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

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ABSTRACT

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

KEYWORDS

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

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

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

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

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

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

METHODS

Modeling the Distribution of O. mykiss

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

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

**Identification of Independent Populations**

Following McElhany and others (2000), we define independent populations as “any collection of one or more local breeding units whose population dynamics or extinction risk over a 100-year time period is not substantially altered by exchanges of individuals with other populations.” Within a basin such as the Central Valley, high summer temperatures at lower elevations fragment otherwise acceptable and continuous habitat into enclaves of interconnected habitats isolated from one another by downstream regions of thermally unsuitable habitat (Rahel and others 1996). If these enclaves are far enough apart, we expect that the enclaves will function as independent populations. We therefore intersected the 24°C mean August air temperature isotherm with the stream network to identify downstream boundaries of habitat patches. We assume implicitly that while discharge, gradient, and temperature all affect the suitability of a habitat, only temperature restricts movement between habitat patches. We computed the distance along the stream network among these downstream edges with the NODEDISTANCE function in the Network Module of ArcInfo, creating a matrix of distances among habitat patches. We used hierarchical clustering with a simple distance-based rule to group nearby patches into independent populations using the LINKAGE function (with the single linkage algorithm) in Matlab (Version 6.5.1, The Mathworks, Natick, MA). Following the Interior Columbia Basin Technical Recovery Team (2003), who reviewed available information on straying of Pacific salmonids, we chose 35 km as the critical dispersal distance: patches that link at 35 km were grouped together as independent populations. The sensitivity of the population delineation to the distance criterion was examined by calculating how the number of clusters declines with increasing linkage distance. If the total length of suitable stream habitat was less than 10 km, we ignored these small areas in subsequent analyses, on the assumption that isolated populations with less than 10 km of habitat would be unlikely to
persist for long periods without immigration (Bjorkstedt and others 2005).

**Quantification of Habitat Similarities**

In most basins, spawning by salmonids can be successful only if it occurs at certain times, such that development and migration can occur before temperature or flow conditions become unsuitable (Montgomery and others 1996; Beer and Anderson 2001). Thus, climate, through its effects on stream temperature and flow regime, is thought to be an important selective force leading to local adaptation in salmonids (Burger and others 1985; Konecki and others 1995; Brannon and others 2004; Lytle and Poff 2004). As proxies for water temperature and flow, we characterized mean elevation (from the USGS DEM), mean annual precipitation and the temperature regime (annual mean, maximum monthly mean, minimum monthly mean and range of air temperature (all from PRISM)) over the watersheds containing the spawning and rearing habitats of each of the independent populations identified with the procedure above. Watershed boundaries were based on the CalWater 2.2 watershed map1 of 1999, but in cases where CalWater boundaries follow political rather than geomorphic boundaries, we delineated boundaries by hand, following the DEM. We characterized the similarity of watersheds by calculating the Mahalanobis (1936) distance among the centroids of watersheds using the PDIST function in Matlab. The Mahalanobis distance reduces the effect of variables that are highly correlated with each other, and is equal to the normalized Euclidean distance between the centroids if variables are uncorrelated. We then used hierarchical clustering based on the average distance to join groups (using the LINKAGE function in Matlab), and plotted the results as a tree (with the DENDROGRAM function in Matlab).

**Quantification of Habitat Loss to Dams**

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

**RESULTS**

**Distribution of *O. mykiss* Habitat**

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

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1. The CalWater data can be obtained from the California Spatial Information Library, 900 N Street, Sacramento, CA 95814.
Figure 1. Predicted historical distribution of summer rearing habitat for anadromous *O. mykiss* (green). Stream reaches that would be suitable if not for high summer temperatures are shown in orange, and suitable stream reaches that were historically fishless due to natural migration barriers are shown in magenta. For legibility, streams with unsuitable gradient or discharge are not shown. Hydrography is USGS 1:1,000,000; other data are 1:24,000. (Click here for PDF file of larger image).
Independent Populations

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

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

Similarity of Habitats

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

Habitat Loss to Dams

About 80% of habitat identified by our model that was historically available to anadromous *O. mykiss* is now behind impassable dams, and 38% of the populations identified by the model have lost all of their habitat (Figure 5). Anadromous *O. mykiss* populations may have been extirpated from their entire historical range in the San Joaquin Valley and most of the larger basins of the Sacramento River. The roughly 52% of watersheds with at least half of their historical area below impassable dams are all small, low elevation systems. Of the eight population clusters that form at a Mahalanobis distance of 2 (Figure 4), for example, only two clusters contain watersheds with habitat that remains accessible to anadromous *O. mykiss*, suggesting that there has been a significant reduction in the diversity of habitats available to Central Valley *O. mykiss*. 
Figure 2. Spawning and rearing habitat areas of independent *O. mykiss* populations. Green polygons indicate habitat boundaries; color intensity indicates the density of habitat (km stream habitat km⁻² x 100). (Click here for PDF file of larger image).
| Independent Population | Basin                  | Total Stream (km) | Streams                                      |
|------------------------|------------------------|-------------------|----------------------------------------------|
| 1                      | American R.            | 1357.1            | Auburn Ravine, NF                            |
| 2                      | Antelope Cr            | 176.5             | Cold Fork                                    |
| 3                      | Battle Cr              | 122.8             | MF, SF                                       |
| 4                      | Battle Cr              | 349.1             | Knob Gulch, NF, Rock Cr                       |
| 5                      | Bear R (Feather trib)  | 58.5              | NF                                           |
| 6                      | Bear R (Feather trib)  | 356.1             | Long Valley Cr                               |
| 7                      | Bear R (Sac trib)      | 51.5              | Digger Cr, SF Bear Cr                         |
| 8                      | Big Chico Cr           | 30.9              | SF                                           |
| 9                      | Big Chico Cr           | 46.8              | Rock Cr, mainstem                            |
| 10                     | Big Chico Cr           | 114.9             | East Branch Mud Cr                           |
| 11                     | Butte Cr               | 29.2              | MF                                           |
| 12                     | Butte Cr               | 269.4             | mainstem                                     |
| 13                     | Cache Cr               | 1100.0            | Deer Cr, Dry Cr, Wolf Cr, mainstem           |
| 14                     | Calaveras R            | 14.5              | Woods Cr                                     |
| 15                     | Calaveras R            | 22.8              | mainstem                                     |
| 16                     | Calaveras R            | 34.6              | San Antonio Cr, San Domingo Cr               |
| 17                     | Calaveras R            | 71.9              | McKinney Cr, O’Neil Cr                       |
| 18                     | Caliente Cr            | 12.4              | Indian Cr                                    |
| 19                     | Caliente Cr            | 60.5              | Tehachapi Cr                                 |
| 20                     | Caliente Cr            | 75.8              | Walker Basin                                 |
| 21                     | Chowchilla R           | 12.9              | mainstem                                     |
| 22                     | Chowchilla R           | 61.3              | Willow Cr, mainstem                          |
| 23                     | Clear Cr               | 255.7             | Crystal Cr, mainstem                         |
| 24                     | Coon Cr                | 15.6              | mainstem                                     |
| 25                     | Coon Cr                | 38.9              | mainstem                                     |
| 26                     | Cosumnes R             | 587.8             | Cedar Cr, MF, NF, SF                         |
| 27                     | Cottonwood Cr          | 16.8              | mainstem                                     |
| 28                     | Cottonwood Cr          | 44.2              | SF                                           |
| 29                     | Cottonwood Cr          | 55.2              | Jerusalem Cr, Moon Fork, NF Bear Cr          |
| 30                     | Cottonwood Cr          | 62.4              | Duncan Cr, Soap Cr, mainstem                 |
| 31                     | Cottonwood Cr          | 96.8              | Wells Cr                                     |
| 32                     | Cottonwood Cr          | 121.2             | mainstem                                     |
| 33                     | Deer Cr (Kaweah trib)  | 46.2              | Bull Run Cr, Chimney Cr, SF                  |
| 34                     | Deer Cr (Sac trib)     | 299.4             | Little Dry Cr                                |
| 35                     | Del Puerto Cr          | 33.8              | Whisky Cr                                    |
| 36                     | Elder Cr               | 59.3              | NF, mainstem                                 |
| 37                     | Feather R              | 14.4              | Briscoe Cr                                   |
| 38                     | Feather R              | 41.7              | Rocky Honcut Cr                              |
|                         |                        |                   | Canyon Cr, Concow Cr, Little Butte Cr, MF, NF |
| 39                     | Feather R              | 1593.5            | Elk Cr, WB                                   |
| 40                     | Fresno R               | 38.6              | Big Cr, NF                                   |
| 41                     | Kaweah R               | 11.6              | SF Tule R                                    |
Table 1. Proposed historical independent populations of steelhead in the Central Valley (Continued)

| Independent Population | Basin                | Total Stream (km) | Streams                                      |
|------------------------|----------------------|-------------------|----------------------------------------------|
| 42                     | Kaweah R             | 20.9              | Tyler Cr                                     |
| 43                     | Kaweah R             | 42.9              | mainstem                                     |
| 44                     | Kern R               | 35.1              | NF                                           |
| 45                     | Kern R               | 532.2             | French Gulch, Little Poso Cr, Tillie Cr      |
| 46                     | Kern R               | 693.0             | Fay Cr, Kelso Cr, Marsh Cr                   |
| 47                     | Kings R              | 20.6              | SF                                           |
| 48                     | Kings R              | 123.3             | Bitterwater Cyn, SF, mainstem                |
| 49                     | Little Cow Cr        | 33.3              | Clover Cr                                    |
| 50                     | Little Cow Cr        | 59.4              | South Cow Cr                                 |
| 51                     | Little Cow Cr        | 83.5              | Cedar Cr, mainstem                           |
| 52                     | Little Cow Cr        | 88.5              | Gelndenning Cr, Old Cow Cr                   |
| 53                     | Lone Tree Cr         | 28.5              | EF                                           |
| 54                     | Los Banos Cr         | 10.2              | MF Tule R                                    |
| 55                     | Los Gatos Cr         | 19.5              | mainstem                                     |
| 56                     | Los Gatos Cr         | 20.1              | Rube Cr                                      |
| 57                     | Marsh Cr             | 82.9              | SF                                           |
| 58                     | McCloud R            | 1201.2            | Nosoni Cr, mainstem                          |
| 59                     | Merced R             | 18.1              | Snow Cr                                      |
| 60                     | Merced R             | 227.9             | MF, Miami Cr, mainstem                       |
| 61                     | Mill Cr              | 158.7             | NF Willow Cr                                 |
| 62                     | Mokelumne R          | 53.3              | Sutter Cr, mainstem                          |
| 63                     | Mokelumne R          | 276.8             | NF                                           |
| 64                     | Panoche Cr           | 11.4              | Warthan Cr                                   |
| 65                     | Paynes Cr            | 29.9              | Beegum Cr                                    |
| 66                     | Pit R                | 146.5             | Squaw Cr                                     |
| 67                     | Pit R                | 3948.0            | Potem Cr, mainstem                           |
| 68                     | Poso Cr              | 168.5             | Alamo Cr, Indian Cr                          |
| 69                     | Putah Cr             | 982.2             | Scott Cr                                     |
| 70                     | Stanislaus R         | 218.3             | Curtis Cr                                    |
| 71                     | Stony Cr             | 184.6             | Grindstone Cr, NF, SF, Salt Cr               |
| 72                     | Stony Cr             | 237.2             | Little Stony Cr, Salt Cr, South Honcut Cr    |
| 73                     | Suisun Bay tribs,    |                   |                                              |
|                        | northern Kelso Cr    | 573.1             | Sullivan Cr, mainstem                        |
| 74                     | Sweany Cr            | 127.6             | Jesus Maria Cr                               |
| 75                     | Thomas Cr            | 179.1             | Maple Branch Mud Cr                          |
| 76                     | Toomes Cr            | 34.4              | Big Dry Cr, mainstem                         |
|                        |                      |                   | Bear Cr, Corral Hollow Cr, Maxwell Cr, Moccasin |
| 77                     | Tuolumne R           | 323.8             | Cr, mainstem                                 |
|                        |                      |                   | Backbone Cr, Middle Salt Cr, Salt Cr, Squaw Cr, Sugarloaf Cr, mainstem |
| 78                     | Upper Sacramento R   | 766.6             |                                              |
| 79                     | Upper San Joaquin R  | 205.8             | Clear Cr, Erskine Cr, Mill Flat Cr, mainstem |
| 80                     | Yuba R               | 138.4             | mainstem                                     |
| 81                     | Yuba R               | 1077.1            | Dry Cr, mainstem                             |
Figure 3. Linkage of habitat patches as a function of distance along the stream network. At a distance of 35 km, there are 81 discrete patches.
Figure 4. Neighbor-joining tree based on average Mahalanobis distances, calculated from normalized climatic variables and mean elevation. Colored backgrounds envelope clusters of basins that are largely from the same geographic region: orange—tributaries to the Sacramento below the delta; green—the upper San Joaquin and tributaries draining the southern Sierra Nevada; blue—other tributaries to the San Joaquin draining lower elevation areas; yellow—mostly tributaries to the Sacramento River. The numbers in parentheses after the basin name correspond to the population numbers in Table 1. (Click here for PDF file of larger image).
Figure 5. Percentage of historically accessible habitat behind impassable dams. Numbers indicate populations (see Table 1). (Click here for PDF file of larger image).
DISCUSSION

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

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

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

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

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

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REFERENCES

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

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

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

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

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

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

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

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

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

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

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

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

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

Daly C, Neilson RP, Philips DL. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meterology 33:140–158.
Daly C, Taylor G, Kittel T, Schimel D, McNab A. 2002. Development of a 103-year high-resolution climate data set for the conterminous United States. Comprehensive Final Report for 9/1/97 - 5/31/02. NOAA Climate Change Data and Detection Program.

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

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

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

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

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

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

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

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

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

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

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

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

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

Konecki JT, Woody CA, Quinn TP. 1995. Influence of temperature on incubation rates of coho salmon (Oncorhynchus kisutch) from ten Washington populations. Northwest Science 69:126–132.
Lieberman DM, Horn MJ, Duffy S. 2001. Effects of a temperature control device on nutrients, POM and plankton in the tailwaters below Shasta Lake, California. Hydrobiologia 452:191–202.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Quist MC, Rahel FJ, Hubert WA. 2005. Hierarchical faunal filters: an approach to assessing effects of habitat and nonnative species on native fishes. Ecology of Freshwater Fish 14:24–39.
Rahel FJ, Keleher CJ, Anderson JL. 1996. Potential habitat loss and population fragmentation for cold water fish in the North Platt River drainage of the Rocky Mountains: response to climate warming. Limnology and Oceanography 41:1116–1123.

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

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

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

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

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

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

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

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

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

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

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