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Author:
Lindley, Steven T, Schick, Robert S, Mora, Ethan, Adams, Peter B, Anderson, James JGreene, Sheila et al.

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

Steven T. Lindley*, National Oceanic and Atmospheric Administration

Robert S. Schick, National Oceanic and Atmospheric Administration

Ethan Mora, University of California, Santa Cruz

Peter B. Adams, National Oceanic and Atmospheric Administration

James J. Anderson, University of Washington

Sheila Greene, California Department of Water Resources

Charles Hanson, Hanson Environmental, Inc.

Bernard P. May, University of California, Davis

Dennis R. McEwan, California Department of Fish and Game

R. Bruce MacFarlane, National Oceanic and Atmospheric Administration

Christina Swanson, The Bay Institute

John G. Williams, independent consultant

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

ABSTRACT

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

Central Valley spring-run and winter-run Chinook salmon ESUs are not currently viable, according to the criteria-based assessment. In both ESUs, extant populations may be at low risk of extinction, but these populations represent a small portion of the historical ESUs, and are vulnerable to catastrophic disturbance. The winter-run Chinook salmon ESU, in the extreme case, is represented by a single population that spawns outside of its historical spawning range. We are unable to assess the status of the Central Valley

steelhead ESU with our framework because almost all of its roughly 80 populations are classified as data deficient. The few exceptions are those populations with a closely associated hatchery, and the naturally-spawning fish in these streams are at high risk of extinction. Population monitoring in this ESU is urgently needed.

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

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

KEYWORDS

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

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INTRODUCTION

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

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

Developing objective, quantitative, and biologically meaningful recovery criteria for Pacific salmonid ESUs is difficult. Ideally, these criteria would be population- and ESU-specific, taking into account the constraints

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

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

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

ASSESSMENT FRAMEWORK

Population Viability

Risk Categories

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

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

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

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

[a] Census size N can be used if direct estimates of effective size N_e are not available, assuming $N_e/N = 0.2$.
[b] Decline within last two generations to annual run size $\leq$ 500 spawners, or run size > 500 but declining at $\geq$ 10% per year. Historically small but stable population not included.
[c] Run size has declined to $\leq$ 500, but now stable.
[d] Catastrophes occuring within the last 10 years.
[e] Decline < 90% but biologically significant.
[f] See Figure 1 for assessing hatchery impacts.

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

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

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

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

Risk Criteria

Following Allendorf et al. (1997), the first set of criteria deal with direct estimates of extinction risk from population viability models. If such analyses exist and are deemed reasonable, such assessments may be sufficient for assessing risk; indeed, Allendorf et al. (1997) intended that their other criteria be used when

such analyses were not available. The simplest useful population viability assessments are based on the random-walk-with-drift model (Dennis et al. 1991), and can be extended to account for observation error (Lindley 2003); we use this model where possible in this paper. We note that trying to predict absolute extinction risk is subject to many pitfalls and is viewed with skepticism by many conservation biologists and ecologists (Beissinger and Westphal (1998) provides a review of the various issues). We therefore recommend that population viability analysis (PVA) results be compared to the results of applying the simpler criteria, described below.

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

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

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

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

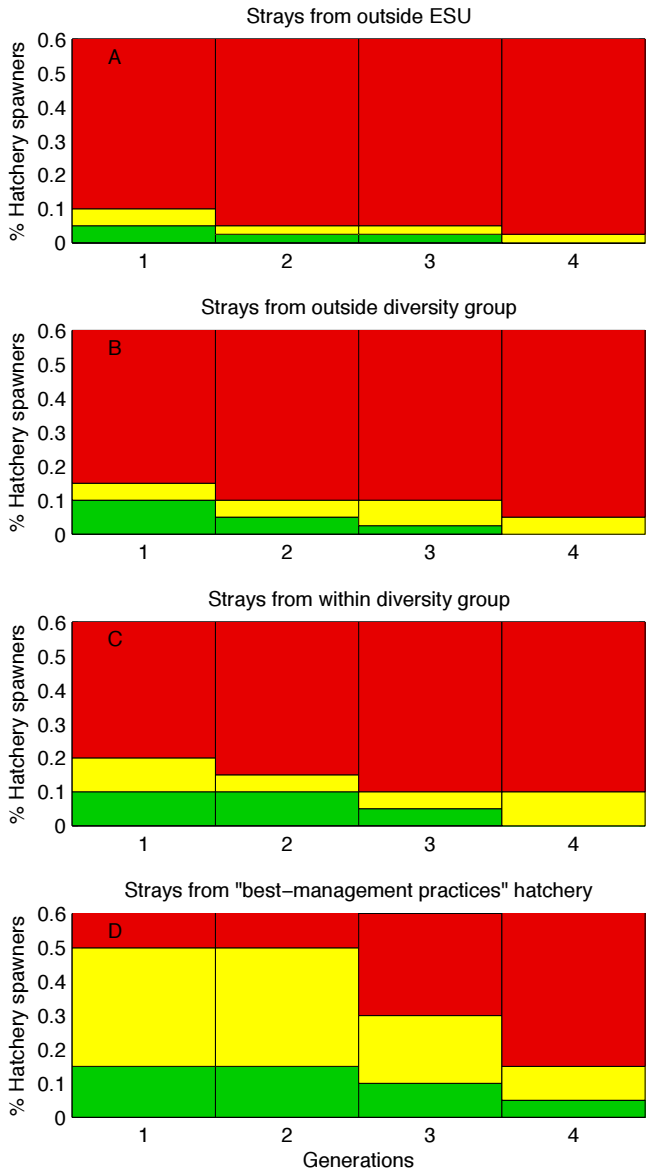

Figure 1. Extinction risk levels corresponding to different amount, duration and source of hatchery strays. Green bars indicate the range of low risk, yellow bars moderate risk, and red areas indicate high risk. Which chart to use depends on the relationship between the source and recipient populations.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

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

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

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

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

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

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

ESU Viability

ESU viability depends on the number of populations within the ESU, their individual status, their spatial arrangement with respect to each other and sources of catastrophic disturbance, and diversity of the populations and their habitats. In the most general terms, ESU viability increases with the number of populations, the viability of these populations, the diversity of the populations, and the diversity of habitats that they occupy. Under natural conditions, most salmonid ESUs have persisted for at least many centuries, and perhaps much longer, given the observed level of genetic differentiation within and among them. How much can an ESU be altered before it is considered at risk of extinction?

While we will not assess ESU viability in absolute terms, we assume that recovery planners will want ESUs to be likely to persist in the face of environmental variation of the sort we know has occurred over the last 500-1000 years. Such variation has included natural catastrophes such as prolonged drought, volcanic eruptions, large wildfires, and anthropogenic impacts such as the 1991 Cantara metam sodium spill. Such catastrophes could occur at any time in the foreseeable future. Therefore, for ESUs to be considered viable, they should at a minimum be able to persist if challenged by any one of these types of catastrophes.

Viability by Representation

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

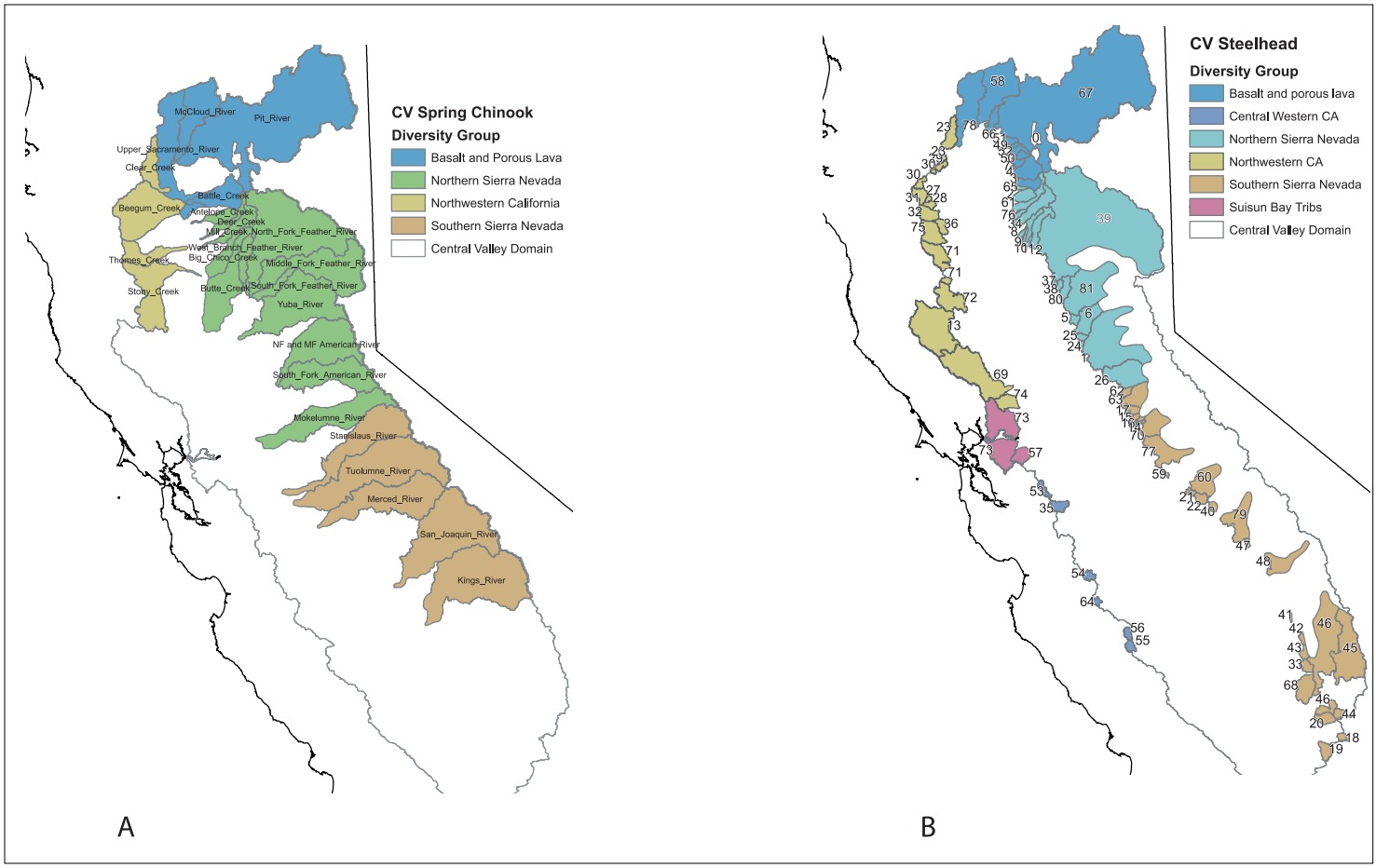

Figure 2. Salmonid ecoregions within the Central Valley. Map A: Central Valley spring-run Chinook salmon. Map B: Central Valley steelhead. Sacramento River Winter-run Chinook salmon not shown because this ESU has only one region (Basalt and porous lava). The numbers identifying steelhead populations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

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

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

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

Viability by Assessment of Specific Threats

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

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

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

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

APPLICATION TO CENTRAL VALLEY SALMONIDS

Central Valley Spring-run Chinook Salmon

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

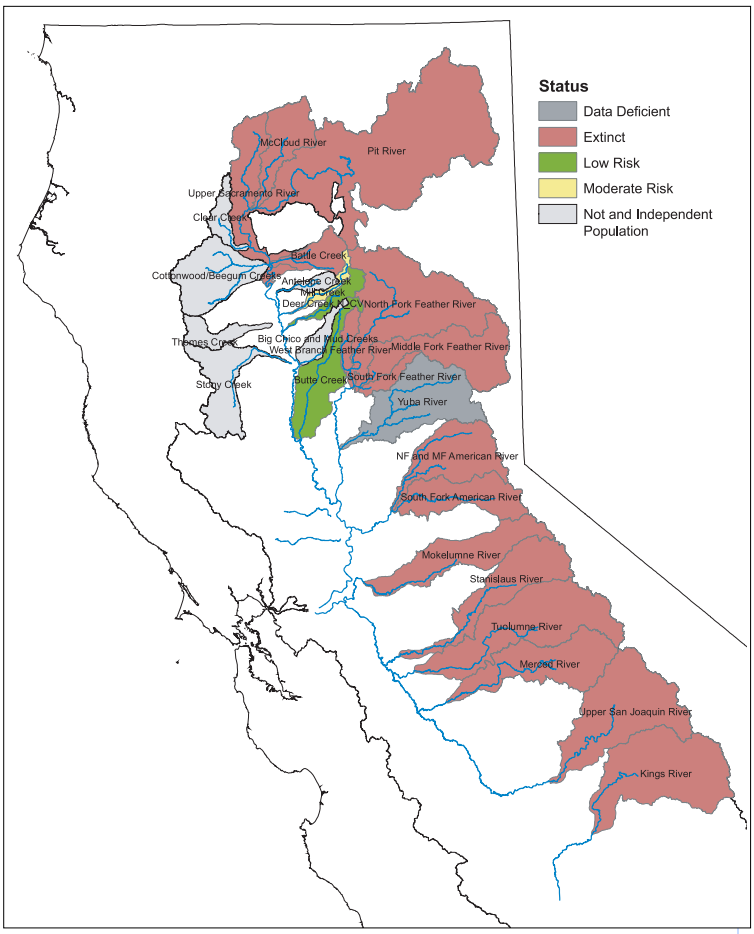

Figure 3. Status of historical Central Valley spring-run Chinook salmon populations.

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

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

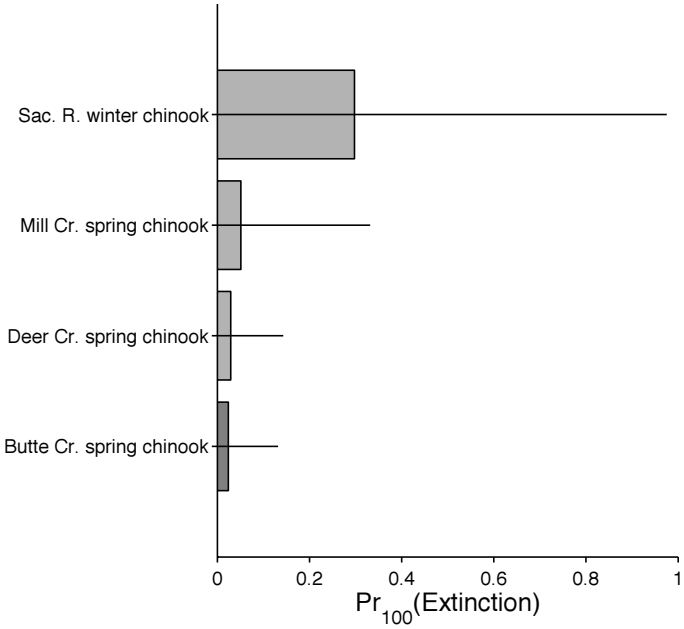

Figure 4. Probability of population extinction as estimated by the random-walk-with-drift model. Bars indicate the expected probability of extinction; lines indicate the 90% central interval for the estimate of the mean.

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

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

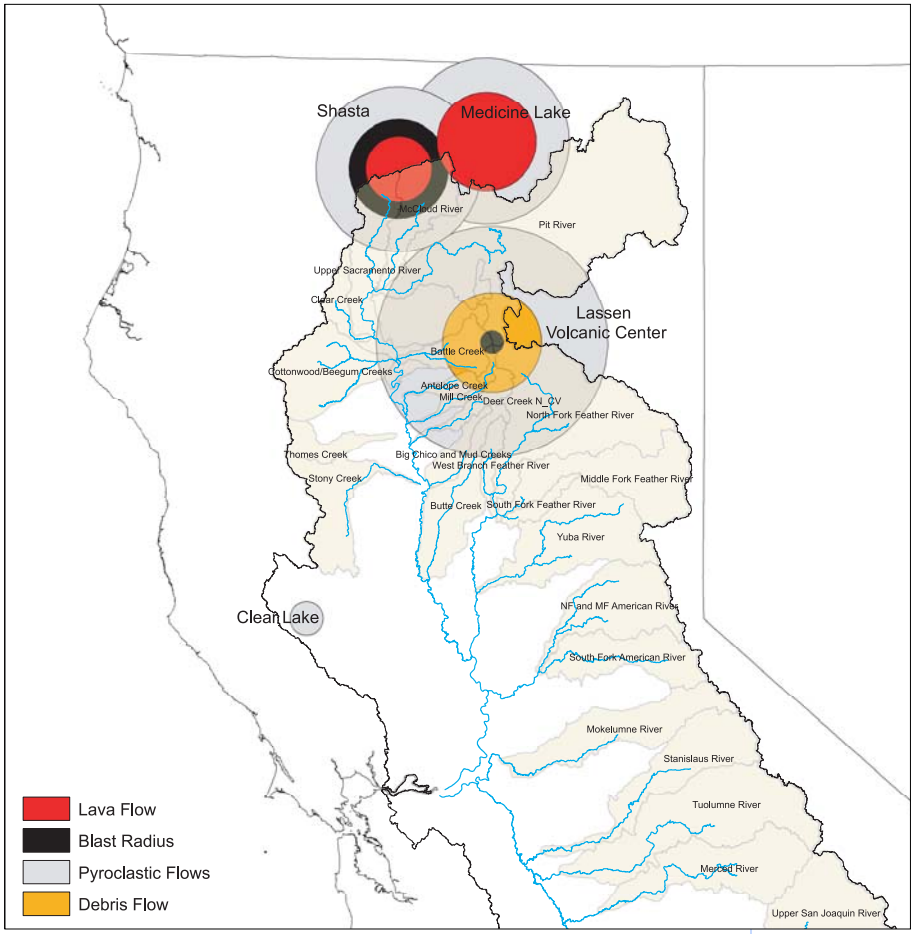

Figure 5. Volcanic hazards affecting the Central Valley recovery domain. Circles indicate the possible spatial extent of various kinds of volcanic effects that could devastate salmonid stream habitat, including lava flow, blast, pyroclastic flow, and debris. Data from Hobblitt et al. (1987)

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

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

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

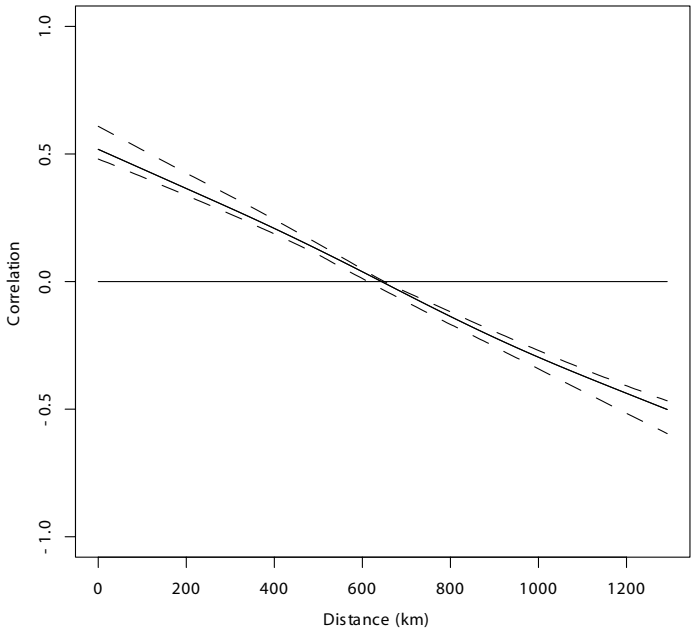

Figure 6. Spline correlogram fit to the gridded Palmer drought severity index data for California of Cook et al. (2004). Solid line indicates the estimated correlation function; dashed lines are the 95% confidence interval. Note that the correlation of drought indices declines with distance between locations,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

Sacramento River Winter-run Chinook Salmon

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

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

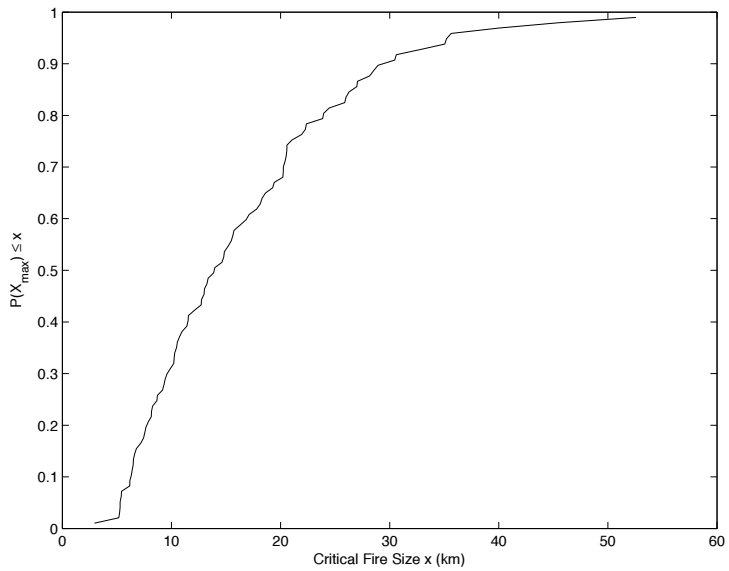

Figure 7. The probability that the largest fire in a year (Xmax) will be smaller than the critical size x. Based on observed fire sizes for the Central Valley recovery domain during the 1908–2003 period.

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

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

Central Valley Steelhead

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

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

Discussion

Population Viability

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

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

ESU Viability

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

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

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

Even if there were adequate data on the distribution and abundance of steelhead in the Central Valley, our approaches for assessing population and ESU viability might be problematical because the effect of resident *O. mykiss* on the viability of populations and ESUs is unknown. From one perspective, resident fish may reduce the extinction risk of the ESU through the production of anadromous individuals that can bolster or rescue weak steelhead populations. Such life history diversity also confers risk spreading, in that members of the ESU are spread among habitats that are subject to independent sources of disturbance. For instance, fish in the ocean are unaffected by flooding, while fish in rivers

are immune to poor feeding conditions in the ocean. At the margins of a species' range, where conditions may be more frequently unfavorable, such life history diversity could be an adaptation to the unpredictable environment (Jonsson and Jonsson 1993.)

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

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

Summary

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

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

CLIMATE VARIABILITY AND CHANGE

Introduction

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

response to management actions. Anthropogenic climate change may preclude some otherwise attractive recovery strategies, depending on future greenhouse gas emissions and the response of regional climate.

Natural Climate Variability

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

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

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

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

Climate Warming

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

Climate forecasts for the Central Valley

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

The recent paper by Hayhoe et al. (2004) examines multiple emissions pathways using two global models to make regional forecasts for California. Their results

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

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

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

Possible Effects on Salmon and Steelhead

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

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

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

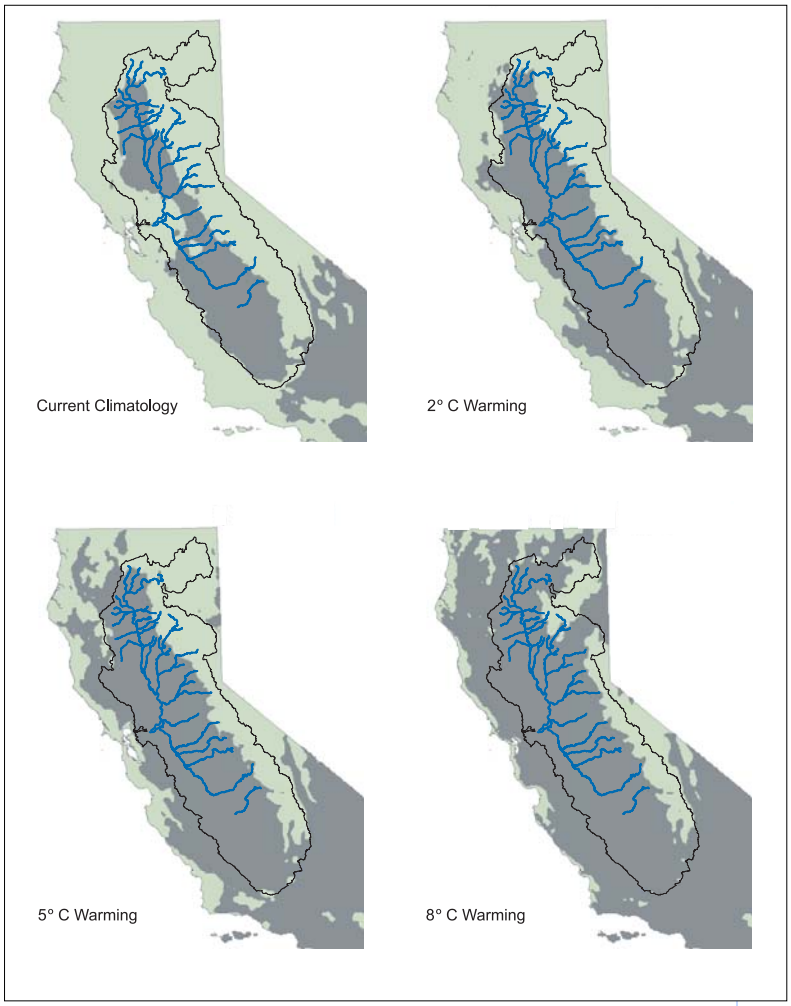

Figure 8. Effects of climate warming on availability of over-summer habitat. Mean August air temperatures exceeding 25°C are shown in gray; blue lines indicate the historical distribution of spring-run Chinook salmon.

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

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

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

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

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

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

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

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

SUMMARY AND RECOMMENDATIONS

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

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

Recovering even a few populations may therefore be a challenging and slow process, although we stress that there appear to be some opportunities that, if successful, would greatly increase the viability of all three ESUs. Some possibilities that are being considered include restoring flows and habitat in the San Joaquin River below Friant Dam and in Battle Creek, and

restoring access to the Yuba River above Englebright Dam. All of these actions, in our view, have the potential to significantly improve the status of affected ESUs, but achieving recovery may require access to additional historically-utilized spawning areas that are currently blocked by dams.

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

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

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

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

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

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

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ENDNOTES

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

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

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

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

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