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**CONTRACTION OF THE SOUTHERN RANGE LIMIT FOR
ANADROMOUS *ONCORHYNCHUS MYKISS***

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Abstract

For many species, contraction of the geographic range limit nearest the equator is predicted by current global climate trends. Anecdotal data suggest that the southern range limit for anadromous populations of the fish *Oncorhynchus mykiss* has recently contracted northward; the contraction is consistent with the climate-change hypothesis, but is also consistent with the coincidental urbanization of the species' southern range limit during the twentieth century. Distinguishing between the two mechanisms of range contraction is important in part to plan conservation measures for the species; and in part to accurately account for the impacts of climate change vs other impacts on species' geographic distributions. Here we assess the current occurrence of anadromous *O. mykiss* in each coastal basin of southern California in which it occurred historically. The extent of the study is the region from Monterey Bay (the Pajaro River basin) southward to the US Border with Mexico; the grain of the study (the smallest unit for which occurrence is estimated) is the coastal basin. Two especially large basins—those of the Pajaro and Salinas rivers—were divided into sub-units. Ninety-two historic steelhead basins were identified, and occurrence was estimated in 86 of them through a combination of field reconnaissance and spot checks (snorkel surveys). The spot checks were conducted in the best-occurring habitat of stream reaches with migration-connectivity to the ocean. The results indicated that between 58% and 65% of historic steelhead basins currently harbor *O. mykiss* populations. The pattern of basin-level extirpation showed a latitudinal gradient, with the highest extirpation rates in the south, confirming that a range contraction has taken place. Most of the extirpations (68%) were associated with anthropogenic barriers to fish migration (dams, flood-control structures, culverts, *etc.*). Historically, the probability of occurrence in a basin was correlated with basin area, but this correlation no longer holds. Barrier-associated extirpations were positively correlated with urban/agricultural development, whereas the “other” extirpations (*i.e.*, not associated with barriers) were positively correlated with mean annual air temperature in the basin. The results suggest that the range contraction is primarily an effect of lost migration opportunities arising from the urban/rural infrastructure; however climate and other stressors may have played a subsidiary role.

Introduction

Large-scale range contractions of species are notable events. One reason for this is that range contraction on the equatorial side of a species range is considered to be evidence for biologically-significant climate warming (Kareiva *et al.* 1993, Easterling *et al.* 2000). This sort of global warming in the twentieth century has been well-documented (Houghton 1997), and range shifts consistent with global warming have been observed in climatically sensitive species such as butterflies (Parmesan *et al.* 1999), even as the uniqueness of the recent warming trend itself is vigorously debated (Mann *et al.* 1998, McIntyre and McKittrick 2003).

In fact range contractions may occur for any number of non-climatic reasons as well—broad-scale habitat alteration may cause population extinctions throughout a species' range, with the effect of shrinking the spatial envelope encircling the extant populations; or local-scale impacts of human activity may happen to coincide geographically with the species' range limit, driving a range contraction. Whatever the primary cause, range contractions on the order of thousands of square kilometers are widely considered to foreshadow species extinction. The IUCN redlist describes significant declines in area of occurrence to be risk criteria (Musick 1999), and the US Endangered Species Act includes extinction in a significant portion of the range as a basis for listing a species as endangered.

The anadromous form of the fish *Oncorhynchus mykiss* is thought to have undergone a significant range contraction at the southern extent of its freshwater range, although the phenomenon is neither well characterized nor well understood (Boughton 2005). Climate may have played a role—since the ending of the “Little Ice Age” in the 19th Century, the southern California climate has become warmer, which would be expected to drive a range contraction (Millar and Woolfenden 1999; Haston and Michaelsen 1997; Scuderi 1993). However, the climate has also become wetter and less erratic, both of which would be predicted to allow the fish to expand their range; the first by making more kilometers of stream suitable to the



Figure 1. The study area.

fish, and the latter by providing for more stable metapopulation dynamics.

The contraction could also be the result of other forces. Population decline is a widespread phenomenon in steelhead, occurring throughout the entire west coast of the USA (Busby *et al.* 1996), and the range contraction may simply be its artifact (*i.e.*, population extirpation may not be any more common in the far south than elsewhere). Also, the southern limit of anadromous *O. mykiss* happens to coincide with the Los Angeles – San Diego metropolitan area, where water diversion and flood control practices have profoundly transformed the region's hydrology, with many negative impacts on the region's freshwater fishes (Moyle 1995). Which combination of the above mechanisms might explain the range contraction is not clear, nor is the precise nature of the range contraction itself.

In this paper we analyze the pattern of population extirpation for anadromous *O. mykiss* (hereafter, “steelhead”) in southern California (Figure 1). First, we systematically assess the occurrence of steelhead in each basin in which it historically occurred. Occurrence was determined using a combination of basin-scale reconnaissance and site-level spot checks (snorkel surveys). To estimate

detection power during the spot checks, we assumed a simple model of detection based on a Poisson process.

Second, we test the hypothesis that the probability of basin-level extirpation is related to latitude; and then test whether two types of extirpations—those associated with barriers and those not—are correlated with certain environmental variables, namely basin size, mean annual air temperature for the period 1961–1990, and percent of the basin that has undergone urban or agricultural development.

Methods

Study system.—Steelhead in the study area inhabit a diverse set of watersheds, from redwood forests in the north to systems of chaparral and sycamore canyons in the south. Despite this diversity a number of ecological features unite the study area and differentiate it from steelhead habitat further north. Rainfall is low, episodic, and quite patchy in space; there is also high interannual variability in total precipitation. Streamflow can vary seasonally over five orders of magnitude,

largely as a result of this patchiness (Figure 2). Summers are hot and dry. Many stream networks discharge so little water in the summer that the surface of the streambed dries up for long stretches (all discharge is groundwater or hyporheic). Perennial flow may be maintained in upper tributaries, particularly in mountainous areas where shallow bedrock pushes groundwater to the surface.

At the ocean, the mouths of most streams become “barred over” during the summer by wave action building up beach sand; migration connectivity to the ocean is lost until the first large storm of the year washes out the sandbar (typically November or December). In the meantime the over-summering juveniles must survive in cool-water refugia within what are essentially small desert streams, or in lagoons isolated from the ocean by sandbars and from the stream system by dry mainstems. Southern California populations are thought to be very sensitive to variation in summer temperatures and annual rainfall.

Under the U.S. Endangered Species Act, the anadromous form of *O. mykiss* is currently listed as threatened or endangered in many parts of the

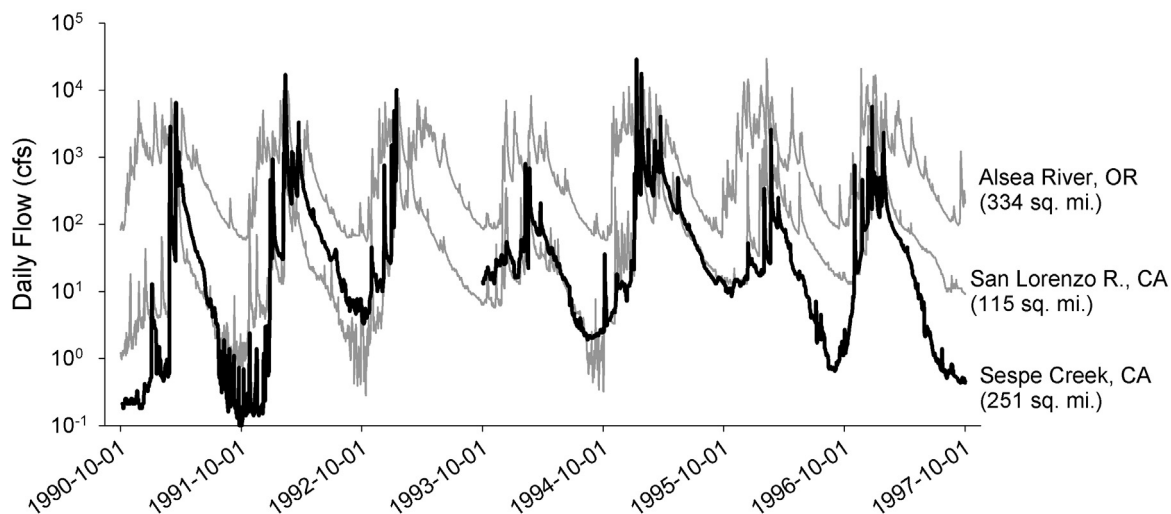


Figure 2. Hydrographs for a river in typical coastal steelhead habitat in Oregon (Alesa River), a system just north of the study area (San Lorenzo River), and a steelhead enclave in the southern part of the study area (Sespe Creek). Watershed area is given in parentheses. The time period includes the end of the California drought in early 1990s.

western USA (Busby *et al.* 1996), and southern California is no exception. The actual entities listed under the act are “Evolutionarily Significant Units” of the species rather than the species itself (abbreviation: ESU; Busby *et al.* 1996). Two ESUs occur within the study area—the South-Central California Coast ESU and the Southern California ESU. The southern-most population in the study area is believed to be the southern geographic limit of anadromous steelhead as a whole. A scattering of isolated *O. mykiss* populations occur further south in Baja California and mainland Mexico (Nielsen *et al.* 1998) but do not appear to exhibit anadromy (*e.g.*, Ruiz-Campos and Pister 1995). Most are considered to be distinct subspecies of freshwater trout by Nielsen *et al.* (1998).

Over the course of the 20th century, the human population of southern California has rapidly expanded, in the process constructing an extensive array of dams, flood-control channels, and road networks, all of which involve the blocking or re-routing of stream channels as well as the re-configuring of the natural hydrology of the region.

Interestingly, much of this activity is focused on the lower mainstems (or lower parts of principal tributaries) of the stream systems. With certain exceptions (*e.g.*, the Big Sur Coast), these lower mainstems tend to occur in wide alluvial valleys with extensive urban or agricultural development, exemplified by the Los Angeles basin and the Salinas Valley respectively. It seems reasonable to believe that such habitats originally served steelhead primarily as migration corridors, and that most spawning occurred higher in the basin in small to medium mountain streams. Despite the occurrence of a rather large human population, many of these mountain streams currently lie within the boundaries of National Forests and military bases, and there are numerous anecdotal accounts of extant non-anadromous *O. mykiss* populations in portions of the basin currently isolated above anthropogenic barriers (Good *et al.* 2005).

Biological Assumptions.— Steelhead are sometimes observed to produce non-anadromous progeny and vice-versa (Zimmerman and Reeves 2000), and in the juvenile stage the two forms are currently considered to be indistinguishable. For

the purpose of this study we assumed that juvenile *O. mykiss* were members of populations capable of exhibiting anadromy (*i.e.*, steelhead) if they were observed in stream reaches with migration-connectivity to the ocean. Our concept of connectivity included stream networks that are seasonally dry in some sections, but exhibit discharge during the rainy season when the fish migrate.

The grain of the occurrence data (the finest-scale unit for which occurrence was estimated; Kotliar and Wiens 1990) was set as the individual coastal basin, defined as the entire catchment area for a stream at the point that it enters the ocean. The two largest coastal basins—the Salinas River system and the Pajaro River system—were divided into subbasins, defined by the catchment areas of each major tributary to the main stem. The extent of the study was the coastal region between the Pajaro River basin (inclusive) in the north and the U. S. border with Mexico in the south (Figure 1).

Historic Distribution.—The basins in the study area were classified as historic steelhead basins, or as having no evidence of historic occurrence, based on one public report (Stoecker *et al.* 2002) and three unpublished manuscripts obtained by the Southwest Fisheries Science Center, Santa Cruz Lab (Titus *et al.* 2003, Sleeper 2002, and Franklin 1999). Titus *et al.* (2003) thoroughly reviewed historic data on steelhead occurrence throughout the entire study area; the others collected “new” historical data in the form of interviews with elderly fisherman, *etc.*, each for a specific region within the study area (Stoecker *et al.* 2002: s. Santa Barbara County; Sleeper 2002: Orange and n. San Diego Counties; Franklin 1999: upper Salinas Basin). Another significant effort at historical research, for Ventura and Santa Barbara Counties, was unavailable to us (E. Henke, personal communication). Data indicating sporadic strays rather than evidence of spawning or rearing were not considered sufficient to establish historic presence of the species in a basin. Historic distribution as determined from these sources is depicted in Figures 3 and 4.

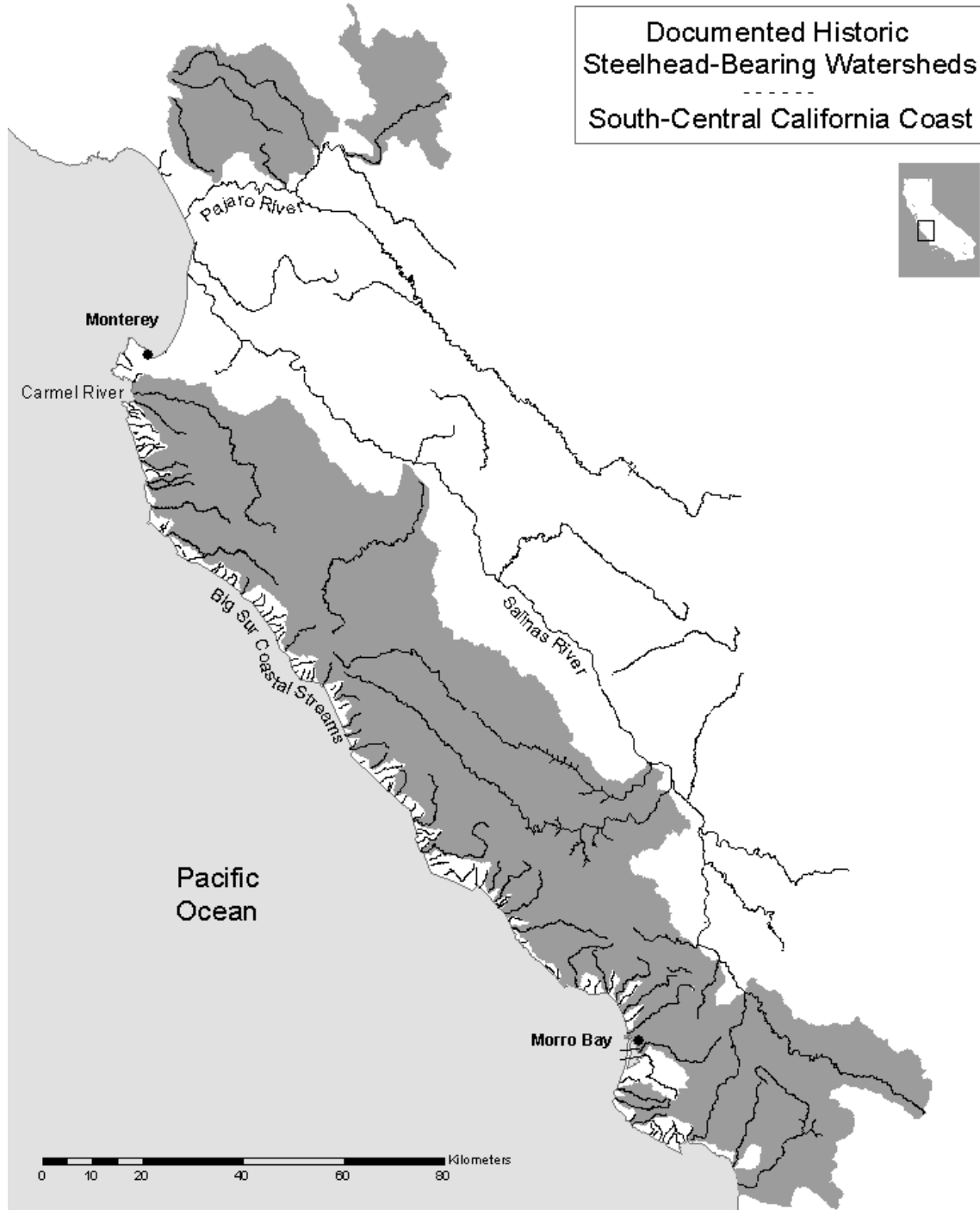


Figure 3. The historic distribution of spawning and rearing basins for steelhead in the south-central California coast. The Pajaro and Salinas systems were disaggregated into sub-basins (for clarity, their mainstems are not depicted as habitat). Historic distribution is based on accounts from Titus *et al.* (2003) and Franklin *et al.* (1999).

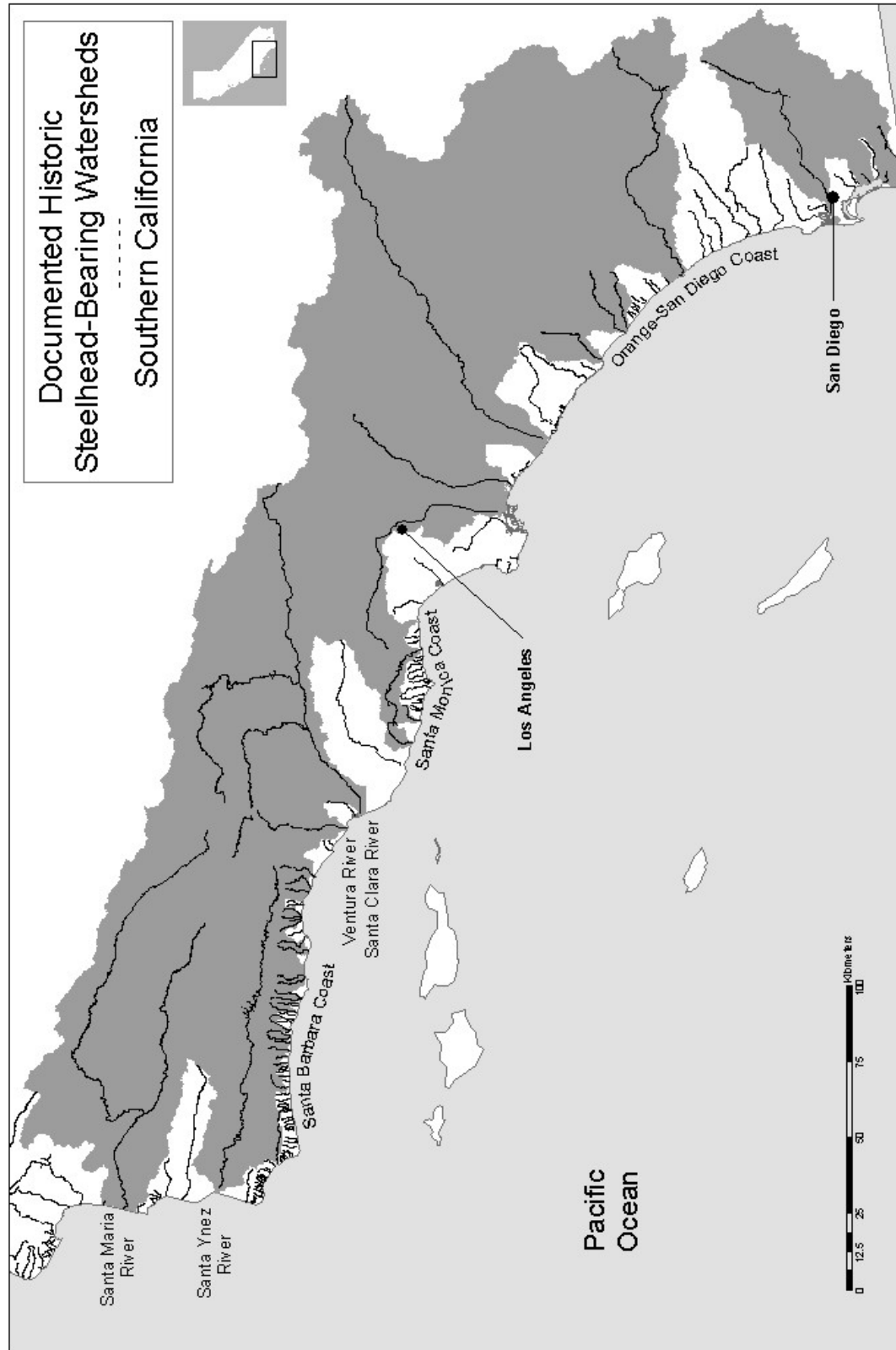


Figure 4. The historic distribution of spawning and rearing basins for steelhead in southern California. Note that the grain of the occurrence data (i.e. the minimum geographic unit depicted) is the coastal basin: Shading of entire basins implies only that steelhead occurred somewhere, not necessarily everywhere, in a basin. Historic distribution is based on accounts from Titus *et al.* (2003), Stoecker *et al.* (2002) and Sleeper (2002).

Determining Occurrence.—Error rates in presence/absence data should tend to be asymmetric—if a species is detected somewhere in a basin it will be known to be present, but if it is not detected it may either be absent or present but overlooked (an error). This implies that the presence of the species is consistent with both a positive and a negative observation, whereas absence is consistent only with a negative observation. We thus considered it parsimonious to treat “presence” as a null hypothesis, to be rejected by one of the following observations:

Dry Stream: Drainages that were dry up to the first barrier to anadromy during summer 2002 or 2003. This determination was made during reconnaissance by experienced field crews.

Barrier Exclusion: Drainages with anthropogenic migration barriers between the ocean and any potential spawning habitat upstream. Our concept of potential spawning habitat was liberal: everything except concrete-lined channels, estuaries, marshes, and channels not exhibiting pool-run-riffle structure. We also placed in this category any stream fitting the definition of “Dry Stream,” but in which the limit to anadromy was anthropogenic and appeared to have spawning and rearing habitat above it.

Spot Checks: If neither of the above criteria could be used to reject presence, we performed a spot check of occurrence using snorkel surveys. To maximize our power to detect fish, we used the method of “best-occurring habitat,” which involves a subjective judgement of relative habitat quality. A reach was judged to be “fishy” (*i.e.* relatively high quality) if it met the following criteria: i) moderate to high stream gradient; ii) pool-run-riffle structure; iii) high vegetative cover; and iv) low turbidity. The criteria were judged by experienced field crew during a period of reconnaissance by car.

To conduct the spot check itself, a crew member conducted a snorkel survey (Dolloff *et al.* 1993) of all pools and runs, omitting riffles due to an assumed low detection-probability, and working

from down- to up-stream. The survey stopped when either one or more steelhead were detected [scored as “spot check (observed)”], or when 100m total linear length of pools and runs had been surveyed without detection [scored as “spot check (not observed)”]. In either case, the linear distance of pools and runs surveyed (“distance-to-detection”) was recorded as a measure of effort.

When we encountered a non-historic basin that looked fishy and had time to survey it, we did so. Occasionally the null hypothesis could not be tested in historic basins, either because landowners would not grant us permission or because the stream posed some hazard such as pollution or overhead bombing. We classified these basins as inaccessible. In some basins, particularly in southern Santa Barbara County, one of us (M.S.) had previously made numerous observations of occurrence during summer 2002; these were scored as “spot check (observed)” if *O. mykiss* had been unambiguously detected; otherwise the basin was submitted to a formal spot check. In several cases steelhead had been documented within the past 3 yr (2000 – 2002) by practicing fisheries biologists; we also scored these basins as “spot check (observed)” without applying the formal method.

Estimating detection error.—To estimate detection error at the site-level, the effort data (distances-to-detection for each spot check) were calibrated by a statistical model that assumed detection of fish to be a Poisson process (so to speak). The model is based on the idea that the longer the distance surveyed without detecting a fish, the more likely the species is truly absent; or to put it more precisely (see Appendix A), the complete absence of fish in 100m of habitat allowed us to reject the hypothesis of 100 or more juveniles per km of habitat at $p = 0.01$ and an assumed per-fish detection probability of 0.5. This last assumption is slightly conservative with respect to demonstrating absence; measured detection rates in snorkel surveys are about 0.6 (comparison with electrofishing counts in Ten-mile Creek, California; T. Williams and B. Spence, unpublished data).

The survey design has an important limit: if juvenile populations commonly occur at densities less than 100 per km in the best-occurring habitat, they would frequently go undetected. In fact, our

results (to be described further on) suggest that nearly all populations have much higher densities.

We also pursued two strategies for assessing detection error at the level of entire basins. First, in a subset of basins we replicated spot checks by performing them at two or more sites within a basin. Error was estimated by the probability of disagreement between replicated spot checks. Second, in five subbasins of the Salinas, we compared the “best-occurring habitat” method with a concurrent general fish survey performed by a separate field team. The general method was designed to characterize the typical fish community of each sub-basin, and did not have a specific focus on identifying *O. mykiss* habitat (potentially quite patchy). We predicted that if the “best-occurring” strategy was effective, it should detect occurrence of *O. mykiss* for basins in which the general survey did not; but not the reverse.

In the general survey, one or more 500m reaches typical of the basin were selected and then surveyed. A snorkel-survey was performed if maximum depth was > 25cm; otherwise bank-side observations were made using either polarized glasses or *Aqua-Vu* underwater viewing equipment (Nature Vision Inc.). Riffles were included in the survey; two divers sometimes performed the survey in wide streams; and all fish species present were identified and counted.

Hypothesis tests.—Logistic regression was used to test a series of hypotheses against the occurrence data. To test hypotheses about the range contraction, the data were coded as “extant” vs “extirpation,” the latter defined as an observed absence in a historical steelhead basin. For preliminary analysis of latitudinal clines in extirpation, basins were grouped into geographic positions according to the county containing the centroid of each (Table 1). We then examined underlying reasons for extirpations. Specifically, we tested the statistical significance of the following predictors: mean annual air temperature by basin; basin size; and the percent of basin that has been developed by the human population (Table 1). The relationship with basin size (area) is a general biogeographic prediction; the relationship with temperature would be expected if mean annual temperature is a limiting factor in the study area; and

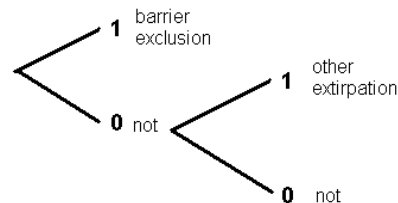
TABLE 1. INDEPENDENT VARIABLES USED IN LOGISTIC REGRESSIONS.

Geographic position codes	
1	Santa Cruz/Monterey Counties
2	San Luis Obispo County
3	Santa Barbary County
4	Ventura/Los Angeles Counties
5	Orange/San Diego Counties
Environmental predictors	
Mean annual air temperature (°C, 1961 – 1990)	
Basin area (ln[Ha])	
Percent Developed (% , from NLCD database)	

the relationship with development would be expected if direct human impacts were the primary cause of the range contraction.

Basin areas (hectares) were estimated using ArcMap software and then log-transformed. Mean annual temperatures for each basin were taken as the mean PRISM temperature across each basin, where PRISM refers to interpolated climate data computed as in Daly *et al.* (1994) (obtained from the Climate Source, Corvallis Oregon; mean °C for the period 1961 - 1990). Percent development was estimated using National Land Cover Data (NLCD), California-South section, version 04-28-2000, available from the USGS EROS data center. NLCD categories were reclassified as a boolean coverage, in which the NLCD categories “Developed,” “Non-natural Woody,” and “Herbaceous Planted/Cultivated” were reclassified 1, and all other categories as 0.

Regressions were done separately for the “barrier exclusions” and “other extirpations,” *i.e.*, extirpations left over after barrier exclusions were removed from the dataset. The two regressions were made conditionally independent by coding the data thus:



Significance tests were Bonferroni-corrected for multiple comparisons.

TABLE 2. COMPARISON OF *O. MYKISS* DETECTION USING TWO SURVEY METHODS.

Sub-watershed	Historical occurrence	General fish survey method ¹		Best-occurring habitat method ²	
		Current occurrence	Number of detections	Current occurrence	Number of detections
Arroyo Seco	Yes	Present	4 of 7 sites	Present	1 of 1 sites ³
Paso Robles	Yes	Absent	0 of 1 sites	Present	2 of 3 sites
Atascadero	Yes	Absent	0 of 2 sites	Present	1 of 1 sites
Santa Margarita	Yes	Absent	0 of 1 sites	Present	1 of 1 sites
Chalone	No	Absent	0 of 2 sites	Absent	0 of 1 sites

¹ General method did not focus on best-occurring *O. mykiss* habitat, but rather stream habitat typical of the sub-basin, for the purpose of characterizing the most common fish species in the sub-watershed.

² Best-occurring method focused on detection of *O. mykiss* only.

³ Data collected in 2001 under a different detection protocol, but similar site-selection protocol.

Results

Overall we examined 86 of 92 historic steelhead basins (the remaining 6 were inaccessible), and 55 of 101 non-historic basins. These numbers include 22 subbasins of the Salinas and Pajaro, 11 of which were historic steelhead basins.

Occurrence.— Assuming negligible detection failure, the overall probability of occurrence in historic basins was between 0.59 and 0.65 ($n = 92$); the uncertainty is due to the 6 basins not assessed. For the south-central California ESU, the probability of occurrence was 0.80 – 0.87 ($n = 45$); for the southern California ESU it was 0.38 – 0.45 ($n = 47$).

Detection error.— Was detection failure truly negligible, as assumed by the above calculations? To answer this question, we made 17 revisits to basins already spot-checked. In all 17 revisits the score (detected; not detected) was the same as that of the previous spot check, for an error probability of 0.00 (95% c.i.: [0.00, 0.162] by the binomial distribution). Additionally, we compared the best-occurring habitat method with a general survey method in 5 sub-basins of the Salinas. The best-occurring habitat method detected *O. mykiss* in 3 sub-basins in which it was not detected by the general method, and agreed with the general method in the other two sub-basins (Table 2).

When steelhead were observed during a spot check, they were usually observed within 30m of the start point of the snorkel survey (32 of 36 cases), suggesting that surveying 100m of pools and runs was sufficient effort to detect the species with fairly high confidence. This assertion can be quantified by fitting a probability-density function to the dataset (the distances-to-detection), and estimating error rate as the area under the right-hand tail of the distribution,

$$\text{probability of detection failure} = \int_{100m}^{\infty} pdf(x) dx .$$

This is a simple failure-time model (Smith 2002). In words, the above quantity is the probability of not detecting the species in the first 100m, conditional on it being present and detectable under infinite effort. A truncated log-normal distribution (Johnson *et al.* 1994) was found to fit the data ($\chi^2 = 1.914$, $df = 2$, $p = 0.384$); the estimated probability of detection failure was 0.0175. Overall this analysis suggests that few extant populations tend to be sparser than 1 observable fish per 100m of habitat, and that our spot-check method had a decently low error rate. This implies, via the statistical model described in Appendix A, that most juvenile populations have densities well above 100 fish per km in the best-occurring (or “fishy”) habitat.

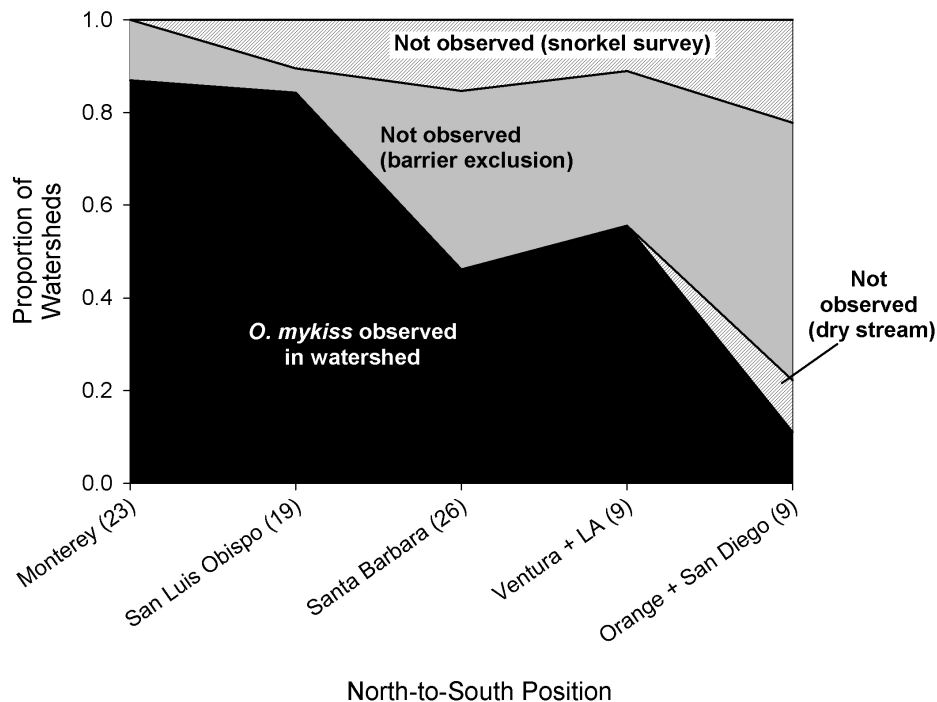


Figure 5. Extirpation north to south in the study area. Data are for all historical steel-head basins except six that were inaccessible ($n = 85$). Numbers in parentheses are the number of basins for each geographic position.

Geographic patterns.—The historic steelhead basins exhibited a latitudinal trend in extirpation rate (null hypothesis: $p = 0.00008$; Table 3A), clearly depicted in Figure 5. Most of the extirpations were associated with migration barriers: Of those historic basins that were assessed, 26% had barrier exclusions, 1% were dry, and 11% were observed to be vacant during the spot check ($n = 85$). The rest were occupied.

Historic occurrence of steelhead was related to both basin area and mean annual temperature (Table 3B); however current occurrence of steelhead was no longer statistically associated with basin area ($p = 0.083$; Table 3C). Inspection of the confidence limits for this predictor in Table 3B and 3C suggests that the relationship of basin area and species occurrence is now quite different from what it was historically. In contrast, the confidence limits for the historic and current effect of mean annual temperature are quite similar.

The extirpations classified as barrier-exclusions tended to be associated with percent development of the basin (Table 3D); there was no

significant association with basin area, nor mean annual temperature. In contrast, the other “other” extirpations tended to be associated with warmer mean annual temperatures but not percent development (Table 3E).

New records of occurrence.—Five new records of occurrence were made in the 56 non-historical basins surveyed. One of these was Gabilan Creek, a tributary to the old Salinas River Channel. Gabilan Creek is the only subbasin on the arid east slope of the Salinas Valley known to harbor juvenile *O. mykiss*. The other four new records were scattered along the Big Sur Coast and Morro Bay region. They occur amidst other basins of similar size and environmental character that also harbor steelhead, and in addition have been said to harbor resident populations of *O. mykiss* above impassable barriers (Titus *et al.* 2003)

TABLE 3. HYPOTHESIS TESTS USING LOGISTIC REGRESSION.

Predictor	Estimate (95% c.i.)	t(df)	p	Odds Ratio*
A. Is there a latitudinal cline in extirpation rate?				
Indep. var.: All basins, classified as extirpations vs. not ($\chi^2 = 20.73$; df = 1; p = 0.00001).				
Intercept	-2.95 (-4.32, -1.60)	-4.33 (84)	0.00002	
Geographic Position	0.904 (0.45, 1.36)	3.95 (84)	0.00008	2.47 (1.57, 3.89)
B. Is the historic occurrence of steelhead in a basin related to basin size or to climate?				
Indep. var.: All basins, classified as historic steelhead vs. not historic ($\chi^2 = 33.29$; df = 2; p = 0.00002)‡.				
Intercept	2.74 (-1.26, 6.74)	1.35 (193)	0.18	
Mean Annual Temp.	-0.41 (-0.67, -0.15)	3.17 (193)	0.0018	0.66 (0.51, 0.86)
Ln(Basin Area)	0.42 (0.27, 0.61)	4.49 (193)	0.0001	1.53 (1.27, 1.84)
C. Is the current occurrence of steelhead in a basin related to basin size or to climate?				
Indep. var.: All basins, classified as currently occupied vs. not ($\chi^2 = 19.90$; df = 2; p = 0.0010)‡.				
Intercept	8.28 (3.03, 13.54)	3.12 (139)	0.0022	
Mean Annual Temp.	-0.67 (-1.02, -0.32)	3.77 (139)	0.0002	0.51 (0.36, 0.73)
Ln(Basin Area)	0.16 (-0.02, 0.35)	1.75 (139)	0.083	
D. Are cases of barrier exclusion correlated with certain environmental predictors?				
Indep. var.: All basins, classified as barrier-exclusions vs. not ($\chi^2 = 12.57$; df = 3; p = 0.012)‡.				
Intercept	-9.44 (-18.9, 0.037)	1.98 (83)	0.051	
Mean Annual Temp.	0.52 (-0.075, 1.11)	1.74 (83)	0.086	
Ln(Basin Area)	-0.04 (-0.35, 0.28)	0.24 (83)	0.81	
Percent Developed	5.24 (0.96, 9.53)	2.43 (83)	0.017	1.69 (1.10, 2.59)
E. Are other types of extirpations correlated with certain environmental predictors?				
Indep. var.: Basins without barrier-exclusion, classified as extirpated vs. not ($\chi^2 = 10.38$; df = 3; p = 0.03)‡.				
Intercept	-18.4 (-29.4, -7.33)	-3.32 (64)	0.0015	
Mean Annual Temp.	1.00 (0.33, 1.67)	2.99 (64)	0.0040	2.72 (1.40, 5.31)
Ln(Basin Area)	0.20 (-0.22, 0.62)	0.94 (64)	0.35	
Percent Developed	0.33 (-6.6, 7.2)	0.09 (64)	0.93	

* Odds ratio is for a unit change in the predictor (i.e. 1°C increase in mean annual temp; approximate tripling of basin size; or 10 percentage points of urban/agricultural development). 95% confidence intervals in parentheses

‡ p-values for model significance are Bonferroni-corrected for multiple comparisons.

Discussion

Detection failure.—We classified a population as “extirpated” if we failed to observe fish during a spot-check; naturally, this rapid-assessment technique may miss some extant populations—a so-called detection failure. Yet our efforts at measuring error suggested that such detection failures were rare: about 1.75% at the reach level, and about 0% at the basin level given an accurate detection at the reach level (however, the latter had a confidence interval that included 16%). These estimates suggest that the rapid-assessment technique had a reasonably low error rate, and most of the apparent extirpations were true extirpations. Even so, a more intensive study might turn up additional extant populations, either because error rates were higher than thought, or because some of the vacant basins subsequently got colonized.

Similarly, some of the “barrier exclusions” that we report may turn out to be partial impediments to steelhead migration, rather than outright barriers. Since many of these barriers have extant populations of *O. mykiss* above them (see below), these populations might have to be reclassified from freshwater-resident to possibly anadromous. Unfortunately, the passability of small instream barriers by adult steelhead appears to be an intricate and poorly understood subject. Opinion varies widely about the abilities of steel-head with respect to barriers/impediments.

Patterns of extirpation.—Given that the rate of detection failure appears to be low, the data indicate that a large range contraction of anadromous *O. mykiss* has occurred. In the study area, steelhead populations have apparently been extirpated from at least a third of the basins in which they are known to have occurred historically. The evidence suggests that most of these extirpations occurred in the south, and about two-thirds of them were associated with human-built barriers that block migratory access.

On the other side of the ledger, occupancy was surprisingly high in the Big Sur – San Luis Obispo region, even in quite small coastal basins. Occurrence was in fact discovered in four small basins that had no previous record of occurrence. The

TABLE 4. OCCURRENCE OF RESIDENT, RESIDUALIZED, OR STOCKED *O. MYKISS* ABOVE ANTHROPOGENIC BARRIERS, FOR BASINS IN WHICH *O. MYKISS* HAS BEEN EXTIRPATED BELOW THE BARRIERS.

Type of extirpation below barriers	Observations of <i>O. mykiss</i> above barriers		Proportion
	Recently observed*	Not observed	
Barrier exclusions	15	7	0.68
Other extirpations	2	8	0.2

* observed sometime within the past 10 yr, cf. Good *et al.* (2005) or Stoecker *et al.* (2002). See appendix C for names of basins.

high occupancy rate of steelhead populations in the tiny basins is surprising—not because the habitat seems unsuitable, but because the stream networks seem too small to support persistent populations. Typically one would expect that small populations periodically go extinct naturally, leaving a period of natural extirpation before being recolonized by fish from nearby areas. If this were the case in the Big Sur, there should have been some fraction of basins vacant at any given time, including the time of our survey. Yet there was really only one site that was both vacant and accessible: Cayucos Creek. This suggests that Big Sur populations are quite resilient to extinction despite being small. Perhaps there is much inter-basin movement fish, effectively linking the various coastal basins into one large population.

As for basins suffering from barrier-exclusion, some points are worth noting. Strictly speaking, the existence of a barrier exclusion does not indicate that the barrier was actually responsible for the extirpation—the population could have gone extinct even if the barrier had never been built. However, if this were the case the portion of the population trapped above the dam should also have gone extinct. In fact in 15 cases the opposite is true: the resident form of the species continues to occur above the barrier (Table 4; data from Good *et al.* 2005 and Stoecker *et al.* 2002). These populations are not functionally anadromous, yet indicate that at least this number of basins contin-

ues to possess suitable *O. mykiss* habitat. If migration-connectivity were restored for the 15 residualized populations noted in Table 4, and they responded by becoming anadromous, the total number of extirpations in the study area would be halved. The overall rate of extirpation would then be no greater than what has already been inferred from our data on “other” extirpations: about 16%. Note that the figure could be larger, because the “not observed” category in Table 4 probably includes some undetected residualized populations.

The logistic regressions suggest extirpations of two types: those associated with temperature, and those associated with barriers arising from urban and agricultural development. In particular,

- 1) Occurrence of steelhead at the basin level is no longer related to basin size, though it apparently once was. The original pattern was an example of the species-area relationship, one of the most general ecological patterns observed in nature. It probably no longer holds because the barrier exclusions have made the effective size of many stream networks much smaller than the actual size. The amount of accessible habitat is no longer closely related to basin size.
- 2) Barrier exclusions tended to be associated with highly-developed basins, whereas the other extirpations had no relationship with development. At least half of the barrier-exclusions still have extant *O. mykiss* populations in streams above the barrier, indicating suitable conditions for the non-anadromous form of the species.
- 3) The other extirpations tended to be associated with warmer basins, whereas the barrier exclusions were not. There is no *a-priori* reason to expect barriers to be built in warmer basins. In contrast, there *is* an expectation that at the southern extent of the range, the populations in the warmest basins would be most vulnerable both to short-term climate fluctuations and long-term trends.

A role for climate is not surprising, since climate variability at the scale of decades is thought to strongly influence marine productivity of

salmon across the northern Pacific (*e.g.*, Hare and Francis 1995, Hare 1996, Mantua *et al.* 1997) as well as having local effects on the hydrology and sediment load of southern California rivers (Inman and Jenkins 1999). Over the long term, there has been a warming trend in California and elsewhere following the end of the “Little Ice Age” in the 19th century (Mann *et al.* 1998, Millar and Woolfenden 1999), and shifts in faunal abundance and distribution have been attributed to long-term climate trends in California for both terrestrial and marine organisms (Parmesan 1996, Barry *et al.* 1995).

On the other hand, in the twentieth century southern California has also seen a trend toward wetter conditions (Inman and Jenkins 1999) that would presumably benefit the fish. Indeed, during the 1990s steelhead recolonizations were observed to reverse extirpations in two basins, currently the two southernmost populations of steelhead in the study area (T. Hovey, pers. comm.; Dagit and Webb 2002). To complicate the picture even more, certain climate models suggest that if the current warming trend continues in California over the next century, it will have particularly strong effects in the south in terms of temperature and rainfall (Snyder *et al.* 2002, Snyder *et al.* 2003).

Despite the importance of climate, extirpations associated with barriers were twice as common as extirpations associated with temperature. The strong association between range contraction of an aquatic species and the regional development of water resources and flood control is consistent with Moyle’s (1995) vision of the threats facing freshwater fish in southern California, and Frisell’s (1993) analysis of threats to freshwater fishes throughout the west coast of the USA. Our study is the first to do a basin-by-basin accounting of *O. mykiss* in the south, and unambiguously demonstrates a large-scale range contraction and a strong association of barriers with that range contraction. Unlike the myriad impacts of climate change on natural systems (Parmesan and Yohe 2003), and the numerous negative effects of urbanization on native species, the major anthropogenic limit on southern steelhead occurrence at the basin scale appears to be quite specific: anthropogenic barriers are preventing migration to suitable habitat.

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Appendices

Appendix A. Statistical model used in spot checks

If w is the probability that a small stream segment contains an observable fish, then the probability of not observing fish in n independent identical segments is $(1 - w)^n$ (McArdle 1990, Kéry 2002, Bayley and Peterson 2001). Assume the segments to be joined end-to-end in a single transect; subdividing each by an integer m gives the probability of not observing the species,

$$\left(1 - \frac{w}{m}\right)^{nm},$$

in which individuals are randomly distributed among the new subdivided sites. At the limit $m \rightarrow \infty$, the expression becomes e^{-wn} , where e is the base of natural logarithms. Now, n is simply the length of the transect and w is the rate of detections per unit distance, or equivalently, the density of observable animals. This is a description of a Poisson process.

An important conclusion immediately follows: Choose a random point on the transect and the distance Y to the next animal is exponentially-distributed, satisfying the equation

$$(1) \quad S(y) = \Pr\{Y > y\} = \frac{(wy)^0 e^{-wy}}{0!} = e^{-wy}$$

(see Smith 2002:20), where the notation for n has been changed to y for clarity. Smith (2002: 123) also describes the corresponding likelihood equation,

$$(2) \quad L(w) = c \prod_{i=1}^D f(Y_i) \prod_{j=1}^R S(y_{\max})$$

in which $f(y)$ is a probability-density function associated with $S(y)$ [$f(y) = -S'(y)$]. The D observations of the first product denote transects that terminated in species detections (distance-to-detection for transect i is Y_i). The R observations of the second product denote transects in which the species was not observed and the transect ended at a maximum length y_{\max} . The value c is an arbitrary constant. If the species is not detected, equation (2) simplifies to

$$(3) \quad L(w) = c \prod_{j=1}^R S(y_{\max}) = c S(y_{\max})^R = c e^{-Rwy_{\max}},$$

which has the maximum-likelihood estimate $\hat{w} = 0$ [i.e., the maximum value of $L(w)$ is at the lower bound $w = 0$]. For our purposes we are more interested in the uncertainty about this estimate, which can be obtained by deriving a cumulative density function (this is done by noting that the upper bound of w is infinity and solving the appropriate integral). The result is

$$(4) \quad \Pr(\text{data} \mid w > w_{\text{crit}}) = CDF(w_{\text{crit}}) = e^{-w_{\text{crit}} R y_{\max}}.$$

To “establish” an absence one would reject this hypothesis at a specified p -value and critical density w_{crit} , the latter being set close enough to zero to be biologically satisfying. Substituting $R = 1$ and $y_{\max} = 0.10$ km, and solving for a p -value of 0.01 yields $w_{\text{crit}} = 46 \approx 50$ fish per km. If one makes the conservative assumption that only about half of the fish are observable, then surveying 100m is sufficient to reject the hypothesis of 100 or more juveniles ($= 50 \div 0.5$) per km of stream habitat, at the level of $p = 0.01$.

Appendix B. The occurrence data by basin.

Historical Occurrence	Current Occurrence	Basin (north to south)	Area (ha)	Year (and external source for data)
X	X	Pajaro River	337558	
		Principal subbasins		
X	X	Corralitos Creek		2001 (C. Garza <i>et al.</i> pers. comm.)
X	X	Pescadero Creek		2003
X	X	Uvas Creek		2003
X	Dry	Llagas Creek		2003
	Absent	San Benito River		2003
X	X	Pacheco Creek		
		Elkhorn Slough	17526	
X	X	Salinas River	1137371	
		Principal subbasins		
	X	Gabilan Creek		2000
	Dry	El Toro Creek		2003
	Dry	Chualar Creek		2003
X	X	Arroyo Seco River		2002
		Stonewall Creek		
	Dry	Chalome Creek		2003
	Dry	San Lorenzo Creek		2003
	Dry	Pancho Rico Creek		2003
X	Barrier	San Antonio River		2003
X	Barrier	Nacimiento River ¹		2003
	Dry	Big Sandy Creek		2003
	Dry	Estrella River		2003
	Dry	San Marcos Creek		2003
	Dry	Huerhuero Creek		2003
X	X	Paso Robles Creek		2003
X	Extirpated	Graves Creek		2003
X	X	Atascadero Creek		2003
X	X	Santa Margarita Creek		2003
		Del Rey Creek	6965	
	Barrier	Seal Rock Creek	393	2002
	Absent	Pescadero Canyon Creek	375	2002
X	X	Carmel River	65822	2002 (D. Dettman, pers. comm.)
X	X	San Jose Creek	3572	2002
	Barrier	Gibson Creek	249	2002
	X	Malpaso Creek	881	2002
	Barrier	Soberanes Creek	828	2002
	Absent	Doud Creek	736	2002
X	X	Garrapata Creek	2782	2002
X	X	Rocky Creek	1359	2002
X	X	Bixby Creek	2940	2002
X	X	Little Sur River	10379	2002
X	X	Big Sur River	15125	2001 (C. Garza <i>et al.</i> pers. comm.)
	Dry	Sycamore Canyon	678	2002
	Barrier	Grimes Canyon	213	2002
X	X	Partington Creek	978	2002
		Hot Springs Canyon	1111	
	Barrier	Lime Creek	208	2002

¹ Marginal habitat below Nacimiento dam was snorkel surveyed in 2003; no *O. mykiss* observed.

Historical Occurrence	Current Occurrence	Basin (north to south)	Area (ha)	Year (and external source for data)
X	X	Big Creek	5774	2001 (C. Garza <i>et al.</i> , pers. comm.)
	X	Vicente Creek	920	2002
X	X	Limekiln Creek	2201	2002
	Absent	Kirk Creek	362	2002
X	X	Mill Creek	1670	2002
	Absent	Wild Cattle Creek	449	2002
X	X	Prewitt Creek	1633	2002
X	X	Plaskett Creek	512	2002
X	X	Willow Creek - Monterey	4214	2001 (T. Laidig, pers. comm.)
X	X	Alder Creek	1085	2002
	X	Villa Creek - Monterey	1140	2002
	Absent	Soda Spring Creek	174	2002
X	X	Salmon Creek	2188	2002
X	X	San Carpofo Creek	9229	2002
		Arroyo de los Chinos	481	
X	Inaccessible	Arroyo de la Cruz	11075	2002
		Oak Knoll Creek	1672	
X	Inaccessible	Little Pico Creek	1886	2002
X	Inaccessible	Pico Creek	3496	2002
X	X	San Simeon Creek	8498	2001 (C. Garza <i>et al.</i> , pers. comm.)
X	X	Santa Rosa Creek	12324	2001 (Alley (2001))
X	X	Villa Creek - SLO	5186	2002
X	Extirpated	Cayucos Creek	2834	2002
	Absent	Little Cayucos Creek	565	2002
X	Barrier	Old Creek	5324	2002
	Barrier	Willow Creek - SLO	887	2002
X	X	Toro Creek	4023	2002
X	X	Morro Creek	6452	2002
X	X	Chorro Creek	11947	2001 (Payne & Assoc. (2001))
	X	Los Osos Creek	6096	2001 (Payne & Assoc. (2001))
X	X	Islay Creek	2452	2002
X	X	Coon Creek	2099	2002
X	X	Diablo Canyon	1400	2002
	Dry	Little Irish Canyon	111	2002
	Dry	Irish Canyon	911	2002
X	X	San Luis Obispo Creek	21339	2002 (Morro Group, Inc. (2002))
	Barrier	Wild Cherry Canyon	400	2002
	Barrier	Pecho Creek	432	2002
	Dry	Rattlesnake Canyon	357	2002
X	X	Pismo Creek	9706	2002
X	X	Arroyo Grande Creek	37996	2003 (M. Kilgour, pers. comm.)
X	X	Santa Maria River	481084	2002 (K. Cooper, pers. comm.)
	Dry	Shuman Canyon	5978	2002
	Absent	San Antonio Creek	45161	2002
X	X	Santa Ynez River	232543	2000 (Anonymous (2000))
	Absent	Honda Creek	3058	2002
X	Extirpated	Jalama Creek	6389	2002
	Inaccessible	Wood Canyon	1026	2002
	Inaccessible	Damsite Canyon	427	2002
	Inaccessible	Canada del Cojo	824	2002
	Inaccessible	Barranca Honda	634	2002
	Inaccessible	Canada de la Llegua	202	2002

Historical Occurrence	Current Occurrence	Basin (north to south)	Area (ha)	Year (and external source for data)
	Inaccessible	Arroyo San Augustin	462	2002
	Inaccessible	Arroyo El Bulito	640	2002
	Inaccessible	Canada del Agua	570	2002
X	X	Canada de Santa Anita	829	2001
	Inaccessible	Canada de la Cuarta	414	2002
	Inaccessible	Canada de Alegria	925	2002
		Agua Caliente	666	
X	X	Canada de la Gaviota	5216	2001
X	Extirpated	Canada San Onofre	538	2002
	Dry	Canada del Molino	399	2002
X	X	Arroyo Hondo	1133	2001
X	Barrier	Arroyo Quemado	779	2002
X	Barrier	Tajiguas Creek	1613	2002
X	Extirpated	Canada del Refugio	2107	2002
X	Barrier	Canada del Venadito	520	2002
X	Barrier	Canada del Corral	1701	2002
X	Extirpated	Canada del Capitan	1607	2002
	Inaccessible	Las Llagas Canyon	716	2002
X	Inaccessible	Gato Canyon	911	2002
	Inaccessible	Las Varas Canyon	748	2002
X	Barrier	Dos Pueblos Canyon	2183	2002
X	Inaccessible	Eagle Canyon	1204	2002
X	Barrier	Tecolote Canyon	1467	2002
X	Barrier	Bell Canyon	1589	2002
X	X	Goleta Slough Complex	12393	2001
X	Barrier	Arroyo Burro	2651	2002
X	X	Mission Creek	2814	2000
	Barrier	Sycamore Creek	1050	2002
X	X	Montecito Creek	1719	2001
X	Barrier	Oak Creek	389	2002
X	X	San Ysidro Creek	1057	2002
X	X	Romero Creek	1507	2001
	Inaccessible	Toro Canyon Creek	953	2002
X	X	Arroyo Paredon	1218	2000
X	Barrier	Carpinteria Salt Marsh Complex	2636	2002
X	X	Carpinteria Creek	3961	2000
X	Barrier	Rincon Creek	3796	2002
		Los Sauces Canyon	2980	
X	X	Ventura River	58666	2001 (C. Zimmerman, pers. comm.)
		Hall Canyon	1884	
		Arundell Barranca	2829	
X	X	Santa Clara River	420965	2001 (M. McEachron, pers. comm.)
		Calleguas Creek	89197	
	Dry	La Jolla Canyon	975	2002
X	Extirpated	Big Sycamore Canyon	5523	2002
		Little Sycamore Canyon	1538	
X	X	Arroyo Sequit	2839	2002
X	X	Malibu Creek	28622	2002
		Carbon Canyon	945	
	Absent	Las Flores Canyon	1075	2002
	Barrier	Piedra Gorda Canyon	190	2002
	Barrier	Pena Canyon	248	2002

Historical Occurrence	Current Occurrence	Basin (north to south)	Area (ha)	Year (and external source for data)
	Absent	Tuna Canyon	413	2002
X	X	Topanga Canyon	5106	2002 (Dagit & Webb 2002)
		Santa Ynez Canyon	1829	
		Santa Monica Canyon	4132	
	Barrier	Solstice Canyon	1154	2002
	Absent	Corral Canyon	944	2002
	Dry	Trancas Canyon	2372	2002
	Dry	Escondido Canyon	933	2002
	Absent	Ramirez Canyon	895	2002
	Absent	Zuma Canyon	2405	2002
		Ballona Creek	33981	
		Dominquez Channel	19579	
X	Barrier	Los Angeles River	216969	2002
X	Barrier	San Gabriel River	183514	2002
X	Barrier	Santa Ana River	661050	2002
		San Diego Creek	31946	
	Barrier	Los Trancos Canyon	495	2002
	Barrier	Muddy Canyon	376	2002
	Dry	Moro Canyon	868	2002
	Inaccessible	Emerald Canyon	581	2002
		Laguna Canyon	2088	
	Inaccessible	Aliso Creek	9300	2002
		Salt Creek	2543	
X	Extirpated	San Juan Creek	46125	2002
		Canada de Segunda Deshecha	2966	
X	X	San Mateo Creek	34789	2002 (T. Hovey, pers. comm.)
X	Dry	San Onofre Creek	11159	2002 (C. White, pers. comm.)
		Las Pulgas Canyon	7087	
		Aliso Canyon	2350	
X	Extirpated	Santa Margarita River	190851	2000 (Swift <i>et al.</i> 2000)
X	Barrier	San Luis Rey River ²	146185	2002
	Inaccessible	Loma Alta Creek	2558	2002
	Inaccessible	Buena Vista Creek	5883	2002
	Inaccessible	Agua Hedionda Creek	8037	2002
		Canyon de las Encincas	1037	
		San Marcos Creek	15489	
	Absent	Escondido Creek	22289	2002
	Barrier	San Dieguito River	90308	2002
	Absent	Los Penasquitos Creek	24616	2002
		Rose Canyon	10257	
		Tecolote Creek	2549	
X	Barrier	San Diego River	113741	2002
		Chollas Creek	8755	
X	Barrier	Sweetwater River	59501	2002
		Telegraph Canyon	2179	
X	Barrier	Otay River	37840	2002
X	Inaccessible	Tijuana River	4149	2002

Note: During the final phases of preparing this technical memorandum, we received reports of historic occurrence in Sacate Creek and Sycamore Creek.

² Road crossing at mouth assumed to be migration barrier.

Appendix C. Resident, residualized, or stocked *O. mykiss* above barriers.

Data are for occurrence within the past 10 years, for historical steelhead basins with barrier exclusions or other extirpations.

Basin (north to south)	Recent occurrence of <i>O. mykiss</i>		
	Below lowest barrer (this study)	Above barrier (obs. 1994 – 2003)	Source of observation
Llagas Creek (Pajaro)	Dry stream	X	J. Smith, pers. comm.
San Antonio River (Salinas)	Barrier exclusion	X	H. Fish, pers. obs.
Nacimiento River (Salinas)	Barrier exclusion	X	D. Boughton, pers. obs.
Graves Creek (Salinas)	Spot check (absent)		
Cayucos Creek	Spot check (absent)		
Old Creek	Barrier exclusion	X	Good <i>et al.</i> (2005)
Jalama Creek	Spot check (absent)	X	Stoecker & CCP (2002)
Canada San Onofre	Spot check (absent)	Last obs. 1991	Stoecker & CCP (2002)
Arroyo Quemado	Barrier exclusion	No recent records	Stoecker & CCP (2002)
Tajiguas Creek	Barrier exclusion	X	Stoecker & CCP (2002)
Canada del Refugio	Spot check (absent)	Last obs. 1990	Stoecker & CCP (2002)
Canada del Venadito	Barrier exclusion	No recent records	Stoecker & CCP (2002)
Canada del Corral	Barrier exclusion	Last obs. 1993	Stoecker & CCP (2002)
Canada del Capitan	Spot check (absent)	No recent records	Stoecker & CCP (2002)
Dos Pueblos Canyon	Barrier exclusion	X	Stoecker & CCP (2002)
Tecolote Canyon	Barrier exclusion	X	Stoecker & CCP (2002)
Bell Canyon	Barrier exclusion	No recent records	Stoecker & CCP (2002)
Arroyo Burro	Barrier exclusion	No recent records	Stoecker & CCP (2002)
Oak Creek	Barrier exclusion	No recent records	Stoecker & CCP (2002)
Carpinteria Salt Marsh Complex	Barrier exclusion	No recent records	Stoecker & CCP (2002)
Rincon Creek	Barrier exclusion	X	Stoecker & CCP (2002)
Big Sycamore Canyon	Spot check (absent)	no barriers?	
Los Angeles River	Barrier exclusion	X	Good <i>et al.</i> (2005)
San Gabriel River	Barrier exclusion	X	Good <i>et al.</i> (2005)
Santa Ana River	Barrier exclusion	X	Good <i>et al.</i> (2005)
San Juan Creek	Spot check (absent)		
San Onofre Creek	Dry stream	no barriers?	
Santa Margarita River	Absent	X	Good <i>et al.</i> (2005)
San Luis Rey River	Barrier exclusion	X	Good <i>et al.</i> (2005)
San Diego River	Barrier exclusion	X	Good <i>et al.</i> (2005)
Sweetwater River	Barrier exclusion	X	Good <i>et al.</i> (2005)
Otay River	Barrier exclusion		Good <i>et al.</i> (2005)

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