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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.

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INTRODUCTION

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

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

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

Habitat modeling is often used to extrapolate from and interpolate between observations of species occurrence to provide

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

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

METHODS

Modeling the Distribution of *O. mykiss*

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

The second model is a set of simple rules, or environmental envelopes, that define whether a given stream segment is suitable for steelhead. The envelopes include mean annual discharge (suitable if >0.028 m^3s^{-1}), gradient (suitable if <12%), and mean August air temperature (suitable if <24°C), and whether the area was considered by Knapp (1996) to be fishless prior to anthropogenic introductions. We are aware of no published data suitable for identifying a lower discharge limit for steelhead, but Harvey and others (2002) found that the density of age one-year-old-or-older steelhead was lower in streams

with lower discharge in tributaries to the Eel River. A discharge of 0.028 $m^3 s^{-1}$ (or 1 cubic foot per second) was taken as a lower bound, although data of Harvey and others (2002) suggest that steelhead occasionally occur in streams with somewhat lower discharge. Steelhead are commonly found in stream reaches with gradients less than 6% (Burnett 2001; Harvey and others 2002; Hicks and Hall 2003), but in some systems they are not uncommon in reaches with gradients of up to 12% (and occasionally higher) (Engle 2002). Stream temperature is linearly related to air temperature between 0 and 24°C (Mohseni and others 1998). Steelhead in southern California are almost never found in areas where mean August air temperatures exceed 24°C (D. Boughton, NOAA Fisheries Santa Cruz Lab, in preparation). Schmidt and others (1979) reviewed available information on thermal tolerance of *O. mykiss*, and found that 24°C was the highest reported maximum temperature for *O. mykiss* rearing. More recently, Nielsen and others (1994) found that 24°C was the upper lethal temperature for juvenile steelhead in northern California. In the Eel River, steelhead were not found in streams with maximum weekly average summer temperatures greater than 22°C (Harvey and others 2002). Knapp (1996) developed a GIS coverage of historical fish distributions through a survey of published papers and unpublished reports. Most areas of the western Sierra Nevada above 1500-m elevation were historically fishless due to Pleistocene glaciation and numerous migration barriers (Moyle and Randall 1998). The final output of this stage of the analysis was a GIS dataset describing a collection of stream segments suitable for *O. mykiss*, connected by unsuitable stream segments.

Identification of Independent Populations

Following McElhany and others (2000), we define independent populations as "any collection of one or more local breeding units whose population dynamics or extinction risk over a 100-year time period is not substantially altered by exchanges of individuals with other populations." Within a basin such as the Central Valley, high summer temperatures at lower elevations fragment otherwise acceptable and continuous habitat into enclaves of interconnected habitats isolated from one another by downstream regions of thermally unsuitable habitat (Rahel and others 1996). If these enclaves are far enough apart, we expect that the enclaves will function as independent populations. We therefore intersected the 24°C mean August air temperature isotherm with the stream network to identify downstream boundaries of habitat patches. We assume implicitly that while discharge, gradient, and temperature all affect the suitability of a habitat, only temperature restricts movement between habitat patches. We computed the distance along the stream network among these downstream edges with the NODEDISTANCE function in the Network Module of ArcInfo, creating a matrix of distances among habitat patches. We used hierarchical clustering with a simple distance-based rule to group nearby patches into independent populations using the LINKAGE function (with the single linkage algorithm) in Matlab (Version 6.5.1, The Mathworks, Natick, MA). Following the Interior Columbia Basin Technical Recovery Team (2003), who reviewed available information on straying of Pacific salmonids, we chose 35 km as the critical dispersal distance: patches that link at 35 km were grouped together as independent populations. The sensitivity of the population delineation to the distance criterion was examined by calculating how the number of clusters declines with increasing linkage distance. If the total length of suitable stream habitat was less than 10 km, we ignored these small areas in subsequent analyses, on the assumption that isolated populations with less than 10 km of habitat would be unlikely to

persist for long periods without immigration (Bjorkstedt and others 2005).

Quantification of Habitat Similarities

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

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

Quantification of Habitat Loss to Dams

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

RESULTS

Distribution of *O. mykiss* Habitat

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

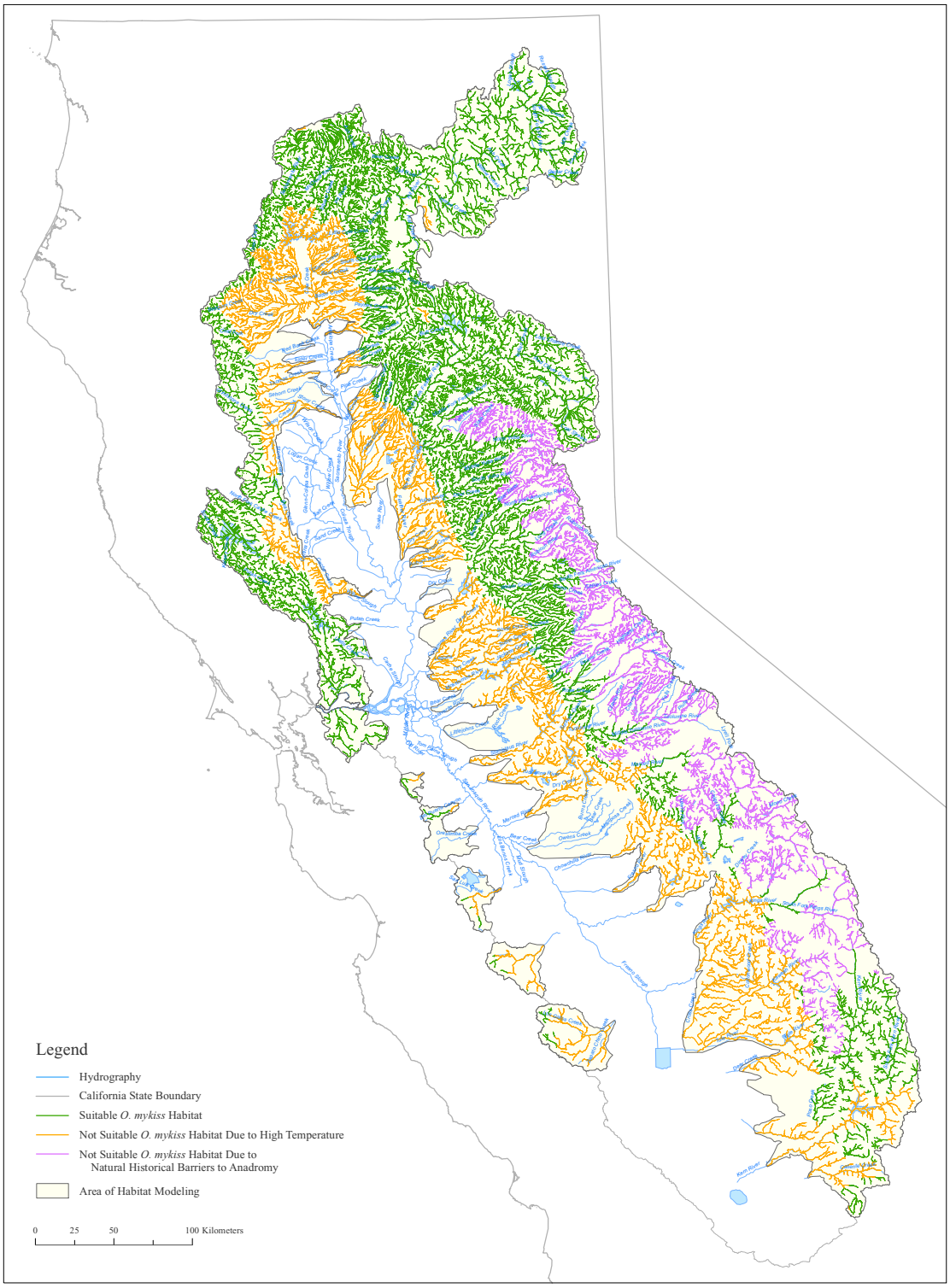

Figure 1. Predicted historical distribution of summer rearing habitat for anadromous *O. mykiss* (green). Stream reaches that would be suitable if not for high summer temperatures are shown in orange, and suitable stream reaches that were historically fishless due to natural migration barriers are shown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

Independent Populations

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

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

Similarity of Habitats

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

Habitat Loss to Dams

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

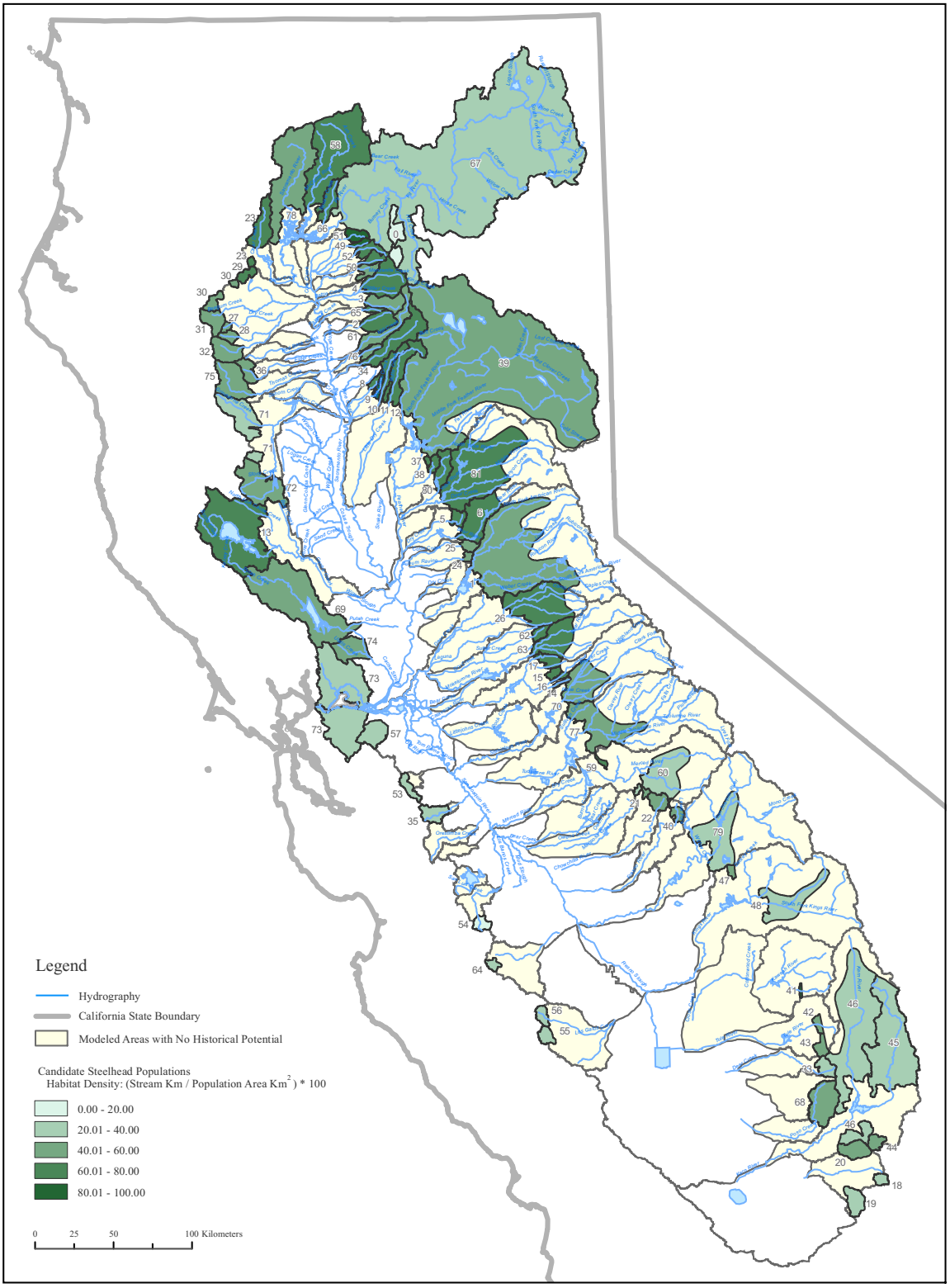

Figure 2. Spawning and rearing habitat areas of independent *O. mykiss* populations. Green polygons indicate habitat boundaries; color intensity indicates the density of habitat (km stream habitat km^{-2} x 100). (Click here for PDF file of larger image).

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

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

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

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

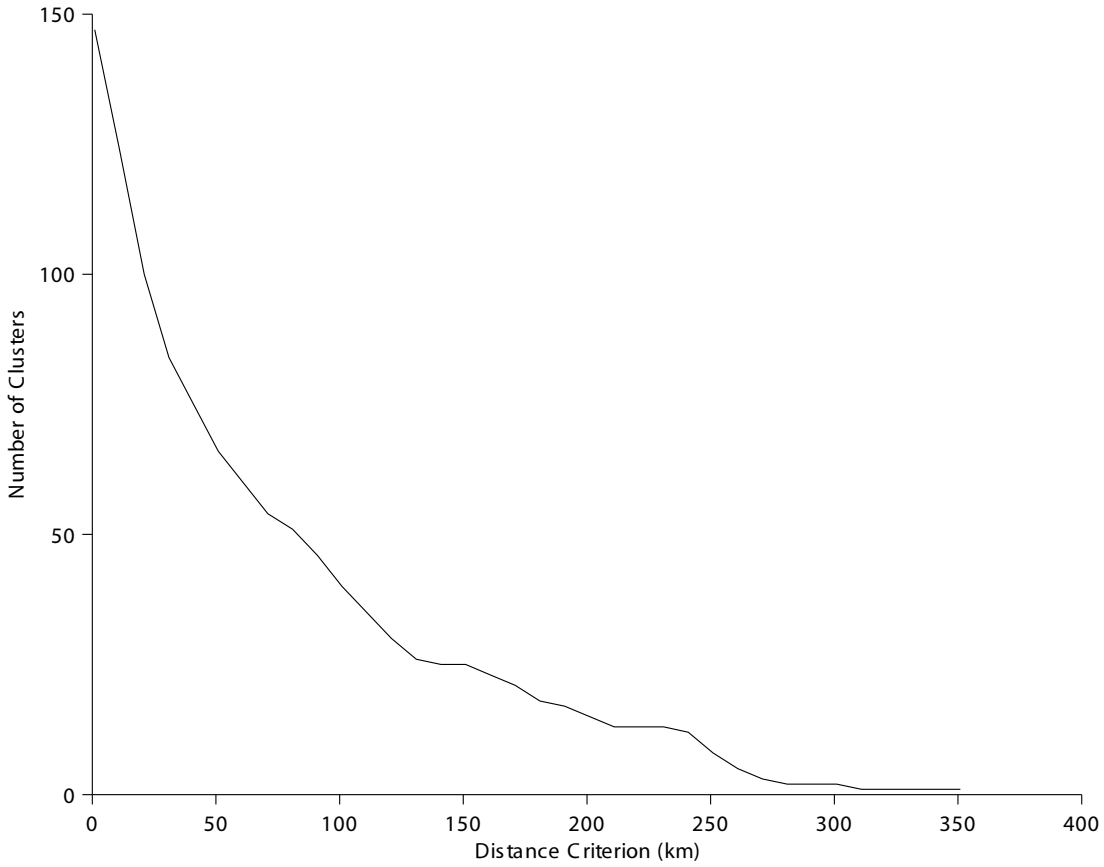

Figure 3. Linkage of habitat patches as a function of distance along the stream network. At a distance of 35 km, there are 81 discrete patches.

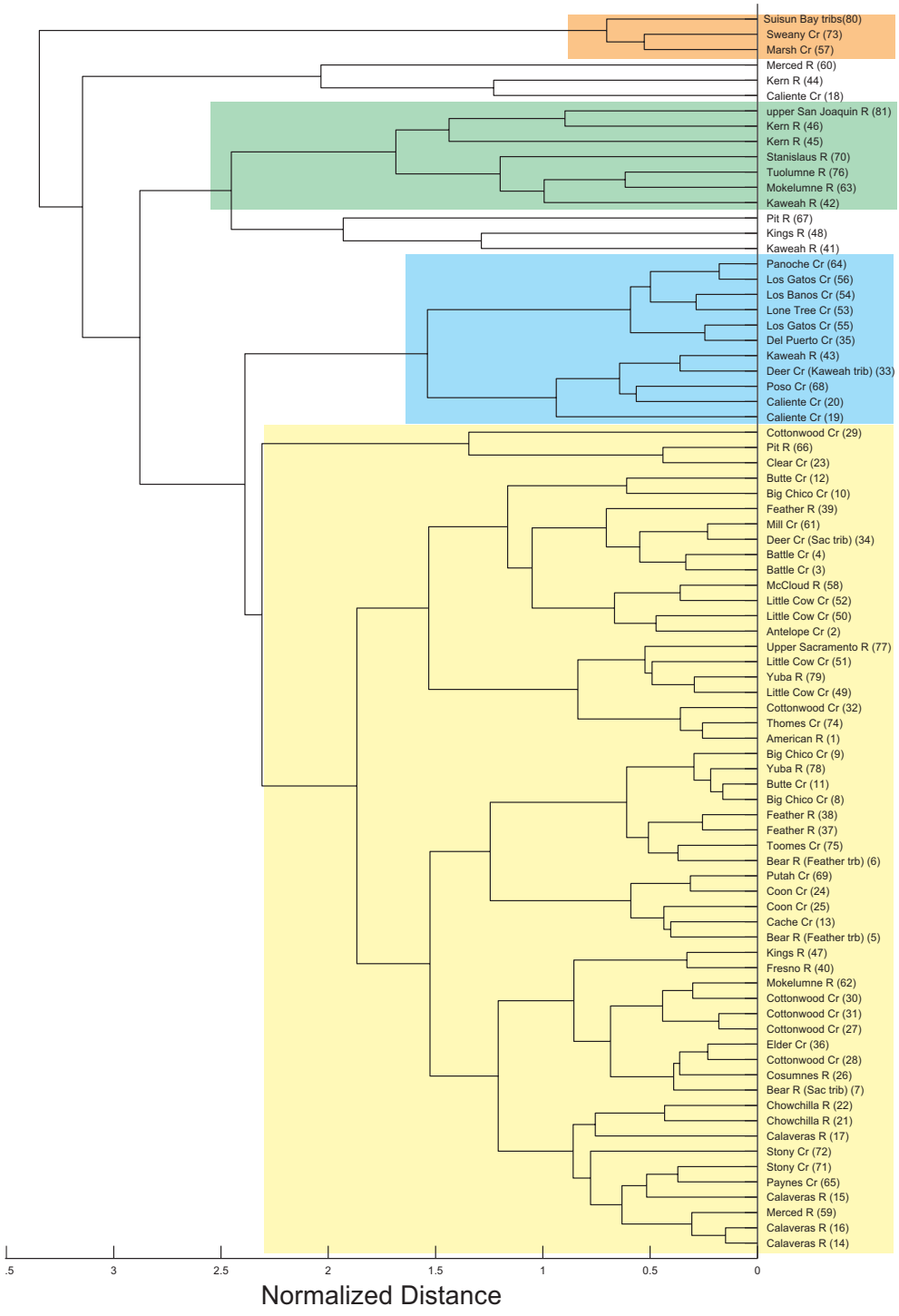

Figure 4. Neighbor-joining tree based on average Mahalanobis distances, calculated from normalized climatic variables and mean elevation. Colored backgrounds envelope clusters of basins that are largely from the same geographic region: orange—tributaries to the Sacramento below the delta; green—the upper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

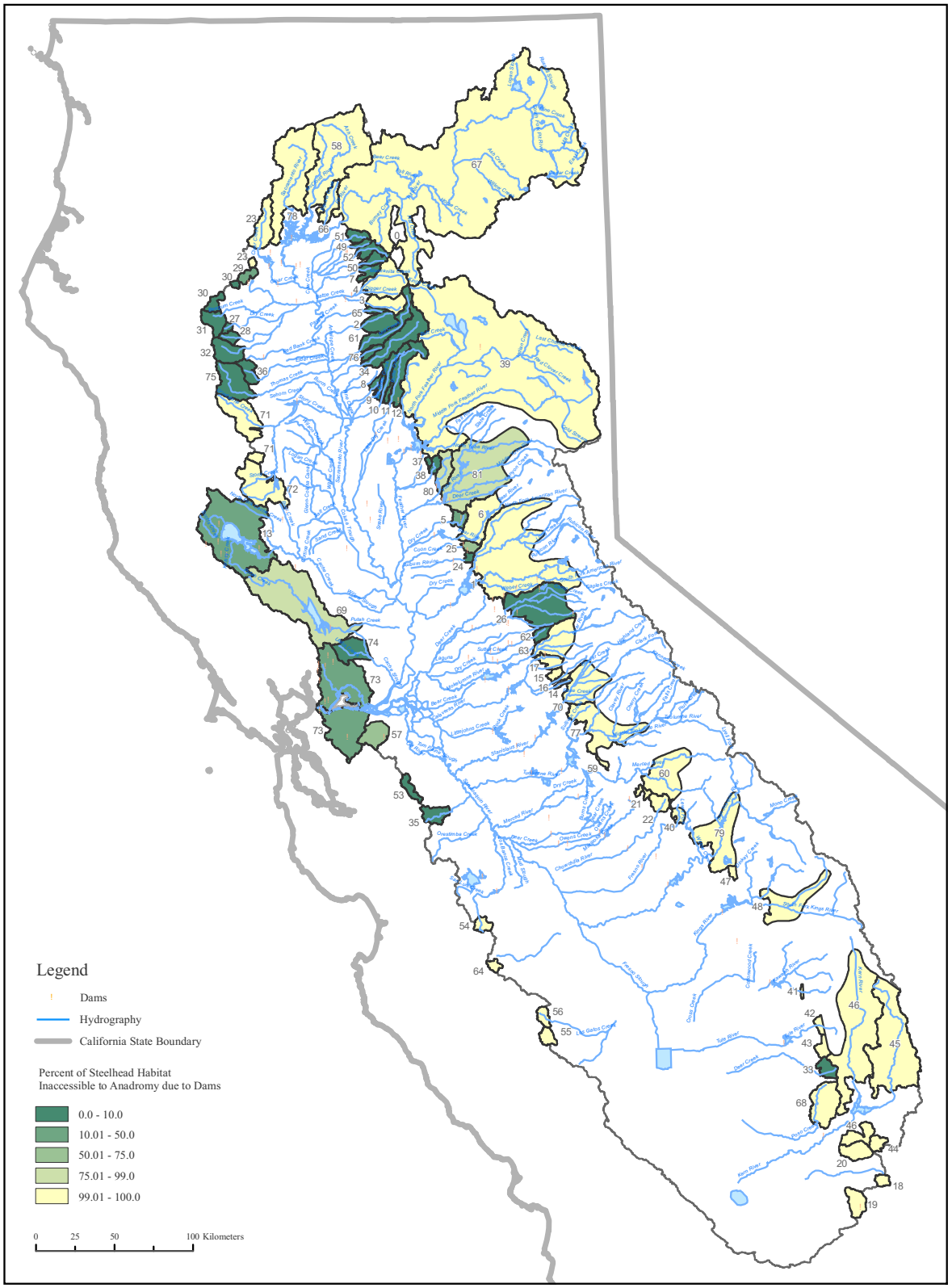

Figure 5. Percentage of historically accessible habitat behind impassable dams. Numbers indicate populations (see Table 1). (Click here for PDF file of larger image).

DISCUSSION

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

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

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

It appears that much of the historical diversity within Central Valley *O. mykiss* has been lost or is threatened by dams. Figure 5 shows that dams have heavily altered the distribution and population structure of

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

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

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