur. Due to size alone, the expectation for within-basin population structure is greater here than for smaller basins.

The Salinas River itself is a moderately large, low-gradient river running the length of the alluvial Salinas Valley. In most areas its bottom is sandy or muddy today, and in summer the surrounding valley can be rather warm. It is possible that these conditions posed a significant barrier to the movement of juveniles between the different tributaries of the Salinas.

On the other hand, the lagoon at the mouth of the river probably did provide important juvenile habitat (especially during the summer), and since this habitat would be shared by all the fish in the basin it would appear to encourage co-mingling. At certain periods in its history, Elkhorn Slough was part of the estuary of the Salinas River (Gordon 1996), and this large and productive slough may have formed high-quality rearing habitat for steelhead Other, fresher sloughs and shallow lakes in the lower basin between Castroville and Salinas once existed (Gordon 1996), and they too may have comprised nursery habitat for rapid growth of juveniles during the summer.

Moreover, a century ago the water table of the Salinas Valley was probably near the surface, and perhaps ground-water exchange kept the mainstem cooler than the surrounding air. This factor may have encouraged basin-wide mixing of fish by facilitating movement. For shorthand we will call this the "juvenile corridor" hypothesis.

Another factor that might have encouraged basin-wide commingling (of adults in this case), is the highly variable pattern of rainfall for the re-

Table 12. Steelhead areas in the Salinas Basin.

Name of area	Spatial Separation*	Alluvial Valley?
Salinas Lagoon		
	65 km	Yes
Arroyo Seco		
	87 km	Yes
San Antonio River		
	8 km	Yes
Nacimiento River		
	38 km	Yes
Upper Salinas		

* Separations between confluences with the mainstem Salinas, measured as the fish swims. Estimated from topographic maps. Beginning of Upper Salinas is marked as the confluence of Paso Robles Creek with the mainstem.

gion. The hypothesis is this: Due to patchy rainfall and variable flows in the region, adult steelhead migrating up the mainstem would frequently be prevented from ascending their natal stream due to low flow, and would instead opportunistically use other tributaries of the mainstem. This process would tend to prevent distinct populations from developing in different parts of the watershed, and in consequence the Salinas would contain a single, widely-distributed population of steelhead. For shorthand we will call this the "hydrologic forcing" hypothesis.

It is possible to work through a more structured assessment of these questions about Salinas Basin population structure, using relevant data. In particular, a reasonable set of steps is to:

1) Divide the Salinas Basin into its principle sub-basins.
2) Determine which sub-basins originally harbored steelhead populations, *cf* Titus *et al.* (2003) and Franklin (1999).
3) Evaluate the juvenile-corridor hypothesis by examining transfer distances between sub-basins.
4) Evaluate the hydrologic-forcing hypothesis using USGS gauge data.

10.1.2. Original Occurrence by Sub-basin

The sub-basins with historical accounts of steelhead occurrence are depicted in Figure 36. All except the Gabilan Creek basin are on the south-west side of the Salinas Valley. Gabilan Creek itself is somewhat exceptional. It was only recently documented to have *O. mykiss* (Casagrande *et al.* 2003), and is only marginally part of the Salinas system, since it is connected via Tembladero Slough. Tembladero Slough roughly parallels the main channel of the Salinas westward from the town of Salinas, and connects to the old Salinas River Channel between the current mouth of the river and Elkhorn Slough. We consider this sufficient to regard the fish in Gabilan Creek as a discrete population.

The remaining fish can be neatly grouped geographically into four units: Arroyo Seco fish; San Antonio River fish; Nacimiento River fish; and upper Salinas Basin fish (Figure 36). This latter entity consists of 5 small tributaries of the headwaters of the Salinas and the southern end of the mainstem Salinas itself.

10.1.3. The "Juvenile-Corridor" Hypothesis

For a juvenile steelhead to have transferred between Arroyo Seco and the next steelhead unit south, it would have had to swim 87 km upstream through the low-gradient meandering channel of the mainstem Salinas (Table 12). It seems unlikely that juvenile transfers between Arroyo Seco and the units upstream were very common.

The remaining three units are closer to one another, particularly the San Antonio and Nacimiento Rivers (Table 12). The channel in this section still runs through an alluvial valley, albeit a much narrower one than lower down in the system. A history of regular juvenile transfers between the three units seems unlikely, but their proximity to one another is such that it cannot be ruled out.

10.1.4. The "Hydrologic Forcing" Hypothesis

The hydrologic forcing hypothesis is that migration choices at stream confluences are dictated by hydrologic conditions rather than the fish's homing ability and preference for its natal stream.

This would occur only when there are high flows in one branch of the confluence and extremely low flows (precluding migration) in the other. It may be possible to estimate the frequency of this situation using USGS gauge data.

Given the four steelhead units in Table 12, the final destination of a migrating fish depends upon its navigation decisions at three confluences, or "decision points," in the system (Figure 36):

Decision Pt. 1:   Arroyo Seco vs. mainstem
Decision Pt. 2:   San Antonio R. vs. mainstem
Decision Pt. 3:   Nacimiento R. vs. Upper Salinas

We made a rough assessment of the forcing at each of these decision points by examining USGS gauge data. The comparison must be made for the period prior to the construction of the three major dams on the Salinas (Salinas Dam in 1942; Nacimiento Dam in 1957, and San Antonio Dam in 1965), because these dams have altered the wintertime discharge patterns at the decision points.

Thirty-four gauges have been operated in the basin over the years[1]. Unfortunately, the Salinas Dam was built early enough that no suitable set of gauges is old enough. However, there is a suitable set of gauges for the period prior to the construction of the other two dams (Figure 36). In some cases (e.g. USGS 11150500), the gauge is considerably upstream of the decision point it is meant to address. This would tend to under-estimate the covariation at the decision point itself, so if a strong covariation is observed in the data, the true covariation at the decision point is likely to be even stronger.

Scatterplots for discharge at the three decision points are shown in Figure 37, along with a system in Oregon that can serve as a standard of comparison. The figure indicates the following. First, discharge at the three decision points routinely dips below 100 cfs, whereas flows in the branches of the Oregon system are always at least 5 times that threshold. This lends considerable credibility to the idea that low-flow constrains migration opportunities more in southern California than in the temperate rainforests of Oregon.

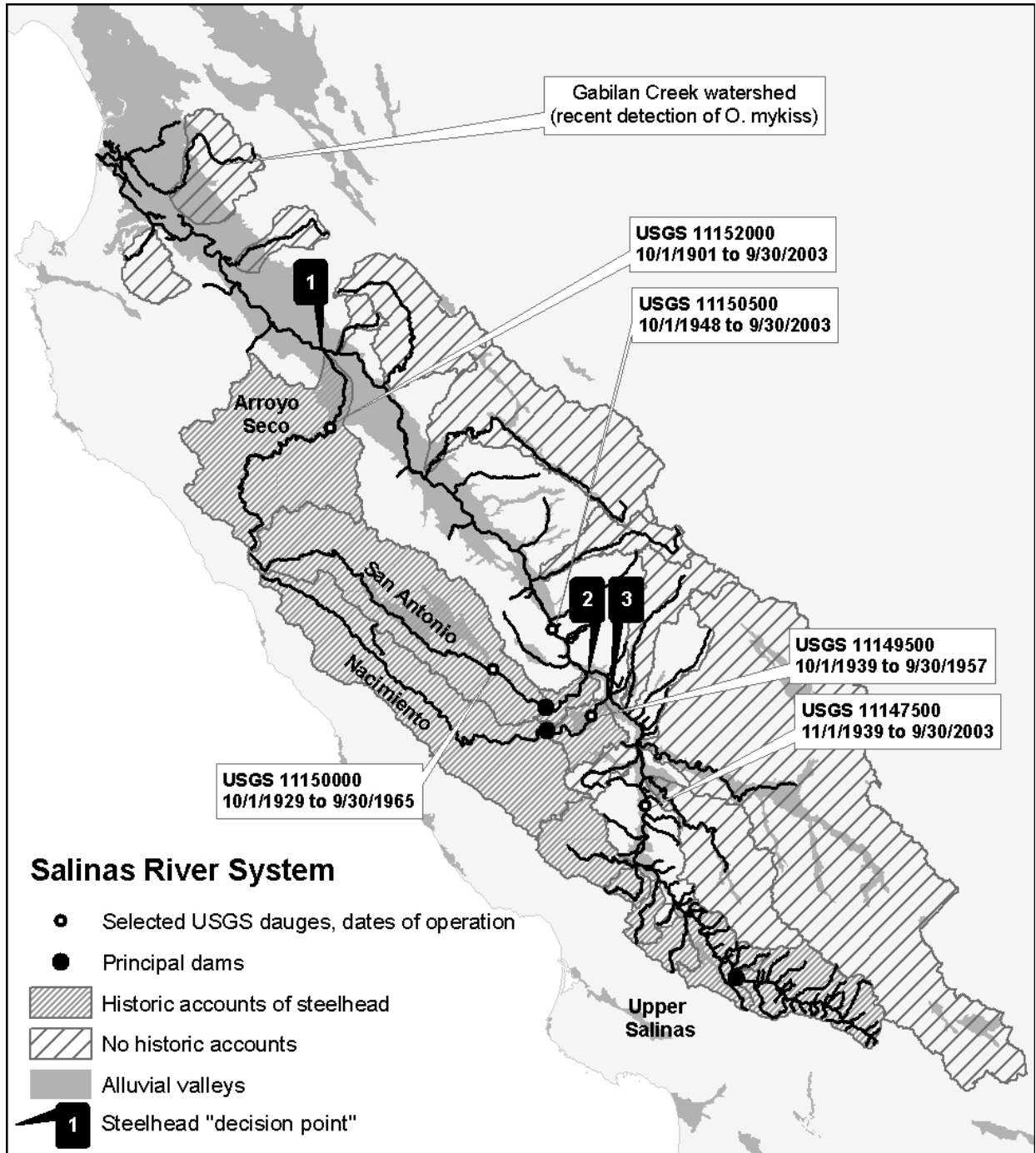[1] see http://waterdata.usgs.gov/nwis

Figure 36. Information pertaining to the population structure of steelhead within the Salinas Basin. Historical accounts can be grouped into four units: the Arroyo Seco, San Antonio, and Nacimiento Rivers, and a group of 6 small watersheds in the headwaters (labeled Upper Salinas above). Movement between these four areas is contingent on movement patterns at three key "decision points," labeled 1 – 3 on the map. Large dams on the San Antonio, Nacimiento and Upper Salinas Rivers were built in 1965, 1957 and 1942, respectively. *O. mykiss* has also been recently documented in Gabilan Creek, at the north end of the Salinas Basin (Casagrande *et al.* 2003).

A. Decision Point 1

B. Decision Point 2

C. Decision Point 3

D. Santiam River (Oregon) comparison
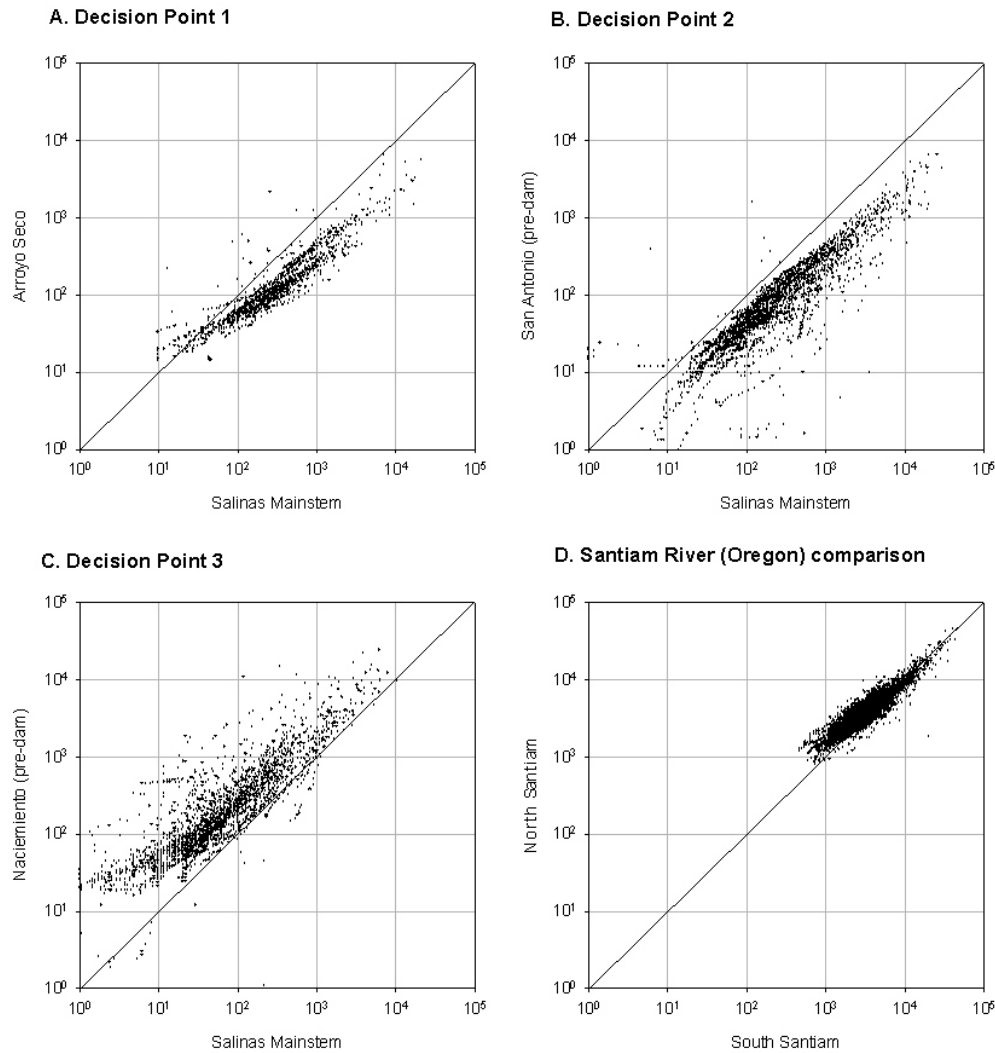
Figure 37. Comparison of daily mean discharge (cfs) at 3 key decision points in the Salinas system. All data are for the migration season (Jan – May), during the period of record prior to dam construction on the San Antonio and Nacimiento Rivers (i.e. before 1957). A: Years 1948 through 1956 (USGS gauges 11150500 vs. 11152000; n = 1210 days. B: Years 1939 through 1956 (USGS gauges 11147500 + 11149500 vs. 1115000; n = 2723 days). C: Years 1948 through 1956 (USGS gauges 11147500 vs. 11149500; n = 2723 days). D. An analogous steelhead decision point on the Santiam River in the Willamette Valley, Oregon. The North and South Santiam Rivers are considered to contain independent steelhead populations.

This leads us to a third interesting conclusion: If one considers the three decision points together, it appears that the discharge pattern of the Nacimiento tended to dominate. A hypothetical steelhead using the rule "At each decision point choose the stream with the highest flow" would tend to end up in the Nacimiento River. The flow data suggest that Nacimiento really is the mainstem of the system.

However, the data from USGS 11147500—which represents the Upper Salinas tributaries—omits the input from the Estrella River, whose confluence is just above that of the Nacimiento. It happens to drain the largest sub-basin of the Salinas, but the sub-basin is very dry—steppe in most places, barely woodland in others. There have been occasional observations of dispersing adults in this tributary, but no evidence for juveniles. Informal observations made over the past few years suggest that it rarely has above-ground discharge during the summer.

To address the hydrologic-forcing hypothesis more explicitly, assume that migration is restricted when a stream drops below 30 cfs[2]. How common is the case where one stream is below 30 cfs and the other above it? Figure 38 illustrates the frequencies of such events for each decision point. Asymmetric flows are rare for decision point 1, but not for decision points 2 or 3. (percentages are 3%, 19% and 28%, respectively).

The asymmetric flows are themselves asymmetric: At decision point 2 all the asymmetries favor the mainstem Salinas over the San Antonio River, and at decision point 3 they nearly all favor the Nacimiento River over the upper Salinas.

It is possible that the asymmetry at decision point 3 is an artifact of Salinas Dam. USGS gauges above and below the dam show that during these years, dam operations did tend to reduce flows during dry weeks in the winter (data not shown). The effect would have been muted, however, by the fact that the watershed above Salinas Dam is only 29% of the total watershed contributing to USGS gauge 1114750, and appears to be in a fairly dry area.

Taking the figures at face value suggests that about one fifth of migrating adults may have been forced up the Salinas at decision point 2, and about a fourth of these would have been forced up the Nacimiento at decision point 3. Perhaps more if these asymmetries followed periods when both routes had low discharge and fish were "stacked up" in the migration corridor; or if the 30-cfs threshold is too low. Perhaps less if migration tends to be associated with higher flow (as it is in the Carmel River; see Boydstun *et al.* 2005) or if adults wait at the decision point until flow in the preferred stream increases. Even so, a "forcing rate" half as large (*c.* 10%) would probably still be large enough to demographically link the three subpopulations upstream of decision point 2. Arroyo Seco fish, on the other hand, seem able to maintain a high rate of fidelity.

Some important cautions temper this statement. The threshold of 30 cfs is expert opinion; if the true threshold were closer to 100 cfs, the forc-
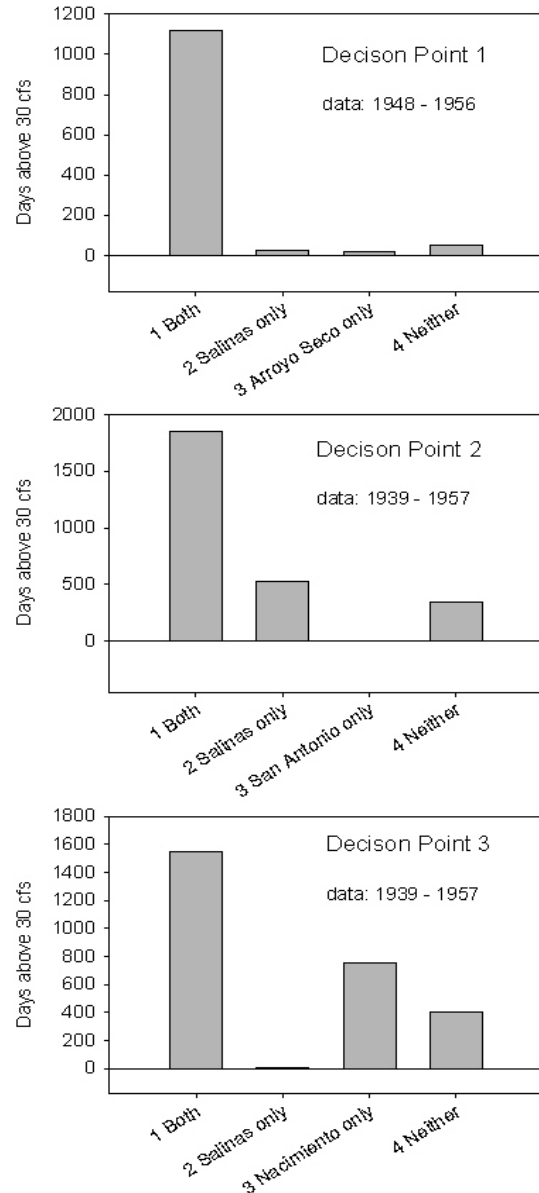
Figure 38. Number of days that each branch at a steelhead decision point had mean daily discharge greater than 30 cfs. Only data for the Jan. – May migratory season are depicted.

ing rate at decision point 1 would increase markedly, and would strongly favor the mainstem Salinas (This can be determined by inspection of Figure 37A). On the other hand, decreasing it to 10 cfs would eliminate any forcing altogether.

Another caveat concerns the gauge data itself. Discharge at one point in a stream may not match discharge just up or downstream due to groundwater flux (*e.g.*, see Figure 3 on page 10). More-

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[2] A conservative guess. Larger flows are probably necessary to avoid restricting migration.

Table 13. Weight of evidence for a separate population in Arroyo Seco

Separate population in Arroyo Seco	A single population in the Salinas system
1. Juvenile transfers unlikely	1. Within-basin dispersal may be highest at the first decision point in a system.
2. Hydrologic-forcing unlikely	
3. Maintains a margin of safety with respect to a mistake	

over, local channel morphology no doubt interacts with discharge to determine migration access for steelhead, meaning that the adoption of a single threshold flow value is quite simplistic.

10.1.5. Other Considerations

A certain fraction of returning adults would be expected to spawn in a different tributary than the one in which they originated. The argument is sometimes made that such within-basin dispersal events are biased toward the lowest major tributary in the watershed. For example, some simple algebra shows that if a fixed probability describes the probablility of choosing the non-natal branch at each successive decision point, then the largest fraction of dispersers will end up at the lowest tributary in the system.

For example, in a study of microsatellite DNA from steelhead in the Pajaro system, Sundermeyer (1999) suggested hatchery fish stocked in Uvas Creek or the lower part of the watershed tended to swamp the lowermost tributaries genetically. Dispersal to the uppermost tributaries (Pacheco and Dox Picachos) was apparently much less. In addition, Tar Creek, a tributary to lower Uvas/Carnadero Creek, has relatively large runs in some years even though it drains a tiny, dry watershed—but it is the first decision point in the Uvas Creek system. Of course, this example involves hatchery fish, which may disperse at greater rates than wild fish.

Since Arroyo Seco is the lowest steelhead stream on the mainstem Salinas, the above argu-

ment suggests that it would receive the greatest fraction of immigrants, and should therefore not be considered a distinct population.

There is another aspect of judging whether the Arroyo Seco fish constitute a separate population: What are the consequences of making a mistake? In terms of recovery, the more risky mistake would be to erroneously lump the populations. In such an event, viability criteria mistakenly applied to the lumped pair would not necessarily be sufficient to protect either one of the pair. For example, suppose that to be viable a population must on average have a run of 1000 fish, and each of the pair has on average a run of 600 fish[3].

The opposite mistake—splitting into two when in reality there is just one population—maintains a margin of safety if both units are recovered to the point that they meet viability criteria. However, if only one unit is "recovered" to meet the viability criteria, it might not actually be viable, due to poor conditions in the other unit. Another risk is that each single unit may not have sufficient conditions to form a viable population on its own. For example, its carrying capacity may be too small, and the recovery effort would fail on its own terms. Still, the bigger risk with respect to recovery appears to be erroneous lumping.

10.1.6. Three Populations Perhaps

The evidence is insufficient to make a strong statement about the number of populations in the Salinas basin. However, the weight of evidence suggests that the southern Salinas basin originally supported a discrete steelhead population, based primarily in the Nacimiento River but also occurring in the San Antonio and Upper Salinas units; and that the northern basin had a second discrete population in Arroyo Seco (Table 13). As noted early, there also appears to be a discrete population in Gabilan Creek, indicating a likely total of three populations in the Salinas River system.

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[3] These numbers are made up for illustration.

10.2. The Historic Condition of Mainstem Habitat

The historic extent and abundance of steelhead populations is more uncertain in the south part of the study area, as is the original condition of stream habitats. It is possible that more information could be gleaned from the period of about 1769 [the first Spanish Land expedition] to about 1880, when the first railroads reached the Los Angeles Basin and hatchery fish began to be transported in by rail. For some areas, such as Lompoc, hatchery fish did not come until later because the railroad between Santa Maria and Santa Barbara was not completed until shortly after 1900. The Santa Monica Mountains had only a wagon road from Santa Monica to Ventura until 1910 or so and unlikely were planted with anything other than local fish before this. Other outlying areas may have been delayed as well. We are not aware of any records of people moving local fish around before the big push to bring hatchery fish began [after about 1880] but perhaps not much would have been affected by such local stock movement if southern steelhead are genetically homogenous. One of the authors (C. Swift) has been able to find some scant data here and there, often not very quantatitive, that gives some indication of the extent of fish, and thus indirectly, numbers (see §10.3).

Much more certain is the general condition of the habitat before European contact because this was better recorded and has been exhaustively researched by workers studying plant communities, grizzly bears, condors, marine mammals, *etc*. Of course fresh water was critically important, so almost immediately after settlement drastic changes were made to water courses. At first it was just diversions, until the late 1860s when there was a post-Civil War population influx. At that time, ground water withdrawal began to lower the water tables for the expanding fruit and citrus agribusiness. At first this produce mostly went to San Francisco by ship, but soon the railroad enabled export to the eastern United States. Very likely, records, diaries, *etc* of the early settlers from this period, including the various water agencies

and their workers, may have more information specifically about fishes.

10.2.1. The Monte

The agricultural effort provided great incentive to clear the "monte" in many areas. The monte was the cottonwood and willow forests that covered the lower reaches of the large rivers. You have to imagine the Salinas Valley with a more or less continuous willow-cottonwood-sycamore forest a few to several miles wide down to within a few miles of the ocean, and also consider this in all or most of its drainages. For the Salinas Valley, the early dramatic change in the monte is well documented by Gordon (1996) and this history certainly applies to all coastal drainages to a greater or lesser degree.

In Vandenberg, one of us (C. Swift) looked at several years of the Lompoc Record [newspaper] for accounts of the steelhead runs. Virtually every issue has several advertisements for laborers to "clear the monte", namely grub out this forest to prepare the land for farming. Massive machinery was also developed to remove the brush [such as coastal sage scrub] from the upland terraces near the river for wheat farming. When you drive down the Santa Ynez River valley from Lompoc to the sea you have to imagine all that flat land [now with flowers and broccoli] covered with a mature willow/cottonwood forest, with the river out in the middle somewhere protected by grizzly bears.

This agriculture also was coming after considerable degradation from cattle and sheep during the late 1700's to the mid-1800s. The trees were also removed for fuel and many historical accounts of southern California note the lack of coal and other fuel sources compared to the better-forested areas farther north. Many complete water diversions in the mountains surrounding the Los Angeles Basin from about 1890 onward were for electrical generating stations. This power accelerated the ability to pump and extract ground water. The lowered ground water went below the reach of tree roots, effectively killing many of them. Finally in the 1930s and 40s many of the remaining

trees were removed to provide uninterrupted flow during high runoff periods to prevent flood damage.

10.2.2. Down-cutting

Another geological or hydrological phenomenon that occurred in the late 1800s and earliest 1900s was arroyo formation or down-cutting of many drainages. This is evident almost every where in the lowlands today where streams are flowing in deeply entrenched soil canyons cut into the surrounding floodplain. There are various attributions or explanations of this, mostly as a culmination of the altered grazing and land practices that descended on the west with European contact. It has also been argued that it is due to a long term climatic effect and anthropogenic effects are only a minor contributor to this result.

One of the most striking contrasts between downcutting and its absence is at San Antonio Creek, on and upstream of Vandenberg Air Force Base. The lower 8 or 9 kilometers on the Base still have dense willow forest across the whole floodplain and the stream flows at the surface of the floodplain as it meanders through the forest. Upstream of Lompoc-Casmalia Road on the Base and for the rest of the lowland portions of the drainage upstream of the Base, the floodplain is plowed and planted right to the edge of the five to ten meter entrenchment of the stream below the flood plain. The entrenchment of Salsipuedes and El Jaro creeks, tributary to the Santa Ynez River, occurred during the high winter flows of 1861-62 (Poett 1991, calling the trench a *barranca*), and possibly in the San Antonio Creek at the same time.

The explanation for the widespread occurrence of down-cutting in the west is that as the area was progressively grazed and relatively more deforested in the riparian corridor, the streams became vulnerable. Eventually the next exceptional high flow event could entrench the stream and recovery would not occur unless land use or management changed dramatically. Western streams are still strongly entrenched in many areas.

Thus by 1900 when the first real USGS maps were being surveyed and drafted, many

"blueline" streams were already intermittent or "desertified" to dry washes. For example, the first colonists to establish the city of San Bernardino in the 1850's reported that they could not farm north of present day Baseline Road because it was too swampy. This area is all dry washes today and was mapped as such in the earliest 1900s because it was already that way by then. Even by 1900, Ballona Creek draining the western Los Angeles Basin through what is now Beverly Hills and west Los Angeles is shown as a blue line stream and springs were common in the Rancho La Brea area.

10.2.3. Formerly Perennial Flow

Many rivers never went dry in the lowlands. Friis (1983) quotes an edition of *Daily Alta California* from 1858 saying Anaheim is located where the [Santa Ana] river never goes dry. Baumgartner (1996) quotes his ancestors that the Santa Margarita River never went dry from about the mid-1800s to about 1900 at the ranch house, about 9 miles up from the ocean in the present day Marine Corps Base Camp Pendleton and the Base Commanders residence. He had historical accounts (early to mid-1800s) of discussions with the previous Spanish and Mexican caretakers from the Mission San Luis Rey. Many of the accounts of the drying of local streams in southern California date from the late 1880s onward when the cumulative effects of much change was already being felt. Keeley (2002b) has argued that wildfires lit by Native Americans may have kept many watersheds in grassland rather than chaparral or sage-scrub, with the effect that streams now intermittent would have been perennial due to the increased water yield of grassland watersheds.

In the Los Angeles basin, records of a cold-water associated fauna indicate there was once a better watered and cooler aquatic system than is currently appreciated. The cool water fauna was apparently less vulnerable to the major interruptions of the main streams, and survived into the early 1900s. As a result it was better documented and was clearly widespread. The fauna included redlegged frogs, unarmored threespine stickleback, freshwater non-parasitic lamprey (cf *Lampetra pacifica*), and the freshwater shrimp *Syncaris*

pasadenae. This species combination occurs in one other place, namely around the tributaries of northern San Francisco Bay. In the Los Angeles Basin the redlegged frog, lamprey, and shrimp have been extirpated since the early 1950s. Carl Hubbs, an eminent ichthyologist at Scripps Institute of Oceanography at La Jolla, remembered the lampreys being fairly common in the Los Angeles Basin in the earliest 1900s, and genuinely regretted not having kept more specimens for the record, since the existence of two species (the non-parasitic one in addition to the migratory Pacific lamprey) was not appreciated at that early time. For more information see Miller (1961), McGlashan (1930), and Mendenhall (1908)

10.2.4. Probable Historic Baseline Conditions

For the reasons summarized above, historical and scientific estimates of steelhead habitat based on the first USGS maps of the 1894-1904 period for blueline streams will probably seriously underestimate the amount and quality of habitat present at European contact. If the extent of habitat originally available is based on blueline stream present below impassable barriers, then numbers based on these first detailed topographic maps would seem to be a minimum to expect and easily a serious underestimate of the extent of steelhead habitat.

The clearing of the monte and downcutting of streams also suggests that much of the original steelhead habitat was lower in the streams and the remaining populations are confined to upstream extremities today. Today, these downstream areas may be too warm and contain elevated levels of fine sediments, but were probably not like this originally. One can use the EPA's Handbook for Assessment of Physical Stream Habitat to calculate the particle size expected in the lower Santa Margarita, Santa Clara, or San Luis Rey Rivers (P. Kaufman, pers. comm.). These streams are now very sandy in their lower reaches, but the calculations apparently indicate that the theoretical "expected" particle size is a few orders of magnitude larger than what we find there today (A. C. Rehn, pers. comm.). This suggests the lower mainstems may originally have had gravel or cobble substrates, more conducive to steelhead spawning and rearing.

Widespread springs, artesian upwellings at the coast and elsewhere indicate that more water was available prior to settlement of coastal southern California. A "San Francisco Bay fauna" of freshwater shrimp, two lampreys, stickleback, a mountain sucker, and speckled dace were all present as well. The springs were probably not continuous along the coast, but there were probably many pockets of habitat that would have supported trout/steelhead. Probably the only genuine hiatus in the distribution of *O. mykiss* was in San Diego county where fish were present in the Santa Margarita and San Luis Rey Rivers, then absent until the Tijuana and/or San Diego River as early noted by Cooper (see Swift *et al.* 1993). Several ichthyologists spent much time in San Diego in the late 1800s and did not record or hear reports of them otherwise. However, there are remains of *O. mykiss* at Native American archaeological sites near Los Peñasquitos Creek (northern San Diego County) (Gobalet *et al.* 2004).

10.3. Historic Accounts of *O. mykiss* in the SOLA Section of the Study Area

This summary was prepared from sources compiled by C. Swift and is not exhaustive; many potential sources of information have not yet been examined.

10.3.1. Santa Ana River

1. Black (1975) referred to the diary of Benjamin Hayes relating a trip from L. A. to Mill Creek on October 6, 1856 when they stopped in the Cucamonga area to catch trout. [This could have been either the San Gabriel or Santa Ana drainages]

2. Black (1975, p. 130) also notes the papers of Nellie Metsinger [Motsinger?], indicating they caught trout in San Antonio Creek near the house in 1874. This house was up in San Antonio Canyon, Santa Ana River drainage. On page 131 she notes E. O. Crosby's memoirs in the Huntington Library to the effect that there were fish to catch in sloughs on Rancho Cucamonga, 1862-1874.

3. Lyman (1996, p. 264) says boys were noted by government surveyors (Railroad Survey party) to be fishing in the lower portion of Lytle Creek in 1853 [this area seldom has water today].

4. Lyman (1996) also notes that the next year (1854) Rich [last name] was convalescing by spending several weeks camped in the mountains [of the Santa Ana River drainage] in pursuit of trout. Lyman, who accompanied Rich on the last of these expeditions caught only sufficient fish for the morning and evening meals, though Addison Pratt was usually more successful, as were Ed Daley and some others.

5. Lyman (1996, p. 261) notes that in May 1857 about 200 persons went to the mouth of City Creek near San Bernardino, and the day before, Addison Pratt caught "...sufficient to furnish much of the party with fresh trout". This indicates a catch of at least tens of fish and possibly as many as 200 or more. City Creek still holds introduced trout, yellowlegged frogs, and speckled dace, all common associates with trout locally today.

6. La Fuze (1971, p. 103) notes that in 1869 a party went to the head of Santa Ana Canyon to get a wagon load of fish and eight deer. On page 112, "[in 1871] fishermen went to the Santa Ana River to open the season, one pair [of persons] got 60 [trout] in two hours and another pair got 90 in one day…"

7. La Fuze, Part II (1971) notes in 1870 one party went up the West Fork of the Santa Ana River, above Knights Shingle Machine and caught 140 trout, some to 4 pounds. On page 113 she notes (1871) a group of sportsmen camped on the South Fork again, caught 60 fish per hour, and caught 350 in three days, "mornings and evenings". Going down Devil Gulch and Hells delight to Bear Creek, fishermen caught 225 fish in 2 hours, [on one occasion] killing 12 trout with one shot. On page 121 she notes that in 1873 George Miller and companion caught 300 trout in one day in the Santa Ana River Gorge [this is the gorge in the San Bernardino Mtns, not the one downstream below Prado Dam]. On page 144 (for 1877) she records that the Cable Boys, who had bought a portion of the Muscpiabe Rancho, had stocked with trout a clear, cold stream stair-stepping down through it. Peirson (1970) identifies this ranch as at the head of Cajon Pass and the Mohave Trail [almost certainly too high and steep for native trout]. On page 154 (for 1879) she notes "Early in the year Tom Baca brought "perch" from Mexico to springs around Waterman's Resort. Dr. Smith had carp in his boating pond. Noting Cable's stocking (Walnut Creek) had become good fishing, Ed Daley published a proposal in the paper that all feeder streams of the Mojave watershed (Deep Creek, Husston Creek, Grass Valley Creek, Little Bear Creek) be stocked with trout from the Santa Ana River. He even offered to subscribe money and time." [This clearly indicates many streams in the Santa Ana drainage had trout originally, that Mohave River drainage streams did not have them, and that local fish where the only ones moved around to about 1880]

8. In 1883 Big Bear Lake was established. Hatcheries were developed on its tributaries and considerable stocking began in the mid 1880s and thereafter. Shebley (1927) claimed to have participated in the first introductions of fish into the Big Bear area in 1891 and 1892, but these were early efforts by CDFG that apparently came after the local efforts just noted.

9. Maynard (1965) quotes (p. 73) a Belle J. Bidwell in seeing San Antonio Creek "abounded with small trout in 1887 when camping about 5 miles up from mouth" [presumably about 5 miles upstream of it opening out onto the Los Angeles Plain just north of Upland]. Possibly these were introduced at this later date but probably not.

10. Willis A. Evans (then DFG biologist) Notes for 6 November 1946 [in Long Beach Office files of CDFG, now in Los Alamitos] recorded that Warden Gyger [Gryger?] caught fish ["rainbow trout"] in the south Fork of San Jacinto River before 1893 when the dam for Lake Hemet was installed and before any stocking had taken place. The San Jacinto River drains into Lake Elsinore and during high flow years over tops its sill downtream through Temescal Creek to the Santa Ana River in the Prado Dam area.

10.3.2. San Gabriel River

1. Rose (1959) related the experience that his ancestor, L. J. Rose, heard of "fair trout fishing in Santa Anita Canyon by schoolboys" in the 1870s or earlier. This canyon is now dammed, and had an impassable barrier about a mile upstream of present day Arcadia. It drains into the San Gabriel River and would later be the Baldwin Ranch and now partly the Wilderness Park [of Los Angeles County].

2. Pfueger (1964, p. 13) notes that food supplies were always constant problems in the 1860s and 70s and that the San Gabriel River and even San Jose Creek provided fish. He does not specify species but this usually meant trout (see below) and other post-1900 accounts mention trout in the San Gabriel River near the mouth of San Jose Creek, just north of the present day Whittier. Pflueger also mentions (p. 200-201) an attempt in October, 1888 to introduce "Tahoe trout" into the San Gabriel River. DFG even had a hatchery in the Whittier area that took steelhead from the river up through the 1930s and 1940s.

3. Jackson (1977) notes that from the mill pond of Henry Dalton on the San Gabriel River [near or above present-day Azusa] from the 1840s to 1870s was well stocked with trout. He means well supplied rather than stocked from elsewhere, very unlikely, as well as unnecessary, at these early dates.

10.3.3. Los Angeles River

We have less information on the Los Angeles River, but Crocker (1990) relates that "A number of persons remember good trout fishing in the Arroyo [Seco] up until the time of the construction of Devil's Gate Dam in the 1920s." Charlie Sommerville recalls that he could easily catch 25-30 seven to eight inch rainbow trout within a couple of hours in pools under the Colorado Street Bridge and elsewhere in the Arroyo. Several times a week he would take such catches early in the morning to be prepared for breakfast at the Annandale Golf Club. These early fish were better than the hatchery fish served at the Club in later years. This is on the western side of the city of Pasadena today.

10.3.4. Context

The historic record summarized in part above gives the impression of a typical scenario, namely initial discovery of abundant trout, rapid decimation of local stocks within a few decades, and then efforts to restore or stock more fish to take their place. This stocking often came from the northern California hatchery fish that could come in by railroad by the 1880s or by transfer of rescued fish from the lower parts of larger streams.

An important distortion in the historic record has to do with the demise of the pre-Columbian human population. Many European settlers noted the super abundance of terrestrial (bear, deer, etc) and marine intertidal (abalone, marine mammals) organisms. However, European diseases and other aspects of early contact severely decimated the native human population, and probably released

considerable predation pressure on the local fauna utilized for food. Prior to European contact, the California coast had human population densities among the highest in North America and many times higher than in other parts of the west (Keeley 2002b). Their decimation occurred in the 100 years or so from the mid-1700s to the mid-1800s. By the mid-1800s many of the organisms they hunted were much more abundant than they would have been under "full" pre-European or Native American population levels.

Thus, numbers of fish based on catches, *etc*. during this time period reflect a relatively high peak over the last few hundred years or so. This has been fairly well documented for grizzly bears, namely that abundant livestock and offal from early whaling and other marine mammal hunting activities led to in increase in these bears in this time period. The same is postulated for intertidal abalone and pismo clams. They were actively fished by the pre-European inhabitants and would have been scarce. But abalone, pismo clams, etc

became very abundant in early 1800s after the sea otters and Native Americans were decimated. Only in the mid to late 1800s did the Chinese fishermen began to decimate these molluscs again. Unfortunately, we do not know of any comparable information on steelhead.

What we do know is that in the early 1970s, our own observations indicate large numbers of naturally-produced *O. mykiss* were present in both the San Gabriel River and upper Arroyo Seco (L. A. River drainage). One of us (C. Swift) often caught and released 50-60 small fish up to six inches long in three to five hours fishing. These densities were confirmed by seining and snorkeling. Observations made along the San Gabriel in the 1980s also showed that hundreds of trout were present in 100 m of stream. Very likely, both the Arroyo Seco (Los Angeles Basin) and the upper San Gabriel populations have been continuously present for 150 years or so, although without any access to the ocean for the last 60 years or so.

10.4. A Note on Sources of Information

"In practical reasoning, a person may have to take anecdotal evidence into account in order to arrive at a prudent decision on how to proceed in a changeable situation where scientific knowledge, based on expert opinion, may be insufficient (by itself) to solve the problem"—Walton (1997: 165).

Standard scientific discourse involves numerous appeals to authority, in the form of citations to the peer-reviewed literature. One would expect that this scientific literature contains much that is relevent to our purposes here, determining the population structure of steelhead ESUs. However, it also seems likely that much relevent and credible information and analysis is omitted from the peer-reviewed literature but can be found in technical reports, individual accounts, and so forth. When we reference such information in this report, implicitly we are making what philosophers term "an argument from authority."

Arguments from authority, routinely made in modern life to justify certain conclusions or courses of action, are nevertheless vulnerable to error. In strict logical terms an argument from authority is a fallacy—an expert claiming A to be true does not imply, in and of itself, that A is true. But complete dismissal of the argument of authority would render intractable the modern way of doing things, in which everyone relies on specialists to advise them. Thus it is useful to briefly review the conditions for a legitimate (non-fallacious) argument from authority.

Walton (1997) has addressed this topic at length. Specifically, Walton (1997: 223) recommended that to establish validity, an expert (**E**) that is giving an answer (**A**) should be tested against six critical questions:

1) Expertise: How credible is **E** as an expert source?
2) Field: Is **E** an expert in the field that **A** is in?
3) Opinion: What did **E** assert that implies **A**?
4) Trustworthiness: Is **E** personally reliable as a source?
5) Consistency: Is **A** consistent with what other experts assert?

6) Backup evidence: Is **E**'s assertion based on evidence?

An argument from authority may be correct even if these critical questions are not explicitly answered, but they must in principle be open to scrutiny via further study, cross-examination, *etc.* For example, a source must be cited by name so as to provide means for testing the critical questions should they be of concern. In a major section of his book, Walton (1997) discussed tactics by which an authority might phrase an opinion or structure a debate so as to deny the legitimacy or tractability of the above six critical questions. This constitutes a fallacious argument from authority, since it implies that the expert's status as an expert is, itself, sufficient to establish the truth of his claims.

In our compilation of this report, we read numerous reports and correspondence, and had many conversations with individuals having direct experience with, and interest in, the steelhead of southern and south-central California. We regarded such individuals as potential experts. Some information was as simple as "I saw steelhead in location X during year Y," whereas other claims were more ambitious, such as "this creek has highly productive steelhead habitat" or "the runs in stream Q were at least Z fish in most years." We tended to be skeptical of quantitative claims such as the latter, unless an underlying statistical approach was specified; but in general we found little reason to be skeptical of presence/absence reports of the first type. In general, when citing information from outside the peer-review literature, we adopted the following standards:

1) Provide citations.
2) Only use observations that sufficiently describe their context and evidence for trustworthiness.
3) Omit interpretations of observations unless the source demonstrates expertise in the relevant field.
4) In stronger, but still questionable, cases, discuss the issues in the main text.

10.5. Gauge Data for Inland/Coastal Comparison

Data used for Figure 25 on page 52:

Stream Name	USGS Gauge ID	Standardized summer discharge	CV (%)	Years of data	Drainage Area (sq. mi.)
South-Central California Coast					
Inland					
Cedar Creek	11152900	0.043	140	21	12.8
Arroyo Seco	11151870	19.195	88	25	113
San Antonio River nr. Lockwood	11149900[1]	4.189	156	45	217
Nacimiento River nr. Bryson	11148900[2]	3.415	125	48	162
Santa Rita Creek	11147070	0.206	160	33	18.2
Salsipuedes Creek nr. Pozo	11144200	0.016	106	14	5.91
Toro Creek nr. Pozo	11144000	0.285	115	21	9.56
Salinas River nr. Pozo	11143500	1.176	76	15	70.3
Uvas Creek above reservoir	11153900	1.694	82	22	21
Coastal					
Big Sur River	11143000	23.460	56	54	46.5
Lopez Creek above reservoir	11141280	3.619	83	37	20.9
Morro Creek	11142080	1.058	123	8	24
Toro Creek nr. Morro Bay	11142100	0.949	100	8	14
Arroyo de la Cruz	11142500	0.917	113	29	41.2
Corralitos Creek	11159150	0.653	119	15	10.6
Santa Rosa Creek	11142200	0.631	126	16	12.5
Southern California (NOLA)					
Inland					
Coyote Creek nr. Oakview	11117600	0.754	106	30	13.2
Miguelito Creek near Lompoc	11134800	0.575	128	31	11.6
Sespe Creek out of Wheeler Springs	11111500	1.429	133	51	49.5
Santa Paula Creek	11113500	5.135	109	76	40
Matilija Creek above reservior	11114500	4.950	108	22	50.7
North Fork Matilija Creek	11116000	2.251	106	54	15.6
Santa Ana Creek nr. Oakview	11117800	0.291	161	30	9.11
Santa Cruz Creek nr. Santa Ynez	11124500	2.434	196	62	74
Cachuma Creek nr. Santa Ynez	11125000	0.197	181	12	23.8
Salsipuedes Creek nr. Lompoc	11132500	1.418	129	63	47.1
Sisquoc River nr. Sisquoc	11138500	5.525	182	60	281
Alisal Creek nr. Solvang	11128400	0.129	199	17	11.6
Coastal					
Carpinteria Creek	11119500	0.220	310	62	13.1

[1] Also gauge 11149700
[2] Also gauge 11148800

Jalama Creek nr. Lompoc	11120600	0.255	123	17	20.5
Gaviota Creek	11120550	0.856	106	20	18.8
Tecolotito Creek	11120530	0.209	65	9	4.42
San Jose Creek	11120500	0.224	164	62	5.51
Atascadero Creek nr. Goleta	11120000	0.173	247	62	18.9
Arroyo Burro nr. Santa Barbara	11119780	0.103	237	23	6.65
Mission Creek at Santa Barbara	11119745	0.342	179	9	6.6
Sycamore Creek at Santa Barbara	11119700	0.150	88	3	3.41

Note: Standardized summer discharge is the mean discharge for the months June through September, divided by the drainage area. Units: $ft^3/s \cdot mi^2$.

10.6. Limiting Habitats and Population Size

The population-ranking scheme described in §5.3 relies on the assumption that over-summering habitat is the key limiting factor determining steelhead population sizes. This is untested, and alternative scenarios are plausible. We are indebted to Dr. Scott Cooper (UCSB), whose comments are the basis for the following discussion.

Besides over-summering habitat, other habitats that may pose bottlenecks to distribution or abundance include 1) oceanographic conditions which affect *O. mykiss* survival in the ocean; 2) natural barriers to spawning migrations up streams; 3) geological conditions which affect stream flow and abundance of spawning substrata.

10.6.1. Ocean Conditions

For most anadromous fish species, oceanographic conditions (*e.g.*, temperature, current patterns, upwelling, *etc*.) can have large effects on survival, growth, and development. In the case of anadromous salmonids, oceanographic conditions can have repercussions for spawning run sizes and reproductive potential. These considerations may be particularly important for southern California because stock sizes are low, and cyclic (El Nino - La Nina) or long-term (global warming) oceanographic changes may have a large impact on adult salmonid stock sizes.

10.6.2. Spawning migrations.

Key limiting factors include river or stream flow, barrier spits across estuarine mouths, and natural or manmade barriers to migration. Because of river discharge and the presence of sand barriers at river mouths, discharge can change dramatically year-to-year, and this is probably a component of year-to-year fluctuations in run size.

A key but unresolved issue is whether spawning steelhead that cannot obtain access to their natal streams simply absorb their eggs and return in subsequent years, or else migrate up nearby streams that do provide access. Both have been argued, but few data exist.

Unlike other Pacific Coast salmonids, steelhead can survive spawning and return to the ocean,

occasionally multiple times. Because of this flexibility, strong adult cohorts can persist in the ocean and repeatedly attempt to enter, or actually spawn, in coastal streams over a number of years, thereby maintaining particular populations (i.e., a storage effect). Thus the ranking scheme should distinguish between rivers with reliable and unreliable migration opportunities. The existing ranking scheme does so using a system of Category 1 and 2 rivers, but a better measure would use an empirically-derived, continuous measure of reliability that does not enforce a two-category structure onto a complex stochastic phenomenon.

10.6.3. Spawning habitat.

The amount of spawning habitat—in terms of suitable flow regimes and substrate particle sizes—can have large impacts on spawning behavior and young-of-the-year (YOY) production. Suitable spawning conditions are often quite local and dependent on fine-scale geological or geomorphic controls (Dvorsky 2000). The amount of surface flow in given stream reaches often depends on the underlying lithology and stream bed substrata, whereas the amount and sorting of different substrate particle sizes will depend on both flow conditions and the delivery of sediments to the stream (Montgomery and Buffington 1997; see also §4.7).

Most salmonids spawn successfully in well-aerated gravel of defined sizes. Salmonids cannot manipulate large substrata in constructing redds, whereas fine sediments often inhibit interstitial water flow and lower oxygen levels. The availability of suitable spawning substrata has been considered a key control on spawning and YOY recruitment (Dvorsky 2000, Suttle *et al*. 2004, Collins and Dunne 1989). Observations in Rattlesnake and Cold Spring Creeks near Santa Barbara suggest that newly emergent steelhead or trout fry are only found in riffles with pea gravel and adjacent pools (S. Cooper, personal communication). Because pea gravel had very limited distribution in those creeks, it may have been the ultimate limit on population size.
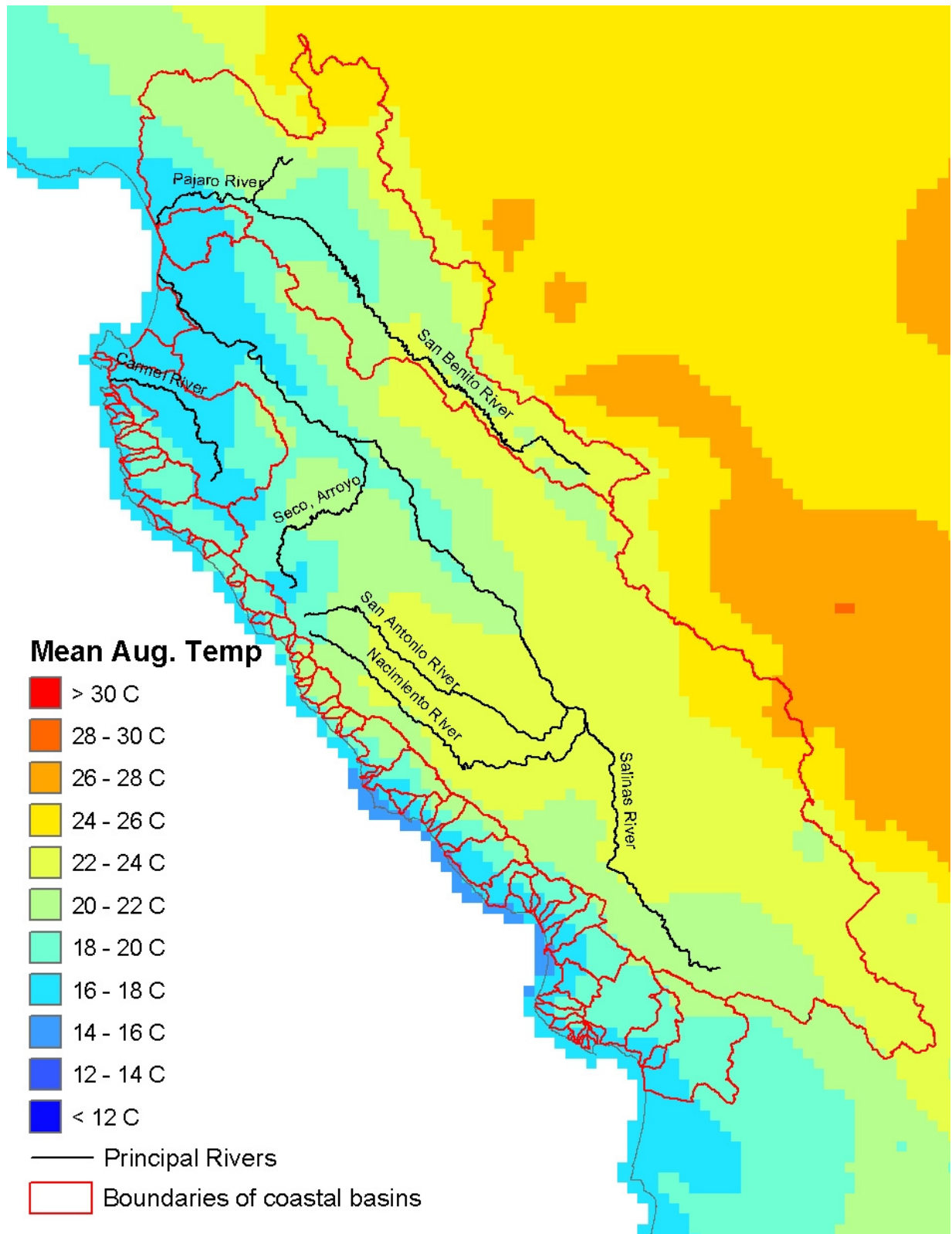
108

Part 11. Color Plates

Plate I. Mean August temperature in the south-central California coast study area, for the period 1961 – 1990. Data *cf*. Daly *et al*. (1994).
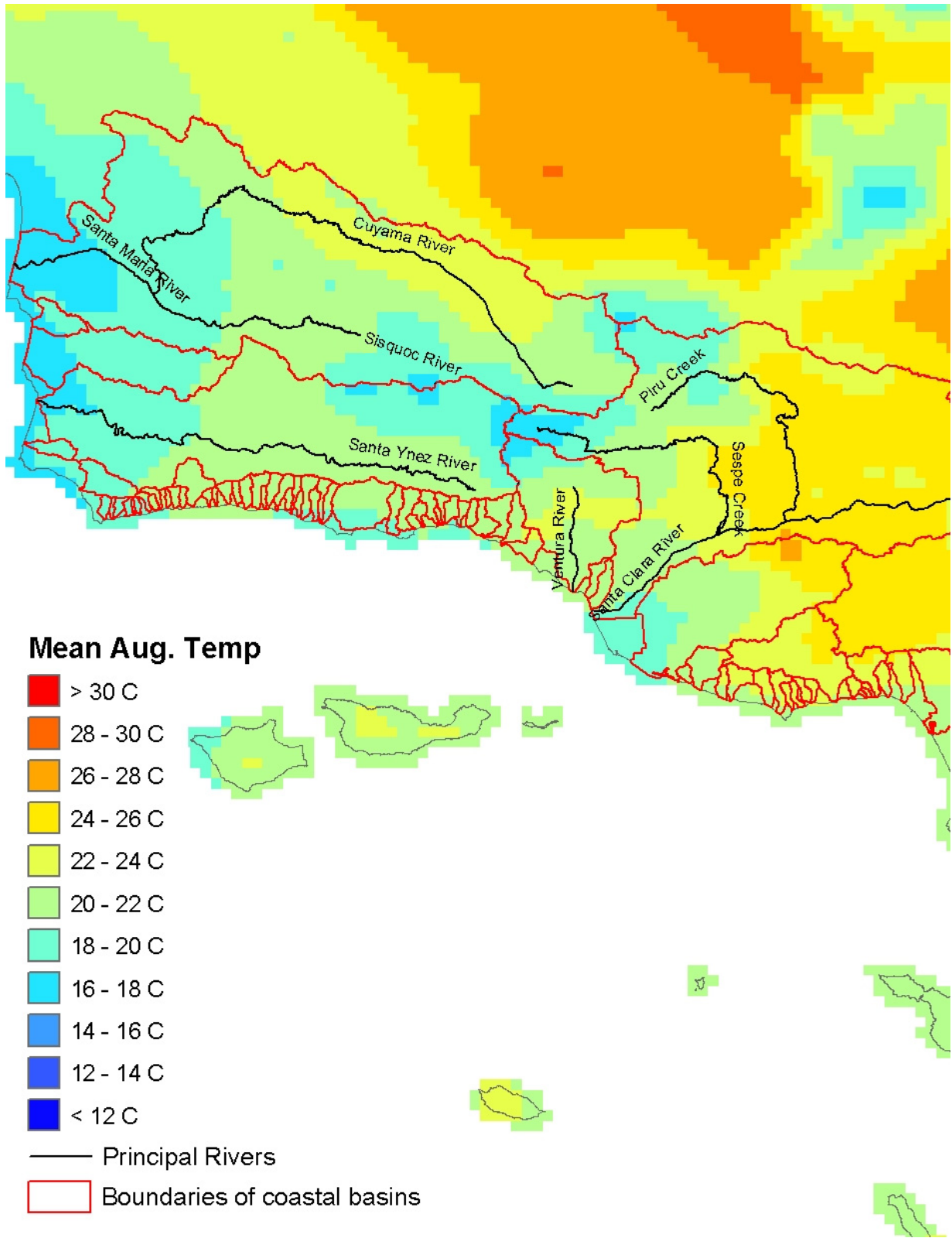
Plate II. Mean August temperature for the NOLA section of the southern California study area, for the period 1961 – 1990. Data *cf*. Daly *et al*. (1994).
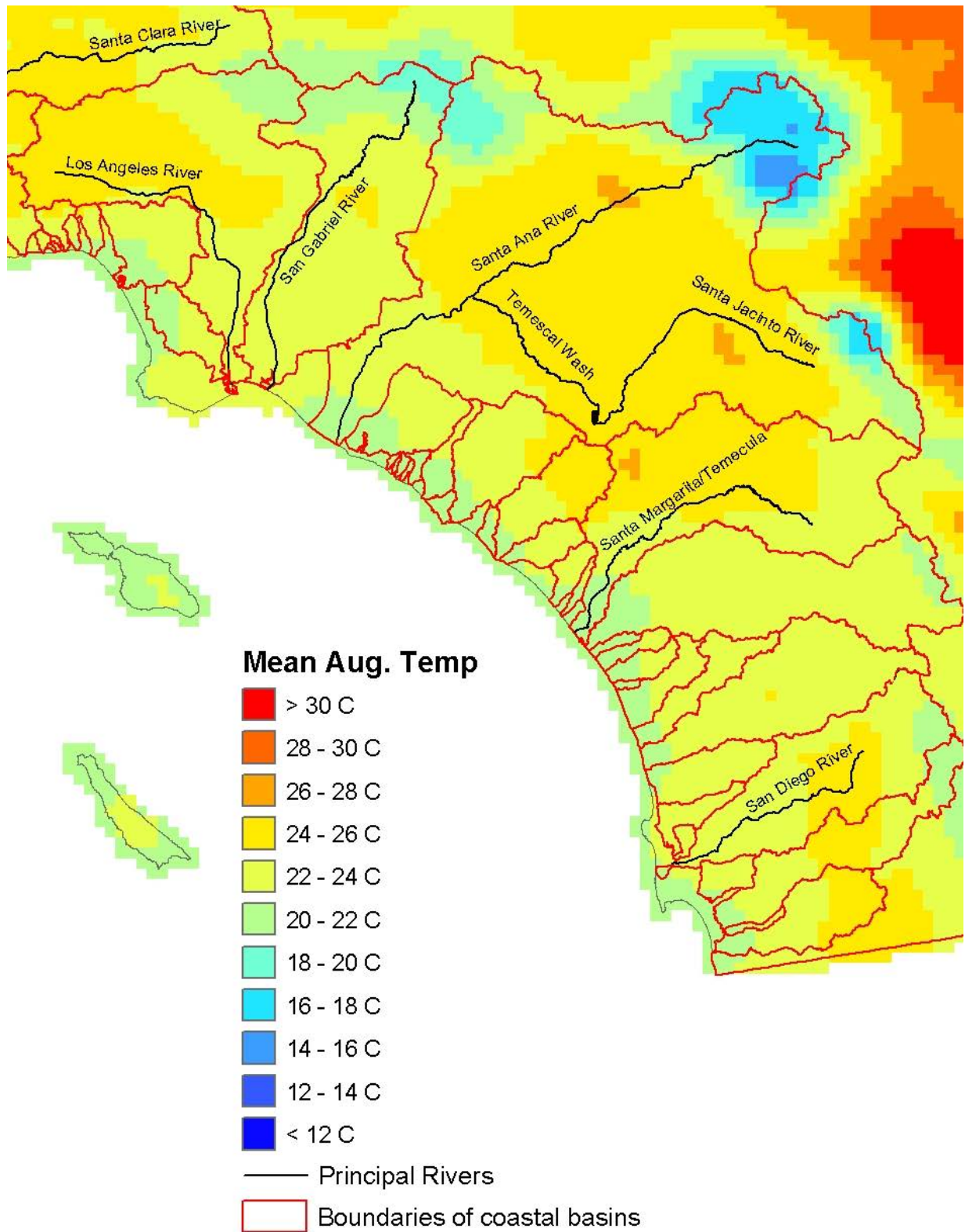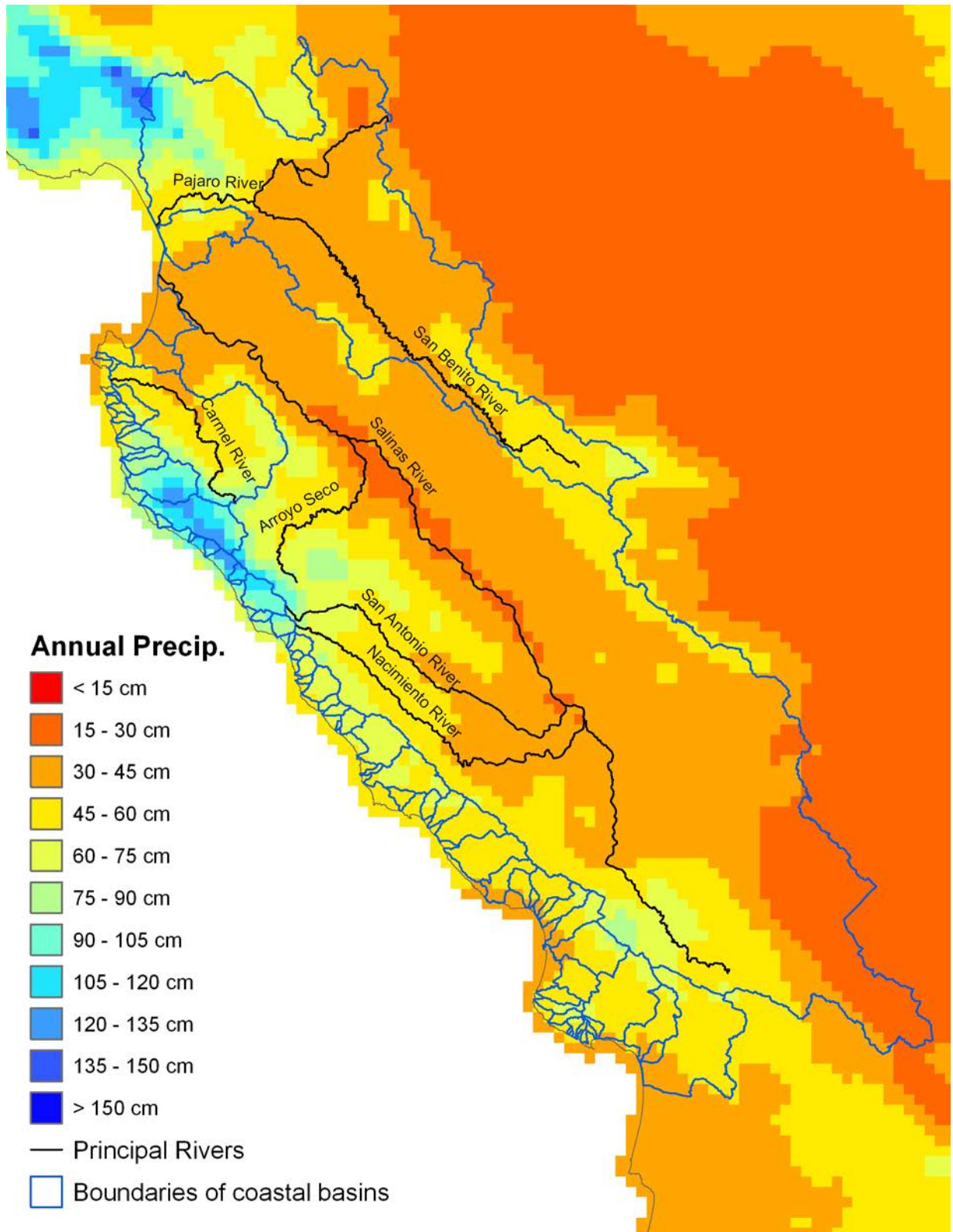
Plate III. Mean August temperature for the SOLA section of the southern California study area, for the period 1961 – 1990. Data *cf*. Daly *et al*. (1994).

Plate IV. Mean annual precipitation in the south-central California coast study area, for the period 1961 – 1990. Data *cf*. Daly *et al*. (1994).
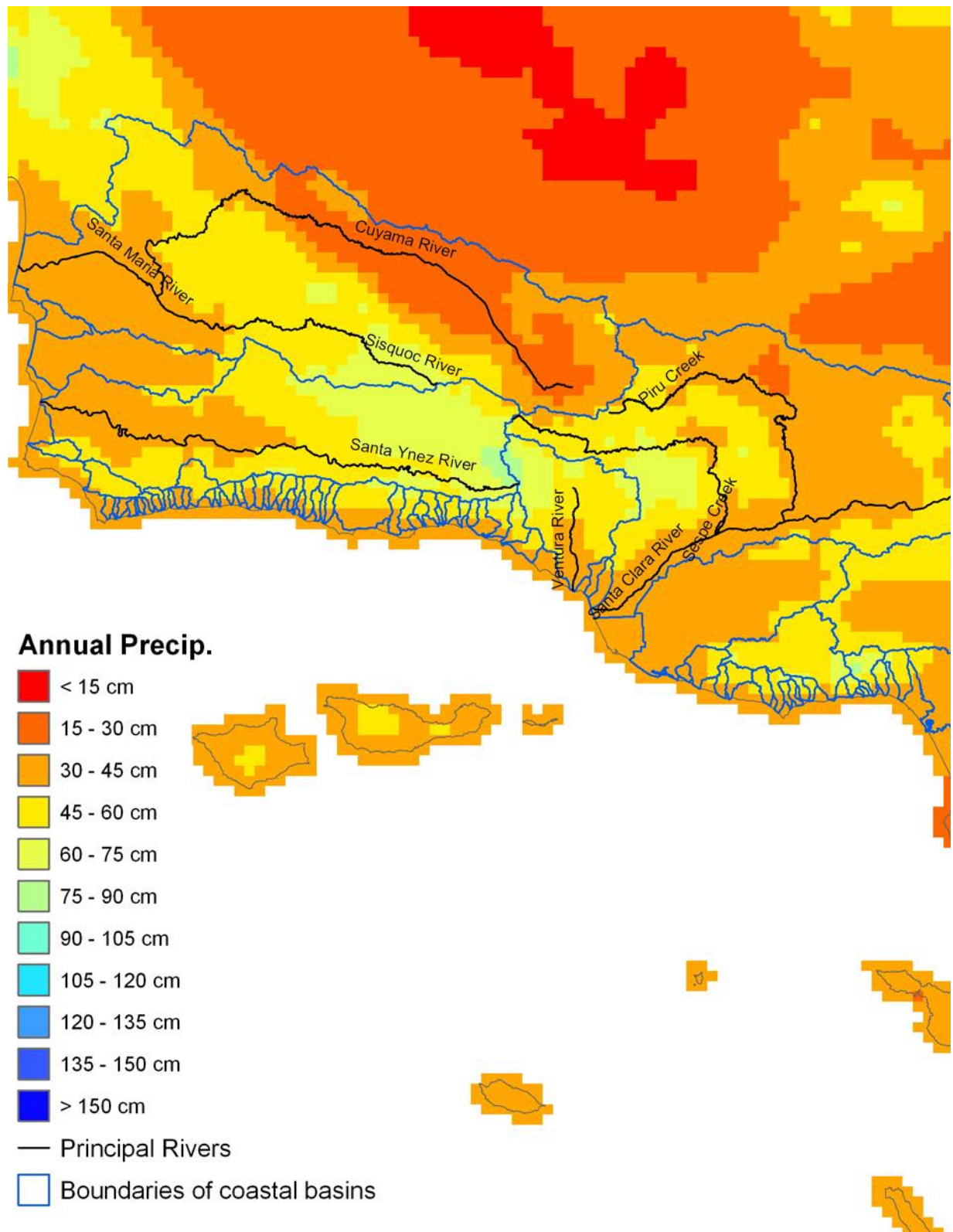
Plate V. Mean annual precipitation for the NOLA section of the southern California study area, for the period 1961 – 1990. Data *cf*. Daly *et al*. (1994).
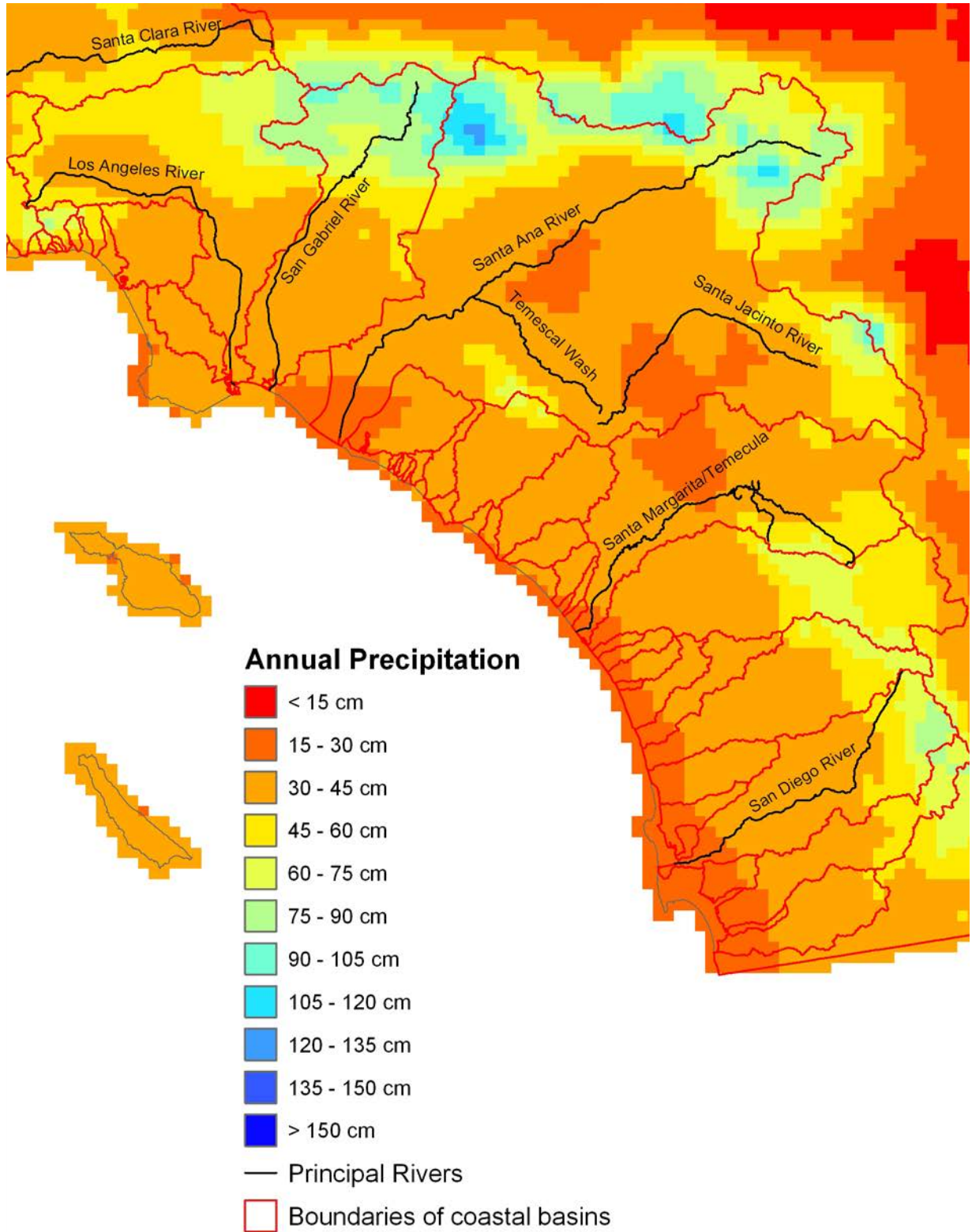
Annual Precipitation

- **< 15 cm**
- **15 - 30 cm**
- **30 - 45 cm**
- **45 - 60 cm**
- **60 - 75 cm**
- **75 - 90 cm**
- **90 - 105 cm**
- **105 - 120 cm**
- **120 - 135 cm**
- **135 - 150 cm**
- **> 150 cm**
- —— Principal Rivers
- ☐ Boundaries of coastal basins

Plate VI. Mean annual precipition for the SOLA section of the southern California study area, for the period 1961 – 1990. Data *cf*. Daly *et al*. (1994).

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Annual Mean Temperature

Degrees Centigrade

High : 18.7

Low : 5.4

Annual Range in Temperature

Degrees Centigrade
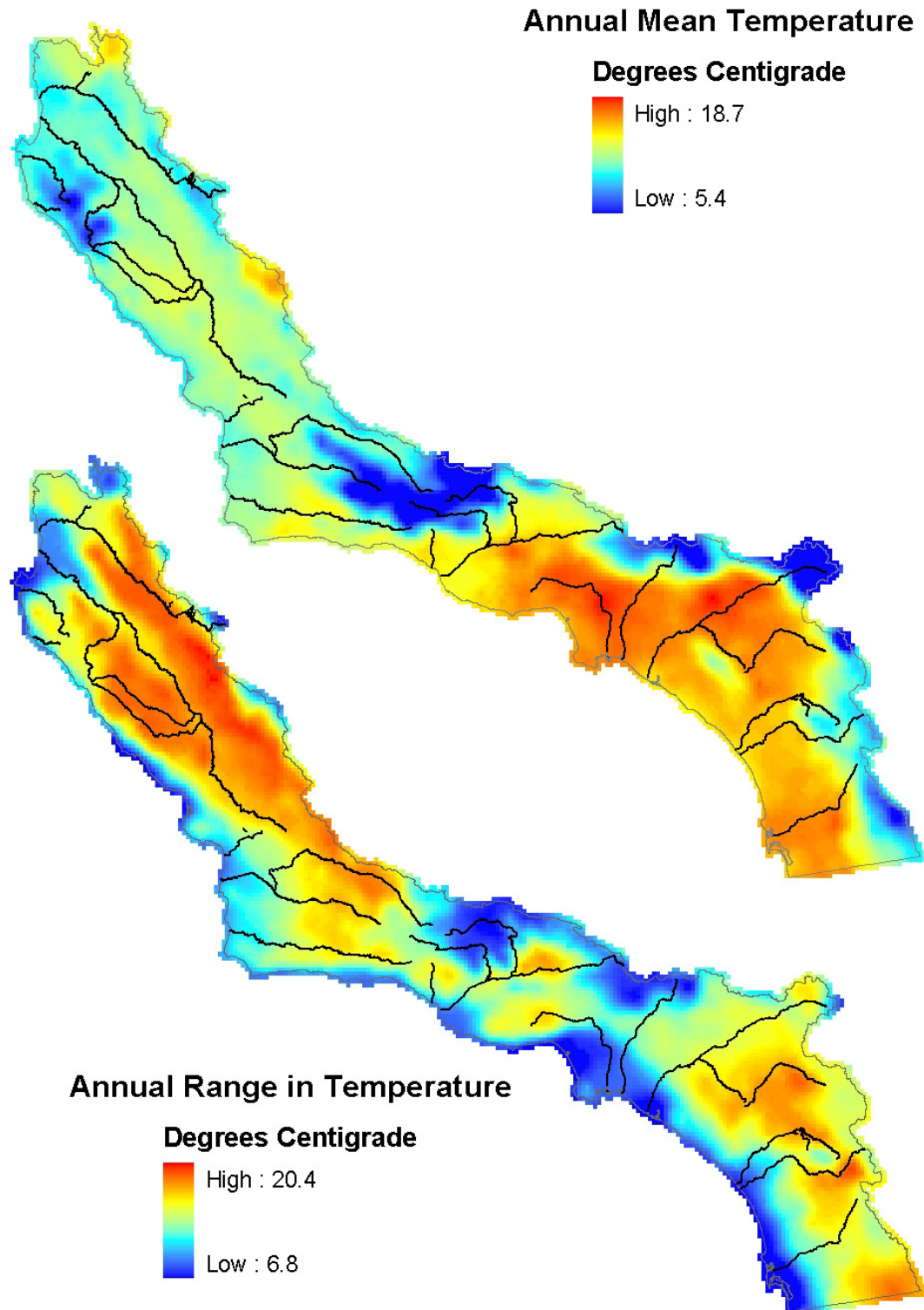
High : 20.4

Low : 6.8

Plate VII. Annual means and ranges of temperature in the study area, for the period 1961 – 1990. Principal rivers depicted are, from north to south: Pajaro+San Benito; Salinas; Carmel; Arroyo Seco; Big Sur; San Antonio; Nacimiento; Arroyo Grande; Cuyama; Santa Maria; Sisquoc; Santa Ynez; Piru; Sespe; Ventura; Santa Clara; Los Angeles; San Gabriel; Santa Ana; Temescal Wash + San Jacinto; Santa Margarita + Temecula; San Luis Rey; and San Diego.

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