UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Science Center
Fisheries Ecology Division
110 Shaffer Road
Santa Cruz, California 95060

30 March 2007

Dear Interested Party,

The Technical Recovery Team (TRT) for the South-Central and Southern California Coast Recovery Domain has recently completed a draft report titled "Viability criteria for steelhead of the south-central and southern California coast". We seek comment from interested parties regarding the scientific content and analysis that underlie the recommendations made in this report.

Viability criteria are ecological and biological conditions that are measurable and that must be met for steelhead to be considered at low risk of extinction. The scientific literature on this topic indicates that predicting the conditions for viability is inherently uncertain due to the complex and stochastic dynamics of wild populations. In addition, a lack of quantitative information on key aspects of steelhead populations in our study area add an additional large component of uncertainty. For this reason, we have suggested two options for viability criteria—one based on the precautionary principle that (for the most part) can be specified now, and one that is based on a future investment in data collection that will address some of the key uncertainties stemming from lack of quantitative information. It is our belief that the framework and the various options laid out in this report will provide coherence to recovery efforts, increase their effectiveness at reducing extinction risk, and ultimately facilitate the recovery of steelhead in the study area. At the same time it offers flexibility in how to deal with the substantial uncertainties.

We emphasize that the conclusions in this document are technical recommendations, and do not represent policy decisions. Throughout, we provide discussion of our assumptions and of the uncertainty in our conclusions. However, we also emphasize a comprehensive view of the species *Oncorhynchus mykiss*, specifically through consideration of how population redundancy and ecological diversity within and among populations contribute to long-term persistence of steelhead. We believe that this emphasis reduces the negative impacts of uncertainty about population dynamics.

In this context, we invite comment on the scientific content and analysis presented in this report. The report is available in electronic form on the website of the Fisheries Ecology Division of the NOAA Southwest Fisheries Science Center (http://swfsc.noaa.gov/textblock.aspx?Division=FED&id=2264). Comment should be sent electronically via email to David.Boughton (David.Boughton@noaa.gov) with "Draft SCSCC Viability Comments" in the subject line, or by mail to the address above. We ask that all comments be submitted by 30 April 2007.

Sincerely,

David Boughton, Ph.D.
Research Ecologist
Chair, SCSCC TRT

NOAA Technical Memorandum NMFS

MARCH 2007 DRAFT

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NOAA-TM-NMFS-SWFSC-XXX

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VIABILITY CRITERIA FOR STEELHEAD OF THE SOUTH-CENTRAL AND SOUTHERN CALIFORNIA COAST

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Abstract

Recovery planning for threatened and endangered steelhead requires measurable, objective criteria for determining an acceptably low risk of extinction. Here we propose viability criteria for two levels of biological organization: individual populations, and groups of populations within the South-Central/Southern California Coast Steelhead Recovery Planning Domain. For populations, we adapt criteria commonly used by the IUCN (The World Conservation Union) for identifying at-risk species. For groups of populations we implement a diversity-based "representation and redundancy rule," in which diversity includes both life-history diversity and biogeographic groupings of populations. The resulting criteria have the potential for straightforward assessment of the risks posed by evolutionary, demographic, environmental, and catastrophic factors; and are designed to use data that are readily collected. However, our prescriptive approach led to one criterion whose threshold could not yet be specified due to inadequate data, and others in which the simplicity of the criteria may render them inefficient for populations with stable run sizes or stable life-history polymorphisms. Both of these problems could likely be solved by directed programs of research and monitoring aimed at developing more efficient (but equally risk-averse) "performance-based criteria." Of particular utility would be data on the natural fluctuations of populations, research into the stabilizing influence of life-history polymorphisms, and research on the implications of drought, wildfires, and fluvial sediment regimes. Research on estuarine habitat could also yield useful information on the generality and reliability of its role as nursery habitat. Currently, risk assessment at the population level is not possible due to data deficiency, highlighting the need to implement a comprehensive effort to monitor run sizes, anadromous fractions, spawner densities and perhaps marine survival. Assessment at the group level indicates a priority for securing inland populations in the southern Coast Ranges and Transverse Ranges, and a need to maintain not just the fluvial-anadromous life-history form, but also lagoon-anadromous and freshwater-resident forms in each population.

Introduction

Steelhead (anadromous *Oncorhynchus mykiss*) occur in coastal stream systems throughout southern and south-central California (Swift *et al.* 1993, Boughton *et al.* 2005), but are currently on the US Endangered Species List due to population declines. Such listings require Federal agencies to develop recovery plans that, "to the maximum extent practicable," incorporate "objective, measurable criteria" for species recovery.[1] Recovery in this context means a return to viability, a scientific concept defined as the conditions for long-term persistence and adaptation of a species or population in a given place (Soulé 1987). If viability can be assessed via objective, measurable criteria, it provides a scientific standard by which to set recovery goals, judge the progress of recovery, and ultimately, remove the species from the US Endangered Species List.

The purpose of this report is to propose viability criteria for steelhead inhabiting the California coast between Santa Cruz and the Mexican Border. Busby *et al.* (1996) described these fish in a coast-wide status review of steelhead Evolutionarily Significant Units (ESUs). The ESU concept was proposed by Waples (1991, 1995) to comprise a group of conspecific populations that are substantially reproductively-isolated from other conspecific populations, and that jointly possess an important component of the evolutionary legacy of the species, understood in genetic and adaptive terms (Waples 1991, 1995).

McElhany *et al.* (2000) argued that recovery planning for *Oncorhynchus* would be more effective if each ESU were treated as a collection of demographically independent populations, where the time-extent for assessing independence was 100 yr. Boughton *et al.* (2006) later used this concept of demographic independence to propose a population-delineation scheme within the two ESUs of *O. mykiss* addressed in this report. There were four central theses of Boughton *et al*. (2006). First, direct empirical data on independence were not available, but the generally-recognized homing ability of the species suggests that each coastal basin generally supports a discrete population. Second, one especially large basin (of the Salinas River) probably supports three discrete populations. Third, the population delineation scheme was uncertain and might require significant revision if better information became available. Fourth, anadromous populations may have a co-existing non-migratory component (also *O. mykiss*), though the biological details of this co-existence are not well understood. In addition, a simple habitat model was used to approximately rank populations in terms of their potential viability and independence under unimpaired conditions.

The effort by Boughton *et al.* (2006) to delineate populations was intended to specify the fundamental components –demographically independent populations— on which to base a recovery strategy for securing the viability of anadromous populations. Currently, the anadromous populations within each ESU are listed on the US Endangered Species List as a threatened or endangered "Distinct Population Segment," or DPS[2], whereas the non-migratory, freshwater populations are not listed. The anthropogenic reasons for the decline of the anadromous populations are summarized in NMFS (1996).

The purpose of this report is to propose viability criteria for populations with anadromy, and for the ESUs of which they are part, that would ensure persistence of the anadromous form of the species over the long term. Viability criteria at the ESU level can be directly defined in the sense of Soulé (1987) described above, namely criteria ensuring the long-term (1000+ yr) persistence of the ESU and retention of its evolutionary potential in natural ecosystems. However, viability criteria at the population level often cannot meet this standard, mostly for two reasons. First, in natural ecosystems populations are sometimes extirpated by environmental catastrophes (Lande 1993), as when the eruption of Mount Saint Helens extirpated the salmonid populations in the Toutle River in Washington (Jones and Salo 1986) (In this case steelhead later recolonized; Bisson *et al.* 1988). Second, indi-

[1] Endangered Species Act, 16 U.S. Code § 1533(f)(1)(B)(ii); see also SELS (2001)

[2] Federal Register 70: 67130 [2005] & 71: 834 [2006].

vidual populations generally do not contain the full evolutionary potential of a higher level of organization, such as an ESU, subspecies, or species, because different populations may harbor different collections of genes.

To reflect these differences, viability for populations is generally defined less stringently than for higher levels of organization, and groups of viable populations are considered necessary for protecting an ESU or species. Here we define viability at the population level as a negligible risk of extinction due to threats from demographic variation, non-catastrophic environmental variation, and genetic diversity changes over a 100-year time frame, following McElhany *et al.* (2000). A viable ESU is thus a set of populations with enough of them viable and sufficiently well-connected to maintain long-term (1,000-year) persistence and evolutionary potential of the ESU. In considering viability, we focus on protection from risks that are inherent to the ecosystems inhabited by the ESUs. Anthropogenic effects pose additional risks, but are beyond the scope of this report.

Uncertainty and Types of Criteria

Assessments of viability must account for uncertainty due to the prevalence of stochastic processes in birth, death, and migration (Lande 1993, Burgman *et al.* 1993, Hanski 1991). Assessments of viability must also account for the complexity of estimating these vital rates, along with their functional relationships with population density and habitat (Williams *et al.* 2002, Borchers *et al.* 2002, Amstrup *et al.* 2005, Thompson *et al.* 1998, Buckland *et al.* 1993). Harwood (2000) reviewed techniques for coping with large uncertainties in ecological risk assessment, and identified two general approaches. The first derives from the precautionary principle, which states that irreversible harm (such as a permanent population extirpation) should be actively prevented even if there is significant uncertainty about its magnitude, likelihood or cost. Criteria developed according to the precautionary principle are purposely set high and include a large margin of safety to account for uncertainties. This general approach to uncertainty has precedence elsewhere, for example in numerous engineering applications where it is known as a prescriptive criterion.

The advantages of prescriptive criteria derived from the precautionary principle are that they are readily derived using existing general information. The disadvantages are that they can be unscientific or biologically infeasible (Harwood 2000; Foster *et al.* 2000). They are unscientific if they favor subjective pessimism over a rigorous evaluation of relevant evidence. They are biologically infeasible if the precautionary "solution" is inherently unachievable—for example, fish productivity requirements that exceed the unimpaired capacity of a watershed.

Adopting prescriptive criteria would lead logically to one of the three following outcomes: 1) Efficient recovery, in which the cost (in either expense or time) of achieving the prescriptive criterion is easier or less than the cost of obtaining additional information to produce a less stringent criterion. 2) Inefficient recovery, in which the cost of achieving the prescriptive criterion is harder or higher than the cost of obtaining data to refine the criterion and then achieving the refined criterion. 3) Biologically infeasible recovery, in which the criterion is impossible to achieve. A more scientific approach is unwarranted for case (1), but advisable for case (2) and necessary for case (3).

The second framework for dealing with uncertainty is formal quantitative risk assessment and decision analysis (Harwood 2000). This approach differs from the prescriptive approach in two key ways: first, the criteria involve direct estimates of risk, and second, the guess at a margin of safety is replaced by a full quantitative accounting of uncertainty and its implications for decision-making. In engineering design, such criteria are called "performance-based" because they define standards for the final performance of the product, rather than standards describing how the product is constructed. Often performance standards are met by analytic techniques. For example, classic population viability analysis (*e.g*. Burgman *et al.* 1993) is a special case of an analytic performance-based criterion (*i.e.* "model prediction of less than 5% risk of extinction in 100 yr given business-as-usual"). The general approach of risk assessment plus decision analysis is broader, with conservation- and fishery-oriented introductions given in Harwood and Stokes (2003) and Punt and Hilborn (1997).

The advantages of performance-based criteria are scientific rigor, quantitative estimates of risk, greater scope for innovative solutions, and especially the potential for efficient management strategies that avoid a bias towards unwarranted or unachievable precaution. The principle disadvantage is the stringent requirement for data-gathering and analysis (which can be expensive and time-consuming). In situations where data are scarce and uncertainty is high—which appears to be the case for the steelhead populations in our study area (Busby *et al.* 1996, Boughton 2005)—the approach more or less collapses to prescriptive criteria. It should also be noted that even when the relevant data are available and rigorously analyzed, viability models retain inherent limits on the accurate forecasting of absolute risk (Beissinger and Westphal 1998).

Here, based on existing information, we propose a set of simple prescriptive criteria for viability at the level of population and ESU. Some of the criteria derived for the population level may be excessively stringent, and thus biologically infeasible for some populations and probably inefficient for many others. Therefore, for these criteria we also provide an alternate set of performance standards for deriving more refined criteria. It should be noted however that the performance-based criteria cannot be characterized given existing information, but instead require an investment in research and monitoring. Therefore, we provide general recommendations about the types of data that, if collected in the future, would have high utility for assessing viability using a performance-based approach (Figure 1).

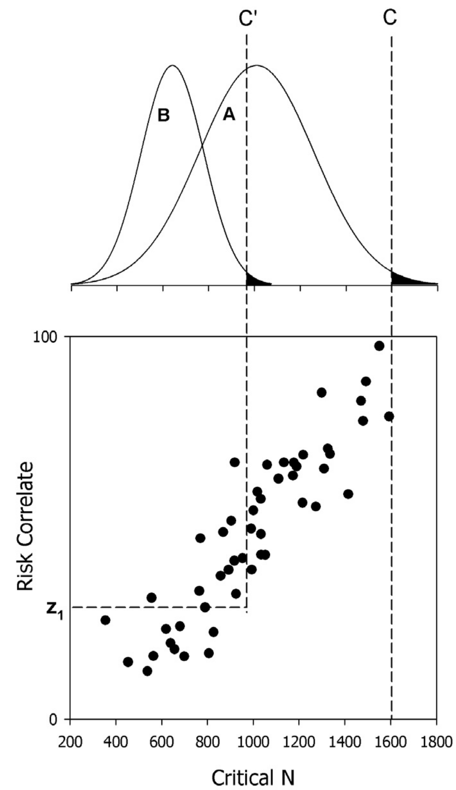

Figure 1. Schematic depiction of the relationship between information and the stringency of criteria. Critical N is the mean population size necessary to ensure low risk of extinction. The scatterplot depicts 50 hypothetical populations for which Critical N is known. Curve **A** depicts their probability distribution. When the Critical N for a particular population is unknown, it must be treated as a random draw from this distribution, leading to a relatively stringent criterion **C**. Curve **B** depicts the probability distribution for populations in which a risk correlate has been measured and found to be less than z_1, leading to a less stringent criterion **C′**. In our nomenclature **C** is a prescriptive criterion, whereas the data and modeling standards necessary for estimating **C′** comprise a performance-based criterion. Due to the large difference between **C** and **C′**, the data used to estimate z_1 had high utility.

Population Viability

Prescriptive Criteria

Conservation biologists have developed several widely-used sets of prescriptive criteria for identifying species at risk of extinction (Mace & Lande 1991, IUCN 1994, Gardenfors *et al.* 2001). These approaches were adapted to Pacific salmonids by Allendorf *et al.* (1997), and further discussed by Lindley *et al.* (2006), who added a "low risk" category corresponding to viability, and a "data deficient category" for poorly known populations. In general we follow the approach of Allendorf *et al.* (1997) and Lindley *et al.* (2006), but with revisions as described below and summarized in Table 1 . In discussing the criteria, it is useful to make a distinction between "criterion type" and "viability threshold," the former being the parameter measured and the latter the smallest acceptable measurement.

Adult population size.— Lindley *et al.* (2006) proposed a low-risk criterion of 2500 spawners per generation, or 834 spawners per year assuming a 3-year generation time. The basis was genetic, in which 2500 adults contributing to the next generation were, on average, sufficient to maintain an effective genetic population size (N_e) of at least 500 (Allendorf *et al.* 1997). However, Allendorf *et al.* (1997) noted that $N_e = 500$ may in some cases be insufficient, and Lande (1995) suggested a minimum N_e of 5000 (see Lindley *et al.* 2006 for a brief discussion of issues). On the other hand, small amounts of migration—one or two adults per generation—would be expected to relax the need for an N_e of even 500 (Wright 1931).

Other risks arising from too-small population size stem from demographic stochasticity and environmental stochasticity. Demographic stochasticity generally poses a significant risk only at very small population sizes. Environmental stochasticity is more complex. Defined as year-to-year variation in a population's mean survival and/or fecundity, it can cause large fluctuations in population growth rate irrespective of population size. Consequently, extinction risk has a non-linear dependency on environmental stochasticity and its relationship with the sizes and mean growth rates of populations (Lande 1993, Foley 1994). Essentially, larger variance causes the number of fish to fluctuate more, increasing the chance of it fluctuating to zero; but a large mean growth rate lowers this risk by shortening the recovery time from downward fluctuations, and a large mean population size keeps the population further away from zero to begin with.

Foley (1994) and Lande (1993) describe what is probably the simplest reasonable extinction model incorporating environmental stochasticity. A numerical analysis of this model (see Appendix A) suggests that, lacking specific information on population variability, it is necessary to maintain a mean population size of at least 12,500 spawners per generation (*c.* 4,200 spawners per yr) in order to achieve 95% chance of persistence for 100 yr in the steelhead populations of our study area.

This criterion applies to the generalized situation in which no quantitative data are available for estimating population variability. Alternatively, quantitative data on specific populations, if collected, could be used to determine a more refined criterion that for many populations would be less stringent, but equally risk-averse. We discuss this alternative in the section on performance-based criteria.

The "12,500 rule" is very sensitive to managerial risk tolerance. For example, a change of ±1% in the performance standard produces:

For 94% assurance: $N > 5{,}900$
For 96% assurance: $N > 32{,}900$

In addition, vastly different criteria might result from slightly different estimates of the two key parameters, the mean and variance of log-transformed annual rate of population increase (see Appendix A). This sensitivity suggests that acquiring data on population growth and environmental stochasticity would have high utility for developing a performance-based criterion, where "high utility" is in the sense of Figure 1.

In the absence of such data, we are left with the "12,500 rule," a precautionary, prescriptive criterion. From one perspective, this rule seems reasonable and intuitive—based on the irregular inter-annual patterns of precipitation in the study area; anecdotal accounts of highly variable spawning runs; the robust theoretical result that large population fluctuations pose high extinction risks; and knowing nothing else about a given population, we would expect that 12,500 spawners per generation (4,200 spawners yr^{-1}) is both necessary and adequate to safeguard a population. From another perspective, however, the rule seems unnecessary for some relatively small populations that appear to have already proven themselves viable in practice. For example, the Big Sur Coast between Carmel and Cambria has numerous small coastal basins containing *O. mykiss* populations (Boughton *et al.* 2005). These populations appear to have very low background extinction rates, and yet all appear to have average run sizes well below 4,200.

Table 1. Summary of prescriptive viability criteria.

Population-level Criteria

Criterion Type[1]	Viability Threshold	Notes
Population Size[2]	N > 12,500	See Figure 3 for alternatives (requires pop. monitoring).
Ocean Conditions[3]	Size criterion met during poor ocean conditions.	"Poor ocean conditions" determined empirically, or size criterion met for at least 6 decades.
Population Density	*Unknown at present*	Research needed.
Anadromous Fraction[3]	N = 100% of 12,500	See Figure 3 for alternatives (requires further research).

ESU-level Criteria

Criterion Type[4]	Viability Threshold
Biogeographic diversity	1) Numbers of viable populations as in Table 5, last column. 2) Viable populations inhabit watersheds with drought refugia 3) Viable populations separated from one another by at least 68 km if possible[5].
Life-history diversity	Viable populations exhibit all three life-history types (fluvial-anadromous, lagoon anadromous, freshwater resident).

1 Population should meet all 4 criteria to be considered viable.

2 Modified from Allendorf *et al.* (1997), Lindley *et al.* (2006); refers to spawning *O. mykiss* per generation.

3 Specified in this report; refers to spawning anadromous *O. mykiss* per generation.

4 ESUs should meet all three criteria for biogeographic diversity and the criteria for life-history diversity

5 Minimum distance between the boundaries of the pair of watersheds harboring each two populations of interest. If meeting the criteria is geographically impossible within a biogeographic group, then the viable populations should be as widely dispersed spatially as possible.

One compelling possibility is that the steelhead habitat in the Big Sur Coast supports populations with high intrinsic growth, low variability, or both, and this allows smaller populations to persist (Boughton *et al.* 2006). If true, this would justify less a stringent criterion for these populations, but determining how much less stringent would require a period of population monitoring (see the section on performance-based criteria). Alternatively, the population delineation scheme of Boughton *et al.* (2006) may be incorrect. In that document we made the provisional assumption that movement of fish among coastal basins is rare enough that each basin can be regarded as containing an independent population. However, if movement is relatively common, then a single population may span multiple basins, meaning fewer but larger populations in the Big Sur Coast, and possibly other areas such as in the southern Santa Barbara Coast and the Santa Monica Mountains. Information on inter-basin movement (straying rates) would therefore have high utility to distinguish these two cases.

Ocean Conditions.—Allendorf *et al.* (1997) considered downward trends in abundance to be an indicator of extinction risk. Although this is valid for persistent trends, short-term downward trends are not necessarily risky, provided that population size is well above its viability threshold. Indeed, short-term downward trends appear to be a normal feature of the dynamics of Pacific salmonid populations, due in part to serial correlation in ocean conditions.

Variation in ocean conditions is known to have dramatic impacts on marine survival of Pacific salmonids. For example, Mueter *et al.* (2002) made a detailed study of chum salmon productivity in Alaska and British Columbia, and found strong evidence of positive covariation in spawner-to-recruit survival for wild stocks within regions and between certain adjacent regions. Sea-surface temperature was the strongest predictor of ocean survival, and the correlations were strongest at times of early ocean survival (Mueter *et al.* 2002). Since sea-surface temperature in the northeast Pacific tends to exhibit serial autocorrelation at the scale of decades (Mantua and Hare 2002, Wang and Schimel 2003), this suggests that ocean mortality of salmon in a given region should likewise be serially-autocorrelated. Ocean catches of Pacific salmon indeed exhibit such patterns, though there are various explanations for the underlying mechanism (Mantua *et al.* 1997, Hare *et al.* 1999, Hilborn *et al.* 2003).

The above findings are relevant to viability because serial auto-correlation of mortality tends to amplify the effects of environmental stochasticity on extinction risk (Foley 1994). Thus, serial autocorrelation implies that the "12,500 rule" described in the previous section is inadequate by some unknown amount. A conservative working assumption is that ocean survival fluctuates widely and is serially correlated, but is otherwise unquantified for our region (studies from elsewhere have found regionally-specific effects; Mueter *et al.* 2002). A population meeting the 12,500 rule during a period of good ocean survival is likely to decline to risky levels when ocean survival deteriorates for long periods.

A simple but effective prescriptive criterion for ocean condition is that the 12,500 rule must be met during a period of poor ocean survival. This criterion could be met via two distinct strategies: 1) monitor population size for at least the duration of the longest-period climate "cycle" (*c.* 60 yr according to Mantua and Hare 2002, though others dispute the notion of predictable cycles), or 2) concurrently monitor population size and ocean survival, so that periods of low ocean survival can be empirically determined. Alternatively, a performance-based approach combined with a comprehensive monitoring program could be applied (described in the next section).

Contrary to Allendorf *et al.* (1997), we do not propose a formal criterion for downward trends *per se*. As argued above, such trends over the short term are a normal occurrence, and only pose a risk if they persist long enough that the population falls below its other viability thresholds (for population size and density). In other words, an ongoing decline may turn out to be short-term in which case it is normal; or it may turn out to be persistent, in which case it provides an early signal that a population may fall below its viability threshold or that there is some unrecognized problem with watershed condition.

Data on ocean survival (derived from smolt counts combined with adult counts) should in principle be useful for separating the effects of ocean cycles and watershed condition on population growth, the former being a kind of autocorrelated noise that obscures the effects of change in the latter. This is because investment in both smolt counts and adult counts allows one to estimate ocean survival as distinct from freshwater production and survival (with only adult counts, the vital rates in the two habitats are confounded and cannot be estimated separately). In addition, short-term improvements in run size due to watershed restoration could be distinguished from short-term improvement due to ocean cycles. Adaptive management probably would be more efficient with an investment in collecting such data, because the feedback loop between doing and learning would be tighter and quicker.

Population density.— A given number of spawners or juveniles may be densely packed into a small section of a watershed, or thinly distributed across its entirety. Both situations have costs and benefits with respect to risk. Dense populations have relatively low risk of depensation (poor population growth rate at low abundance, often caused by scarcity of mates). They have low risk of various genetic problems such as inbreeding depression. However, they are vulnerable to environmental stochasticity since the members of the population all experience similar conditions.

Broadly-dispersed populations benefit from spreading the risk (in the sense of Den Boer 1968) and should be less vulnerable to environmental stochasticity (correlated mortality risks). In addition, they are likely to occupy a broader range of habitats, allowing for the expression and maintenance of phenotypic diversity. In other words, dispersed populations may be less likely to become specialized on, and thus dependent on, a particular environment in a particular part of a watershed. The problem is that, if too-thinly dispersed, the population becomes vulnerable to the risks of depensation and loss of genetic diversity mentioned above.

Allendorf *et al.* (1997) did not propose a density criterion, but our view is that such a criterion is warranted, particularly for populations that were historically large, but are unlikely to be recovered to those historic levels—there is a risk that a thinly dispersed population in such a watershed could meet the criterion for mean size, and yet not be viable (the 12,500 rule seems adequate to prevent the risk of a population densely packed into a small section of the watershed, because the sustained production of 4,200 spawners per year implies substantial spatial dispersion, even at high spawning densities). We also believe that the viability threshold should be high enough to ensure the fish generally inhabit good-quality habitat, which promotes resilience of the population. A potentially suitable threshold for both these purposes is the density at which intra-specific competition for redd sites becomes observable. For coho salmon (*O. kisutch*) this appears to be on average about 40 spawners per kilometer (one spawning pair per 50 meters of stream length), although individual streams vary considerably around this mean (Bradford *et al*. 2000). We could not find data for deriving a corresponding steelhead criterion. It would be a useful topic for research, but would require study areas with sufficient numbers of spawning adults to address the question.

Hatchery influence.—Hatchery fish can have a negative influence on viability if they interbreed with or compete with wild populations (*e.g.* Ford 2002, Goodman 2005), or if their presence masks the decline of a wild population. Currently, hatchery steelhead (anadromous *O. mykiss*) are not being introduced to streams in the study area, and hatchery trout (non-anadromous *O. mykiss*) are only being introduced to stream systems above barriers that are impassable to upstream migrants. The impacts of the hatchery trout are not known; the impacts of hatchery steelhead immigrating from elsewhere are probably very small and do not pose a risk. Should hatchery inputs below barriers be proposed for the future, their expected effect on wild populations can be evaluated. Entries into the literature on this subject are Bilby *et al.* (2005) and Nickum *et al.* (2004), and a rule-set for assessing hatchery risks to viability is in Lindley *et al.* (2006). Given the current situation, we do not propose a viability criterion for hatchery influence.

Anadromous fraction.—Anadromous fraction is the mean fraction of reproductive adults that are anadromous. We believe that juvenile steelhead in our area co-occur with their non-anadromous conspecifics (rainbow trout). Elsewhere, steelhead have been observed to have trout among their progeny, and vice versa (Zimmerman and Reeves 2000). Unfortunately, we do not know how often these transitions occur in south-central or southern California, nor what factors bring them about, though clearly individual populations can be polymorphic for life-history type. Depending on the rate of transition, a group of resident and anadromous fish may function as a single population; two completely distinct populations; or something in between.

Interchange between resident and anadromous fish groups would almost certainly lower the extinction risk of both groups, for the same two reasons that dispersal between separate steelhead populations reduces risk—the existence of a "rescue effect" and the possibility of recolonization (Hanski and Gilpin 1997). The rescue effect would occur at low steelhead abundance, when input from the trout population prevents their complete disappearance. Recolonization occurs when steelhead disappear completely, but are regenerated by the trout population (via "recolonization" of the steelhead niche). These phenomena may have maintained steelhead in the Santa Clara River system in recent times, since modern steelhead runs appear far too small to be self-sustaining (Boughton 2005).

Unfortunately, lack of data on the life-history polymorphism prevents a reasonable estimate for the magnitude of the rescue effect, or for a viability threshold for anadromous fraction. Lacking such data, the prescriptive criterion for anadromous fraction must assume that the rescue effect is negligible, and that anadromous fraction must be 100%—that is, when applying the population size criterion discussed previously, 100% of the spawners must be anadromous.

Further research on this topic is likely to have high utility for estimating a viability threshold that is more efficient than the precautionary "100% rule," using the performance-based approach discussed in the next section. However, in populations where anadromous fish are currently quite rare, it may be necessary to recover run sizes somewhat before numbers are sufficient for useful empirical research on life-history plasticity.

Table 2. General performance-based criteria for population viability.

One or more prescriptive criteria (see Table 1) could be replaced by a quantitative risk assessment satisfying the following:

1) Extinction risk < 5% in the next 100 yr.
2) Addresses each risk that is addressed by the prescriptive criteria it replaces.
3) Parameters are either **a)** estimated from data or **b)** precautionary.
4) Quantitative methods must conform to accepted practice in the field of risk assessment, either Bayesian or frequentist.
5) Must pass independent scientific review.

Performance-Based Criteria

Our proposed framework is in Table 2. Of the various criteria types discussed above, population size is the one we believe would most benefit from a performance-based approach. The prescriptive criterion (N > 12,500 spawners) is rather stringent due to a lack of population-specific data on variability of run sizes and on influences of non-anadromous *O. mykiss*. It also appears to be biologically infeasible for some basins, particularly small coastal basins of the Santa Lucia, Santa Ynez, and Santa Monica Mountains. Below we identify high-utility data (*sensu* Figure 1) that if collected could be used to estimate a more efficient threshold using a performance-based approach.

Environmental stochasticity—One principal reason that the prescriptive criterion is so stringent is the lack of population-specific data on environmental stochasticity (year-to-year variation in mean fecundity and/or survival rate). In general, theory predicts that extinction risk is extremely sensitive to environmental stochasticity (Lande

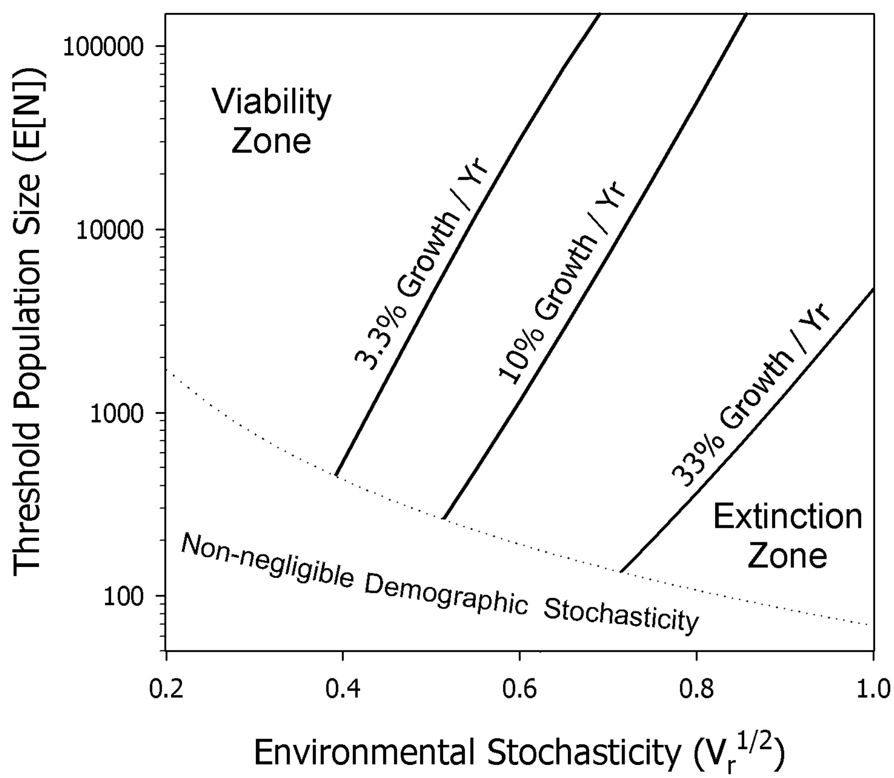

Figure 2. The population size criterion (mean abundance, or E[N]) as a function V_r, under a variety of assumptions about population growth rates. Based on the diffusion-approximation model of Foley (1994). The condition for non-negligible demographic stochasticity was assumed to be $V_1^{1/2}/N > 1\% \cdot V_r^{1/2}$, where V_1 is the demographic stochasticity parameter defined as in Foley (1997); it was computed assuming an annual mortality rate of 33%.

1993). An example is the diffusion-approximation model of Foley (1994), which predicts a log-linear relationship between the population size criterion (E[N]), and the model's environmental stochasticity parameter V_r (Figure 2). This log-linear relationship implies a high utility of acquiring data on V_r, which would then be used to refine the population size criterion. These refined criteria would generally be much less stringent, since they would no longer need to assume a "nearly-worst-case scenario" for V_r (see Appendix A)

Methods now exist for estimating r, V_r, and extinction risk by fitting a density-dependent version of the random-walk-with-drift (RWWD) model to time-series of spawner counts (Holmes 2001, Lindley 2003, Dennis *et al*. 2006). About 20 yrs or more of data are necessary to obtain reasonable confidence in the estimates (Lindley 2003). A recovery effort that includes regular monitoring of spawners could likely use the resulting data to make a better estimate of V_r and obtain a more efficient criterion for population size (see Table 3A). However, some populations may currently have run sizes so low that useful data cannot be collected until they have been recovered somewhat, depending on the field methods used for monitoring.

Anadromous fraction.—Another key uncertainty is the pattern of interchange between resident and anadromous subpopulations. We suspect that extinction risk of the steelhead fraction is likely to be highly sensitive to the details of this interchange, but at present we do not understand it beyond knowing that such interchange does occur, perhaps regularly. Certainly, studies of *O. mykiss* in Alaska indicate that at least some non-migratory populations can spontaneously generate anadromous fish if they had an anadromous fraction historically (Thrower *et al.* 2004). A better understanding of life history plasticity in our study area would allow the derivation of performance-based criteria for population size and anadromous fraction.

The increased efficiency of a performance-based approach has a cost, in that time and resources used to collect the necessary data may pose an opportunity cost on other recovery activities. In Figure 3 we offer a simple decision tree that may help clarify the tradeoffs. Table 3 gives a summary of the two performance-based options.

Table 3. Recommended approaches for deriving performance-based abundance criteria.

A. Random-walk-with-drift model (RWWD)

Necessary Data
20+ yrs of annual spawner counts (anadromous).

Risk Model
Random-walk-with-drift (Lindley 2003, Foley 1994, Dennis *et al*. 2006, and others).

Pro and Con
Pro: Estimate of environmental stochasticity may permit less stringent criterion.
Con: possibly 2+ decades before estimates can be made (see Lindley 2003); assumes negligible rescue effect from freshwater residents, which may be incorrect / inefficient.

Likely Useful For
Establishing viable populations in small coastal watersheds.

B. Standard Population Viability Analysis (PVA)

Necessary Data
1) Annual spawner counts (resident and anadromous).
2) Fecundity (resident and andromous).
3) Anadromous/resident "crossover" rates.
4) Estimates of process error for above quantities.
5) Possibly: Habitat-specific and lifestage-specific data on survival.

Risk Model
Standard PVA methods (*e.g.* Burgman *et al.* 1993).

Pro and Con
Pro: By reducing uncertainty, may allow less stringent thresholds than RWWD or prescriptive criterion.
Con: Highly stringent data requirements; 2+ decades before estimates can be made.

Likely Useful For
Establishing viable populations in watersheds with unreliable migration corridors; or populations known to maintain life-history polymorphisms, especially those with consistently small anadromous fractions.

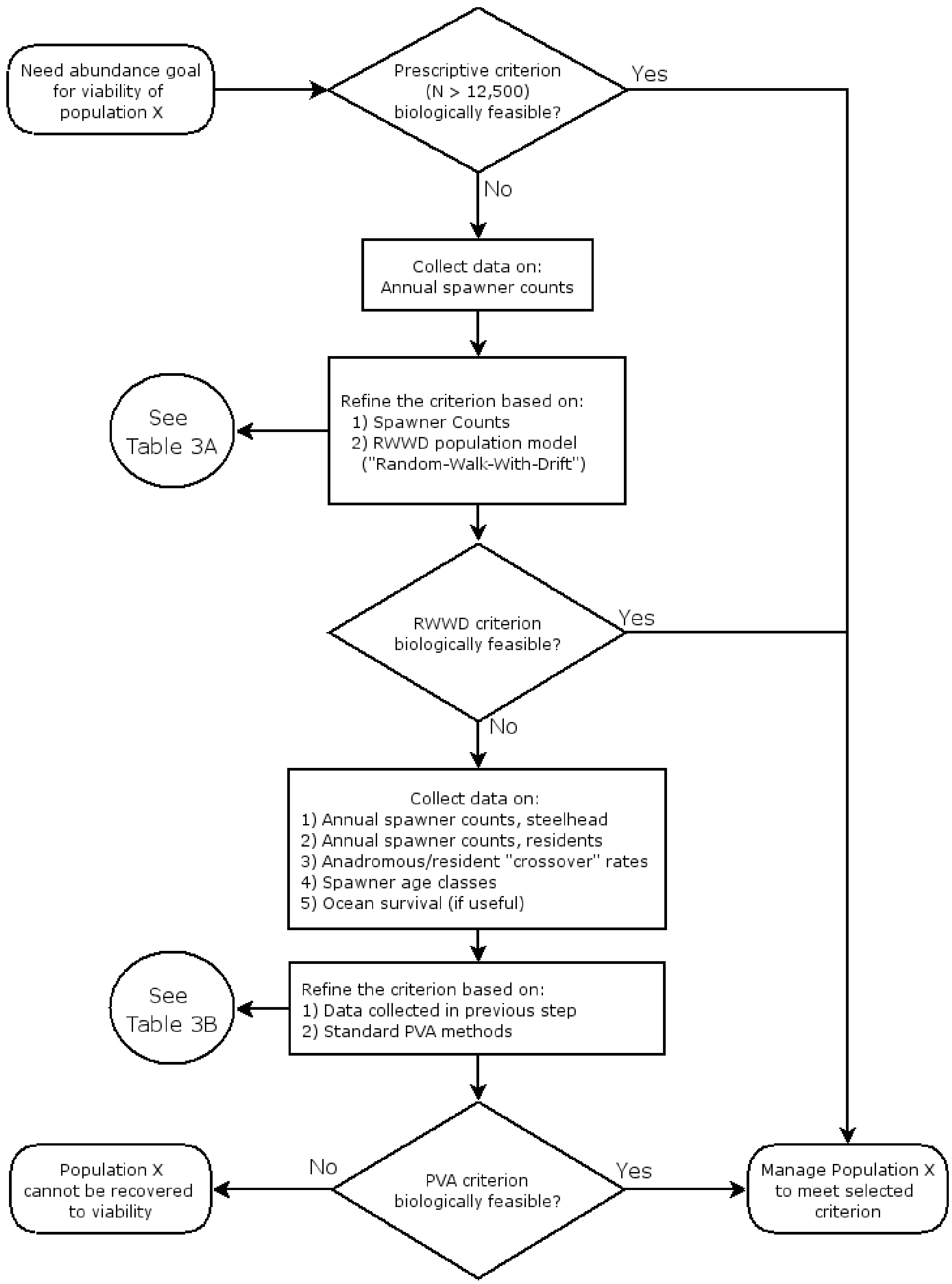

Figure 3. Decision tree for establishing a viability criterion for mean population size (spawners per generation). "Biologically feasible" refers to the ecological capacity of an unimpaired stream network to support enough spawners on average to meet the criterion.

ESU viability

ESU viability depends on sufficient numbers of viable populations to accomplish two ends: preserve the among-population diversity (genetic, phenotypic and ecological) originally present in the ESU, and protect the ESU from catastrophic disturbances. We will assume that recovery planners have a time horizon of at least 500 – 1000 yr in the face of environmental variation that is typical of the study area. The past 200 – 1000 yr offers clues as to what this environmental variation will entail—long-term trends in climate; prolonged drought; large wildfires; and profound anthropogenic disturbance (Gordon 1996, Gumprecht 1999, Haston and Michaelson 1997). For ESUs to be considered viable, they should at a minimum be able to persist under the foreseeable natural disturbance regime of the study area.

For Pacific salmonids elsewhere, ESU viability criteria have followed a straightforward "representation and redundancy" rule (Lindley *et al.* 2006, Ruckelshaus *et al.* 2002, Myers *et al.* 2003), which we adopt here. Under this approach the populations are partitioned into "diversity groups" based on life-history and biogeography. A viable ESU requires *representation* of all diversity groups, and *redundancy* within groups. The redundancy must be sufficient to protect against foreseeable catastrophes.

Life-History Groups

Studies of coastal *O. mykiss* populations in central and southern California reveal three principal life-history groups, which we here designate as fluvial-anadromous, freshwater resident, and lagoon-anadromous (Smith 1990, Hayes *et al.* 2004, Bond 2006). Both anadromous groups classify as winter steelhead, in that adults migrate during the winter rainy season. Fluvial-anadromous fish spend one or two summers (occasionally more) in freshwater streams as juveniles, then smolt and migrate to the ocean, using the estuary only for acclimation to saltwater and as a migration corridor (also occasionally for spring-time feeding). Freshwater residents (commonly known as rainbow trout) complete their entire lifecycle in the freshwater stream network. Finally, lagoon-anadromous fish spend either their first or second summer as juveniles in the seasonal lagoon at the mouth of the stream. This last group may be unfamiliar to most steelhead biologists, so we will describe it a bit more fully below.

In the study area, the estuaries at the mouths of rivers and creeks are typically transformed into lagoons during the dry season, when the combination of low streamflow and coastal wave action allows a sandbar barrier to form between the ocean and the stream's mouth. Several case studies indicate that the resulting seasonal lagoons comprise exceptionally good rearing habitat for juvenile steelhead. Smith (1990) described data collected in 1986 from three creeks between Santa Cruz and San Francisco, in which juvenile steelhead reached high densities and grew extremely fast in the lagoons. Bond (2006) described a more intensive study conducted over 4 years in a fourth creek, with similar conclusions. Fast growth is generally beneficial to fish because large fish have lower mortality rates than small ones, particularly in the marine environment (Sogard 1997; see Ward *et al.* 1989 for a steelhead example). Indeed, of 27 adult steelhead examined by Smith (1990), back-calculation of growth rates (using scale samples) suggested that 60% - 70% had the high juvenile growth rates typically observed in lagoons. Bond (2006) conducted a discriminant-function analysis on scale samples from 406 adults, and concluded that 85% of successfully returning adults had reared in the lagoon. From these and other data, Bond (2006, p. vii) concluded that "estuary-reared steelhead showed a large survival advantage and comprised 85% of the returning adult population despite having been between 8% and 48% of the juvenile population. Although the … estuary comprised less than 5% of the watershed area, it was critical nursery habitat, as estuary-reared juveniles make a disproportionate contribution to the spawning adult pool."

Bond's (2006) work suggests that the lagoon-anadromous life history is very important for the viability of many anadromous populations. However, the other life-history types are also important because lagoons sometimes prematurely breach or become anoxic, with high mortality costs for the lagoon-anadromous component of the population

Table 4. Biogeographic population groups.

South-Central California Coast Steelhead ESU

Population Group	Ecological Characteristics				
	Migration Corridor	**Migration reliability**[1]	**Summer Climate Refugia**	**Intermittent Streams**	**Winter Precipitation**
Interior Coast Range[2]	Long alluvial valleys	Moderate/ Low	Montane	Many	mostly < 75 cm[3]
Carmel Basin	Medium valley	Moderate	Marine + Montane	Some	30 - 90 cm
Big Sur Coast	Short, steep	High	Marine	Few	75 – 135 cm
San Luis Obispo Terrace	Coastal terrace	Moderate	Marine	Some	60 – 90 cm

Southern California Steelhead ESU

Population Group	Ecological Characteristics				
	Migration Corridor	**Migration reliability**	**Summer Climate Refugia**	**Intermittent Streams**	**Winter Precipitation**
Monte Arido Highlands	Long alluvial valleys	Moderate/ Low	Montane	Many	60 – 75 cm (highlands)
Conception Coast	Coastal terrace	Moderate	Marine	Many	30 – 60 cm
Santa Monica Mountains	Short, steep	Low	Marine	Many	30 – 60 cm
Mojave Rim	Long alluvial valleys	Very Low	Montane	Many	75 – 135 cm (highlands)
Santa Catalina Gulf Coast	Coastal terrace & mesas	Low	Marine	Many	mostly <75 cm

[1] Inferred reliability under an un-managed flow regime.

[2] The inclusion of the Pajaro River population in this group is debatable, since much of its best freshwater habitat occurs in the redwood forests at the southern end of the Santa Cruz Mountains—quite ecologically distinct from the chaparral watersheds of the other east-slope populations.

[3] Except in the Santa Cruz Mountains of the Pajaro system, which are wetter.

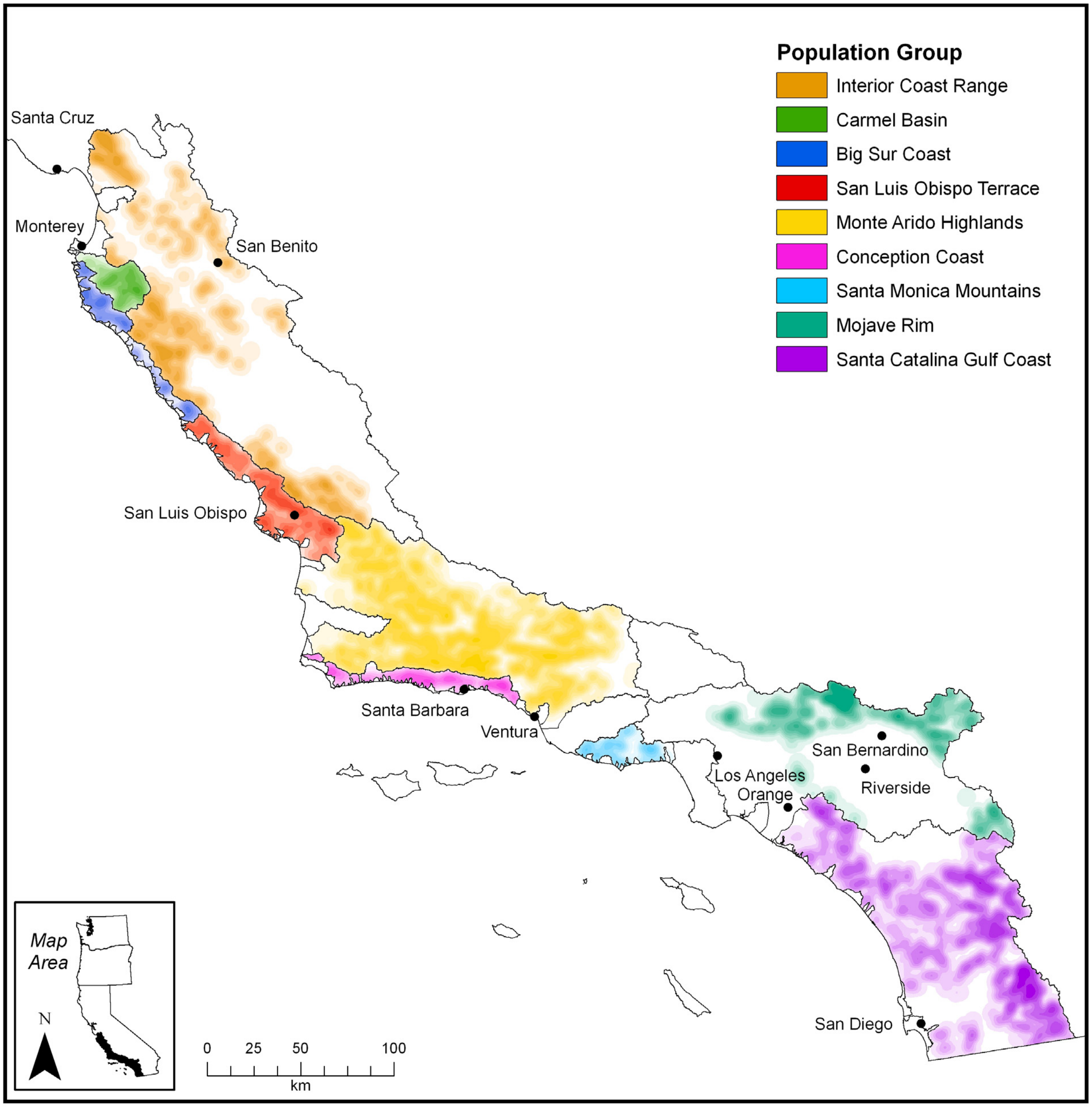

Figure 4. Extent of biogeographic population groups for steelhead in the study area.

(Smith 1990). In the winter following a lagoon failure the fluvial-anadromous life history would tend to predominate in the outgoing smolt run, and thus it probably contributes to the long-term viability of the population.

Finally, the long history of severe droughts in the study area (Haston and Michaelson 1997) leads one to believe that segments of mainstem migration corridors may dry up for multi-year periods, preventing anadromy of any type. During such events the adults in the ocean and the freshwater residents in the perennial segments of streams are the only buffer against extirpation (in the study area, many stream systems are spatially intermittent during dry periods, with alternating segments of surface and subsurface flows). Of these two groups of fish, only the freshwater residents would be capable of reproduction during an extended drought lasting longer than the lifespan of the fish. This suggests that the freshwater-resident component is critical for long-term viability of the ESU through multiple droughts. Conversely, the anadromous life-history types are necessary for migratory recolonization of basins from which the species has been extirpated by a catastrophic event. Additionally, the anadromous types probably allow some populations to maintain a larger size (and thus a lower extinction risk) than if they were solely composed of freshwater-resident fish.

The representation and redundancy rule therefore indicates that each of these life-history types should be represented in each biogeographic population group (see below). We note that intermediate life-history types are common—for example, fluvial-anadromous fish sometimes feed for part of a summer or spring in the lagoon—but that intermediate forms probably do not obviate the need for each of the three main groups. Also worth noting is the fact that some basins do not have lagoons, particularly in steep coastal areas such as the Big Sur Coast. Some of these basins have *O. mykiss* populations. It is not clear whether these 1) are viable despite lacking the lagoon-anadromous form; 2) are a sub-component of a more inclusive multi-basin population that possesses the lagoon anadromous form; or 3) are not naturally viable and hence ephemeral at the time-scale of a century.

Biogeographic Population Groups

To divide the steelhead populations into biogeographic groups, we applied two simple rules. First, we sorted the populations into a coastal super-group and an inland super-group, defined by whether most potential freshwater habitat lay on an ocean-facing watershed subject to marine-based climate inversions and orographic precipitation from off-shore weather systems. The inland populations are not thermally protected by summer climate inversions, have a more seasonal climate, inhabit larger watersheds, and tend to occur in rain shadows of coastal mountains. These differences in climate and topography circumscribe local habitat structure and probably affect the variability, productivity, and resilience of coastal vs. inland populations. Inland populations may require larger runs on average to achieve viability (see discussion in Boughton *et al*. 2006, part 5).

Second, within the coastal and inland super-groups, we sorted populations into groups defined by contiguous areas with broadly similar physical geography and hydrology (Figure 4). The environmental characteristics of each biogeographic area are summarized in Table 4; and the population membership of each group is in Appendix B, based on a list of identified steelhead populations in Boughton *et al.* (2006).

The South-Central California Coast Steelhead ESU has 4 biogeographic groups. The Southern California Steelhead ESU has 5 groups, although it is not clear if all groups are capable of supporting viable populations. In particular, the Santa Monica Mountains and the Santa Catalina Gulf Coast may have originally had so-called ephemeral populations that naturally fail and later get recolonized from neighboring watersheds (*i.e.* metapopulation dynamics). Originally, the Mojave Rim populations probably had quite unreliable migration access and may have consisted mostly of freshwater-resident fish (Boughton *et al.* 2006).

Representation and redundancy means each group must possess a sufficient number of viable populations that a worst-case catastrophe will leave at least one viable population in its aftermath. The assumption is that this population would then serve as a source of colonists to the vacant areas after the habitat has recovered.

Catastrophic Risks

The three most prominent natural disturbances that appear to pose a risk to entire populations are wildfires, droughts, and debris flows, discussed below.

Wildfire.—Although wildfires have long-term benefits for fish habitat, such as producing influxes of spawning gravels to the stream, in the short-term they can be catastrophic. For example, Shapovalov (1944, cited in Titus *et al.* 2003) reported that a wildfire in the Cuyama and Sisquoc watersheds (near Santa Maria) increased the wet-season run-off, with the consequence that dry-season baseflow was decreased. In addition, fine sediment input to the stream buried spawning gravels, filled rearing pools, and absorbed the dry-season baseflow that remained. "As of 1950, there appeared to have been no steelhead fishery for 10-15 years in the Santa Maria River, and very few steelhead were reported to have entered the Cuyama River for a decade," according to Titus *et al.* (2003). In other parts of the southwest, wildfires have been implicated in the extinction of trout populations (Rinne 1996, Brown *et al.* 2001).

To determine a level of redundancy sufficient to withstand catastrophic wildfires, we estimated the expected geographic extent of a thousand-year burn, based on wildfire data from 1910 through 2003 (acquired from the California Department of Forestry[3]). Wildfires in the study area tend to be aggregated in time due to climate forcing (for example, forcing by the hot dry Santa Ana winds out of the Mojave Desert in the southern area; Moritz 1997), so our analysis used total area burned in a year rather than the area of the single largest fire.

Fire return-times were estimated using standard methods: An exponential distribution was found to fit the data (parameter λ = 0.0025084. Fit: χ^2 = 2.32 [df = 3]; p = 0.51), which predicts a thousand-year burned-area of about 2,750 km^2 (parametric curve in Figure 5). Interestingly, the severe fire season of 2003 burned nearly this much area (empirical curve in Figure 5). Note that "thousand year" refers to the median return time expected for an event; actual waiting times are distributed around this median; so the parametric and empirical results are not inconsistent. Since we have a recent example of a thousand-year event, we can examine it in detail to get some insight.

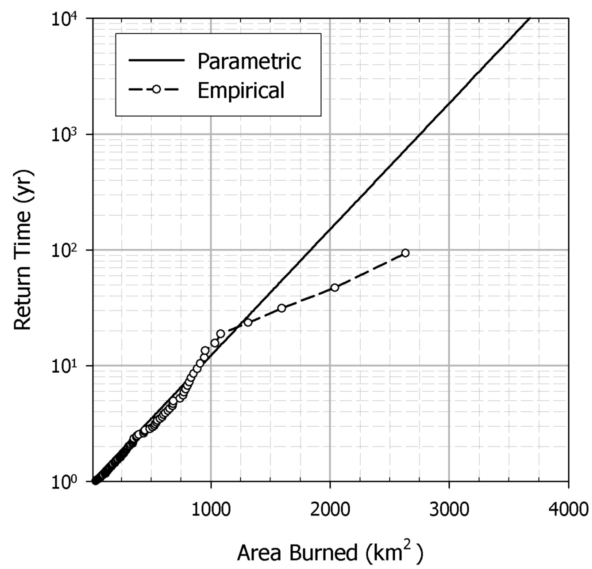

Figure 5. Return-times for wildfire seasons in the study area. Based on a 94-year record as of 2003 (inclusive). The last datapoint on the empirical curve is the 2003 fire season.

In 2003, the study area had 31 fires larger than 1.0 km^2, including some massive conflagrations such as the Simi Fire (435 km^2), the contiguous Padua, Grand Prix, and Old Fires (combined area 617 km^2), and the truly colossal Cedar Fire in San Diego County (1095 km^2). The maximum width of any individual fire at its widest point was 68 km for the Cedar Fire (the combined Padua/Grand Prix/Old Fire was nearly as wide at 63 km), suggesting that two watersheds containing steelhead populations must be separated by at least 68 km of intervening space if they are not to both be affected by the same fire.

If a similar fire season occurred in the future, how many fires might be expected to affect each population group? To make a rough estimate, we noted that the study area as a whole is 56,800 km^2, translating to 0.0005457 "successful" fire-starts per km^2. For each biogeographic population group, we calculated the total watershed area lying within the species' thermal limits (described in terms of August air temperature in Boughton and Goslin 2006), and multiplied it by the rate of fire-starts to

[3] http://frap.cdf.ca.gov/projects/fire_data/fire_perimeters/

Table 5. The number of wildfires in each population group during a thousand-year fire event similar to the events of 2003, and the number of viable populations necessary for ESU viability.

Population Group	Expected Number of Wildfires	Maximum Number of Wildfires		Sufficient Number of Populations*
		95% confidence	99% confidence	
Interior Coast Range	2.567	5	7	4†
Carmel Basin	0.359	1	2	1
Big Sur	0.406	2	2	3
San Luis Obispo Terrace	0.873	3	4	5
Monte Arido Highlands	5.624	10	12	4
Conception Coast	0.327	1	2	3
Mojave Rim	3.209	6	8	3‡
Santa Monica Mountains	0.210	1	2	3†,‡
Santa Catalina Gulf Coast	2.563	5	7	8†,‡

* Viable and spatially separated from other viable populations by > 68 km. Estimated as 1 + the number of wildfires at 99% confidence, or the number of historic populations, whichever is less.

† The number of historically viable populations may be smaller than the table entry, since some historical populations may have been ephemeral and required recurrent colonization.

‡ Evidence is unclear whether anadromy was a consistent feature of *O. mykiss* populations in these groups. Clearly the freshwater-resident form has always been a regular feature of these populations, and anadromous life histories were at least occasionally expressed.

get an expected number of fires in the area inhabited by each population group (Table 5). However, the expectation is not as useful a number as the upper confidence limit—that is, the maximum number of fires that is not unlikely. We estimated this number using the Poisson distribution at 95% and 99% levels of confidence.

A prescriptive criterion for ESU viability is derived as follows: On the face of it, the minimum number of populations would have to be one greater than the maximum number of wildfires in a 1000-year event to ensure sufficient redundancy for a given biogeographic group.[4] However, in some cases this prescription exceeds the number of historic populations (which were clearly sufficient to withstand the aboriginal fire regime). Thus, a reasonable prescription for sufficient population redundancy is: at least 1 + the maximum number of wildfires expected for the biogeographic group, or the number of historic viable populations in the group, whichever is less (see Table 5, last column). Sufficient redundancy also requires that the populations each meet the criteria for population viability; each exhibit all 3 life history types; and each have geographic boundaries separated from other such populations by the long dimension of the largest potential fire (assumed to be 68 km). In cases where such separation is not possible due to geographic constraints, the separation distance should be as much as possible.

Drought.—Drought is likely to have catastrophic effects on fish by causing lack of migratory access during the winter and lack of perennial flow during the summer (the latter is necessary to support rearing to the smolt stage, or in the case of the freshwater residents, completion of their reproductive cycle). In the present day, drought effects may be exacerbated by the lowering of the water table due to groundwater pumping and

[4] This assumes that all fire-starts have the potential for catastrophic effects on populations.

stream diversions. Drought has a long history in the North American Southwest, according to Cook *et al.* (2004) who used tree-ring data to reconstruct Palmer Drought Indices for the entire western USA back to the year 800 (see also Haston and Michaelson 1997).

Lindley *et al.* (2006) used the spatially-explicit reconstructions of Cook *et al.* (2004) to estimate a drought "correlation distance," defined as the minimum geographic distance between two points at which drought conditions are no longer positively correlated. In other words, it is the minimum distance that must separate two steelhead populations if they are to be assured of not both being impacted by the same drought.

The correlation distance they found (640 km) is much longer than the longest dimension of each geographic area occupied by the two ESUs (280 km and 485 km). Thus, redundancy cannot be achieved via spatial separation of populations. It is worth noting, however, that the tree-ring data described by Cook *et al.* (2004) go back to the year 800 A.D., and record at least 4 multi-decade droughts prior to 1300 A.D. These events had far greater magnitudes than anything observed during the historical period. The aboriginal steelhead populations must have either survived in drought-resilient refugia, or have been regionally extirpated prior to 1300 A.D. and recolonized in the subsequent centuries. If the refugium hypothesis is correct, ESU viability is probably contingent on forecasting the location of refugia under future climate regimes. If the recolonization hypothesis is correct, ESU boundaries are currently misspecified. Evaluation of the refugium hypothesis, particularly as it relates to future climate, is an obvious research priority.

Debris Flows.—Flooding can cause debris flows that would be expected to have catastrophic effects on steelhead populations. According to Keller *et al.* (1997), debris flows are the most severe of three types of fluvial transport, moving large amounts of debris of all sizes from fine sediments to large boulders. Keller *et al.* (1997) proposed that debris flows in the study area are usually produced by the convergence of three unusual factors: 1) a pre-existing large geomorphic instability somewhere in the stream network; 2) a large wildfire that removes vegetation, 3) followed within one or two years by an exceptionally large winter storm. This suggests that if an ESU has sufficient redundancy to protect against wildfire risk (discussed earlier), it will also have sufficient redundancy to protect against debris flows.

Summary and Recommendations

Table 1 summarizes the prescriptive criteria we proposed for population viability and ESU viability. At the population level we propose 4 criteria that are objective and measurable, at least in principle. However, one of them (density) is too poorly understood at the moment for us to estimate the minimum threshold necessary for low risk. For two more (population size and anadromous fraction), we have derived a minimum threshold given current information constraints, but feel fairly optimistic that a more efficient threshold could be estimated using a performance-based approach. Table 2 summarizes the standards for the performance-based approach, and Figure 3 gives a simple decision tree for identifying when such an approach is warranted. A performance-based approach would require a long-term investment in obtaining quantitative data on environmental stochasticity and life-history plasticity (Table 3).

At the ESU level we have proposed numbers for sufficient representation and redundancy of viable populations (Table 5), a criterion for life-history diversity in each viable population, and a simple criterion for spatial separation of populations (Table 1). However, we identified a critical lack of information on how the ESUs achieve resiliency to severe drought. In addition, the criteria for redundancy are based on a simple assessment of wildfire risk that is precautionary and perhaps inefficient. A performance-based estimate of wildfire risk would probably be more efficient, but at the cost of a significant research effort.

The recovery of these fish is surely a long-term process, but our work on this report suggests some near-term activities that can and should begin as soon as possible. These include:

Identify and commit to a core set of populations on which to focus recovery efforts. By "core" we mean populations used to meet the criteria proposed in this report—that is, selected to be the focus of recovery. The core set would be selected from the set of all populations composing the two ESUs, previously discussed at length by Boughton *et al.* (2006) and summarized here in Appendix B. The purpose of viability criteria is to provide an objective framework for setting priorities. They become irrelevant if all creeks or basins are given equal emphasis in a recovery plan, or if priorities are based mostly on the ease or popularity of certain recovery activities.

The strategy most likely to achieve recovery and lead to de-listing, in our view, would be to identify how recovery actions and monitoring of the core populations would address the population and ESU viability criteria described in this paper. In general, population viability is more likely to be achieved by focusing on larger watersheds capable of sustaining larger populations, and ESU viability is more likely to be achieved by selecting the most widely-dispersed set of such core populations still capable of maintaining dispersal-connectivity (see Boughton *et al.* 2006). This is not to say that non-core populations are unimportant—Dispersal connectivity and genetic diversity may be aided by also including smaller "non-core" populations that serve as stepping stones for dispersal. However, the core populations are fundamental.

Secure the extant parts of the inland populations. Inland populations comprise the Interior Coast Range, Monte Arido Highlands, and Mojave Rim groups. The original inland populations were relatively few in number, large in spatial extent, and inhabited challenging environments. Due to low redundancy they are necessarily core populations in the sense described above. Unfortunately the inland populations are frequently the most highly impacted by dams, water diversions, and flood control practices, and our wildfire analysis suggests that they had marginal redundancy even before these impacts. Yet the populations of the Interior Coast Range and the Monte Arido Highlands (also the Carmel River) appear to have produced the largest run sizes in the study area during good water years (Boughton 2005).

The extant habitat of these populations—especially the anadromous waters of the Pajaro River, Arroyo Seco, the southern Salinas Valley, the Sisquoc River, the Santa Ynez River, the Ventura River and the Santa Clara River—merit high priority for immediate protection and recovery so that fish passage does not decline further (and should be improved whenever possible, though this is a longer-term effort). The low level of redundancy in the inland groups indicates that ongoing efforts to restore fish passage in the Ventura River are necessary steps to achieving ESU viability, as are future efforts to restore passage in the Santa Ynez River and the Nacimiento River, both of which have a large majority of their steelhead habitat isolated by complete barriers to passage from the ocean. Also, additional efforts to restore passage in the Santa Clara River may be necessary to achieve ESU viability, depending on the number of steelhead that can be sustained by the currently accessible parts of the system.

The role of anadromy in the inland trout populations of the Mojave Rim is less clear; steelhead ascended these rivers in the past (see appendix in Boughton *et al.* 2006) but with what regularity and numbers is not clear.

Identify and maintain sustainable refugia against severe droughts and heat waves. Large changes in the climate are expected by the end of the century and perhaps even mid-century (Hayhoe *et al.* 2004). A direct effect of climate forcing by greenhouse gasses is higher downwelling of infrared radiation, which would be expected to increase surface temperatures and evapotranspiration (Trenberth 1999), with complex, potentially negative effects on summer habitat of *O. mykiss*. Indirect effects include changes in precipitation and temperature patterns; and attendant changes to disturbance regimes, watershed condition, and stream hydrographs (*e.g.* Snyder *et al.* 2002 , Bell *et al.* 2004. Maurer *et al.* 2006). Even a brief description of these effects is beyond the scope of this paper, but it is clear that recovery of steelhead populations will rely on identifying the ecosystem, geomorphological and geologic conditions expected to buffer habitat against the new climatic and hydrologic conditions. Then it will be necessary to adjust recovery efforts according to what has been learned.

Begin collecting population data. The Carmel River population and the Santa Ynez River populations are the only ones with ongoing efforts to monitor steelhead run size, and even these are only partial counts. Yet annual estimates of run size are the single most useful dataset for assessing progress toward recovery. In addition, such data would produce basin-specific estimates of environmental stochasticity, which would allow a more refined criterion for population size (as in Figure 3). It is difficult to imagine a scientifically-based recovery effort that does not involve a serious ongoing effort to monitor run-size in many if not all of the core populations within each of the biogeographic population groups.

Secure and improve lagoon habitat. The work by Bond (2006) indicates that restoration activities in lagoon habitat are likely to produce disproportionate benefits for steelhead populations. However, the work of Bond (2006) and Smith (1990) were case studies in Santa Cruz County, and the robustness of their predictions for areas to the south has not yet been tested. The precautionary approach is to protect lagoons, and the lagoon anadromous life form, irregardless of the generality of Bond's (2006) findings, but it would also be useful to evaluate this assumption empirically.

Estuaries are under serious pressure from suburban development and declines in water quality. Smith (1990) provides a useful discussion of lagoon conditions correlating with high juvenile growth and survival, and concludes that two key elements are integrity of the sandbar barrier during the dry season, and sufficient inflow of freshwater from the stream system during the dry season. Another important problem occurs when the freshwater spawning habitat is distant from the lagoon, and the intervening fluvial corridor has become unsuitable for adult or juvenile migration due to watershed management practices. In addition, current climate trends predict a future of warmer oceans and melting glaciers and icecaps, all expected to raise mean sea levels, perhaps leading to the inundation and displacement of lagoons. Medium greenhouse-gas scenarios project a rise of 0.34m – 0.38m by the year 2100 (Raper and Braithwaite 2006).

Decide on a strategic balance and timeline for investment in better information vs. investment in more recovery activities. Some of the criteria we have proposed are subject to significant revision if quantitative data were obtained. The criteria for population size could be more efficient with basin-specific data on run-size variation and life-history plasticity; and the criterion for spawner density requires basic research. Each of these constitutes a significant research effort that may pose an opportunity cost on recovery activities, but that should also allow better planning that makes recovery activities more effective and efficient. Interested parties should commit to a specific strategy for learning and doing.

Two related issues are that certain research questions require "take" of the fish, and that the anadromous fractions of many populations may currently be too small for tractable research. An example of the first issue: at this writing the only practical way to estimate life-history plasticity at broad scales is via otolith microchemistry (Zimmerman and Reeves 2000). This technique allows determination of the marine-vs-freshwater history of individual fish and their mothers, but requires lethal sampling of fish. Thus it constitutes take under the ESA but ultimately has useful application to recovery planning.

The second issue of small anadromous fractions indicates that for some populations, recovery efforts will probably need to be implemented, and run sizes improved somewhat, before some research efforts can have sufficient sample sizes to be conclusive. Of course, irregardless of how viability criteria might be adjusted in the future, it seems to us clear that run sizes must generally be larger than they are now, if the fish are to be recovered. We see no reason to delay proximal recovery activities because of scientific uncertainty about viability. The principal uncertainty is about how far recovery must ultimately go to achieve viability.

Establish programs for ecosystem-based management of sediment regimes and hydrographic regimes. Sediment regime is a simple term for a complex set of processes governing sediment transport and sorting in stream networks. These processes include the wildfire regime; mass wasting; and the winter flood regime with attendant fluvial transport processes. All these are important for maintaining a dynamic system of spawning gravels and summer pool habitat while preventing too large a buildup of fine sediments (*e.g.* May and Lee 2004). The hydrographic regime plays a role not just in fluvial transport of sediments, but also in maintaining migration connectivity for the steelhead, and in modulating the quality of oversummering habitat in the tributaries and the lagoons. The sediment and hydrographic regimes of many basins have been fundamentally altered by human activities in the region, and are likely to undergo further fundamental changes, both in direct response to future climate change and urban development, and as an indirect responses to both these causes via their effect on the wildfire regime. This is a complex topic beyond the scope of this report, but it is clear that the management of sediment and hydrologic regimes is not amenable to short-term or site-based solutions.

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Throughout the world, *O. mykiss* have thrived when introduced to stream systems having suitable temperatures and hydrographs exhibiting winter flooding and summer low-flows (Fausch *et al.* 2001). This fact suggests to us that steelhead populations of the south-central and southern California coast should have excellent prospects for recovery, if given the appropriate recovery effort. Provided that the regional climate does not warm so much that it becomes prohibitive to the species, we believe that recovery of steelhead in these two ESUs is highly feasible from a biological point of view.

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Appendix A
Derivation of the prescriptive size criterion

The extinction model.—Foley (1994) and Lande (1993) discuss an extinction model in which population growth is treated as a diffusion process, capped by a reflecting boundary representing carrying capacity. Specifically, the model assumes that between $N = 1$ and $N = K$, the population changes according to

$n_{t+1} = r_t + n_t$, where
$n_t = \ln(N_t)$ and
$r_t \sim \mathbf{N}(r, V_r)$ ($\mathbf{N}$ = normal distribution)

The interpretation of the parameters is as follows: r is the expected change in n_t (*i.e.* the mean population growth rate, log-transformed) and V_r is the variance of random variation in r_t (*i.e.* environmental stochasticity) (Foley 1994). When population size N_t = K, the population trajectory is reflected, interpreted as carrying capacity K acting like a ceiling on population size. At $\ln(N_t) = n_t = 0$ the population is considered extinct.

The expected time to extinction of this system is

Eq. 1 $$T_e(n_o) = \frac{1}{2sr}[e^{2sk}(1 - e^{-2sn_o}) - 2sn_o],$$

in which n_o is the initial population size, k is ln(K), and $s = r/V_r$ (Foley 1994, equation 8). For the purpose of deriving a viability criterion, the pertinent risk is for a population currently in its "restored" state, at or near carrying capacity ($n_o \approx k$).

In order to achieve a 95% assurance that a population will persist 100 yrs, one must achieve a T_e considerably larger than 100 yrs. Specifically, the target must be

Eq. 2 $$T_e \approx \frac{100yr}{-\ln(p_{crit})}$$

where p_{crit} would be 0.95 for the risk tolerance given above (Foley 1994, equation 11). Given values of r and V_r, and solving for a T_e that meets the specified risk tolerance, provides an estimate of the minimum carrying capacity that has an acceptably low risk.

However, carrying capacity is difficult to measure and therefore not a useful risk criterion. A better type of criterion is the expected population size, which will be some amount smaller than K due to fluctuations. The equation for expected population size is

Eq. 3 $$E[N] = \frac{e^{2sk}\left[k - \frac{1}{2s}\right] - \frac{1}{2s} - sk^2}{e^{2sk} - 2sk - 1}$$

as reported by Foley (1994), equation A22. To develop a criterion in terms of E[N], it is necessary to derive standards for V_r, r, and p_{crit} that jointly meet the 95% assurance criterion, and then use them to solve Eq. 1 through Eq. 3 .

A standard for *r*.—The assumed value for r should reflect mean growth rate in habitat with good or moderately good quality. The only relevant data we have—steelhead counts from San Clemente Dam on the Carmel River—are somewhat problematic for several reasons: 1) the population appears to have leveled off in recent years, suggesting density dependence (which would violate assumptions for calculating r); 2) earlier counts may reflect not just population growth but redistribution of adults from below the dam to above the dam; and 3) statistical estimates for r have wide confidence limits that include population decline, even though the population was clearly growing during the time period.

Specifically, the 95% confidence interval for the estimator $r = \ln(N_{t+1}/N_t)$ is {-0.20, 0.49} for counts during the years 1992 – 2004. In percent terms this translates to somewhere between -18% and +63% growth per year. This range of plausible values is so uncertain statistically, and of such doubtful biological validity that it is not useful.

We are left to speculate about a cautiously optimistic standard for r in habitat of moderately good quality. We suggest the following standard: 10% per year (= 33% per generation if 3-yr generation time is assumed). Thus the standard for r = ln[1 + 0.10] = 0.0953.

A standard for *V_r*.—We have no data whatsoever on values of V_r in the steelhead populations of our study area. However, S. Lindley (personal communication) has produced estimates of V_r for 20 salmonid populations in the Central Valley,

Table 6. Estimates of V_r for 20 salmonid populations from the Central Valley[1]

Population	sqrt(V_r) {90% c.i.}
Sac. R. winter chinook	0.212 {0.126, 0.344}
Sac. R. spring chinook	0.312 {0.268, 0.354}
Feather R. spring chinook	0.142 {0.100, 0.194}
Butte Cr. spring chinook	0.388 {0.256, 0.588}
Deer Cr. spring chinook	0.192 {0.114, 0.291}
Mill Cr. spring chinook	0.267 {0.141, 0.455}
Sac. R. fall chinook	0.116 {0.087, 0.140}
Sac. R. late fall chinook	0.132 {0.084, 0.214}
Battle Cr. fall chinook	0.170 {0.125, 0.233}
Mill Cr. fall chinook	0.248 {0.153, 0.388}
Deer Cr. fall chinook	0.180 {0.104, 0.319}
Feather R. fall chinook	0.065 {0.032, 0.114}
Yuba R. fall chinook	0.128 {0.086, 0.180}
American R. fall chinook	0.135 {0.087, 0.208}
San Joaquin fall chinook	0.399 {0.331, 0.463}
Mokelumne R. fall chinook	0.383 {0.321, 0.431}
Stanislaus R. fall chinook	0.576 {0.480, 0.656}
Tuolumne R. fall chinook	0.542 {0.404, 0.703}
Merced R. fall chinook	0.418 {0.327, 0.520}
Sac. R. steelhead	0.102 {0.062, 0.174}

[1] Source: S.T. Lindley, NOAA Fisheries. Estimates generated using the state-space method of Lindley (2003)

reproduced above in Table 6. These estimates—mostly from chinook populations—result from a random-walk-with-drift model that was fit to various datasets using a state-space technique described by Lindley (2003) (see also Lindley and Mohr 2003). These estimates for V_r range over nearly an order of magnitude, from 0.065 to 0.576.

A standard can be derived from these data if the following assumptions are true:

1) Each salmonid population can be considered to have a V_r randomly drawn from an underlying distribution that describes all the populations in the Central Valley (sometimes called a "hyper-distribution" of the parameter V_r).
2) The steelhead populations in our study area are described by the same distribution.

It then follows that a standard can be derived by estimating the parameters of the distribution (in our case, the gamma), defining a critical value (p_{crit}) consistent with the overall risk tolerance, and calculating the corresponding critical value of V_r.

Calculations.—There are two critical p-values: one for the extinction model (Eq. 2) and one for the hyper-distribution of V_r (above). Since the product of these two p-values must be at least 0.95, it is convenient to set each at

$$p_{crit} = \sqrt{0.95} = 0.9747 .$$

A gamma distribution fit to the point estimates of V_r (from Table 6) has parameter estimates of alpha (shape) = 3.1571455, and beta (scale) = 0.08088002. The critical value for V_r at p_{crit} = 0.9747 is approximately 0.603.

Likewise, according to Eq. 2 the critical value for T_e at p_{crit} = 0.9747 is

$$T_e \approx \frac{100\,yr}{-\ln(0.9747)} = 3902\ yr \cdot$$

To get the final size criterion, substitute the standards for V_r, r, and p_{crit} into Eq. 1 and solve for k; then substitute V_r, r, and k into Eq. 3 and solve for $E[N]$. The result is $E[N]$ = 4154 spawners per year. Assuming that the generation time for steelhead is 3 yr (*i.e.* the mean age at spawning is 3 yr), a tolerably low risk would be obtained by a mean population size of 3 x 4154, which suggests the following criterion:

N ≥ 12,500 spawners per generation

It should be noted that slightly different assumptions about the parameters V_r and r could yield a vastly more stringent, or less stringent, criterion than the one given here (see Figure 2).

Appendix B
Composition of biogeographic population groups.

Names of populations from Boughton *et al.* (2006); names of groups from Table 4 and Figure 4.

Biogeographic Group	Member Populations (ordered north to south)
Interior Coast Range	Pajaro River, Gabilan Creek, Arroyo Seco, Southwest Salinas Basin.
Carmel Basin	Carmel River.
Big Sur Coast[1]	San Jose Creek, Malpaso Creek, Garrapata Creek, Rocky Creek, Bixby Creek, Little Sur River, Big Sur River, Partington Creek, Big Creek, Vicente Creek, Limekiln Creek, Mill Creek, Prewitt Creek, Plaskett Creek, Willow Creek (Monterey Co.), Alder Creek, Villa Creek (Monterey Co.), Salmon Creek.
San Luis Obispo Terrace	San Carpoforo Creek, Arroyo de la Cruz, Little Pico Creek, Pico Creek, San Simeon Creek, Santa Rosa Creek, Villa Creek (SLO Co.), Cayucos Creek, Old Creek, Toro Creek, Morro Creek, Chorro Creek, Los Osos Creek, Islay Creek, Coon Creek, Diablo Canyon, San Luis Obispo Creek, Pismo Creek, Arroyo Grande Creek.
Monte Arido Highlands	Santa Maria River, Santa Ynez River, Ventura River, Santa Clara River.
Conception Coast[1]	Jalama Creek, Canada de Santa Anita, Canada de la Gaviota, Canada San Onofre, Arroyo Hondo, Arroyo Quemado, Tajiguas Creek, Canada del Refugio, Canada del Venadito, Canada del Corral, Canada del Capitan, Gato Canyon, Dos Pueblos Canyon, Eagle Canyon, Tecolote Canyon, Bell Canyon, Goleta Slough Complex, Arroyo Burro, Mission Creek, Montecito Creek, Oak Creek, San Ysidro Creek, Romero Creek, Arroyo Paredon, Carpinteria Salt Marsh Complex, Carpinteria Creek, Rincon Creek.
Santa Monica Mtns[1]	Big Sycamore Canyon, Arroyo Sequit, Malibu Creek, Topanga Canyon.
Mojave Rim	Los Angeles River, San Gabriel River, Santa Ana River (multiple subpopulations).
Santa Catalina Gulf Coast	San Juan Creek, San Mateo Creek, San Onofre Creek, Santa Margarita River, San Luis Rey River, San Diego River, Sweetwater River, Otay River, Tijuana River.

[1] Population delineation in these groups may be split too finely if there is significant dispersal of fish among neighboring coastal basins. For more discussion see Boughton *et al.* (2006).