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Abstract

Recovery efforts for steelhead are likely to be aided by maps of potential habitat. In the South-Central/Southern California Coast recovery domain, the most geographically restricted habitat type is probably over-summering habitat, due to the mediterranean climate and the general aridity of the region. Here we develop a model of potential over-summering habitat and map it in a Geographic Information System, using the method of environmental envelopes. Under the envelope method, predicted habitat is the set of stream segments falling within the same range of conditions that encapsulate the known occurrences of the species. Thus the method is based on known occurrences described in museum records, environmental reports, scientific papers, and other credible sources. The axes for the "range of conditions" are geomorphic, hydrologic, and climatic features thought to control the broad-scale suitability of stream reaches under natural (unmanaged, unimpaired) conditions. The specific predictors for potential habitat were stream gradient, summer mean discharge, summer temperature, valley width relative to mean discharge, and whether or not the reach occurred in alluvial soils. The resulting model predicts over-summering habitat throughout the recovery domain, as illustrated in 10 synoptic maps included in this report. Various limitations of the model are described at length.

Introduction

The recovery and management of at-risk species usually involves some mix of habitat protection in areas with currently-suitable habitat and habitat restoration in areas that have been somehow degraded. Underlying such efforts must be an objective concept of habitat, preferably one that finds a useful compromise between accuracy, precision, and practicality. Even more useful than a concept is a habitat map encompassing the management area. Such a map can give historical context for, and also serve as a baseline for, management strategies for the species in question.

Steelhead (the anadromous form of *Oncorhynchus mykiss*) are currently considered to be threatened or endangered with extinction throughout much of their range in the state of California. This range includes the coastal basins on the southern half of the state, where the species has a somewhat atypical ecology. In this area, stretching from the heavily forested Santa Cruz Mountains near Monterey Bay to the US border with Mexico, the species inhabits arid areas consisting of oak savanna, grasslands, chaparral, and occasional coniferous forest. During the summer the discharge in many creeks becomes intermittent or dries up completely (Payne and Associates 2004; Spina *et al*. 2005); and in other areas, particularly those too far inland to have a marine-influenced climate, warm summer air temperatures heat up the streams to temperatures unsuitable for steelhead.

For these reasons, steelhead over-summering habitat is thought to have a restricted distribution, more so than winter spawning and rearing habitat. As part of ongoing efforts to develop recovery strategies for steelhead of the south-central and southern California coast, we here derive a model of potential over-summering habitat, and use it to map potential habitat for the coastal basins from the Pajaro River basin at Monterey Bay (inclusive) south to the U.S. border with Mexico. This area is considered to be inhabited by two evolutionarily significant units (ESUs) of steelhead, as described in Busby *et al*. (1996).

Potential habitat, which we focus on here, differs from the term "habitat" as commonly used, in that it refers to areas *potentially* suitable for the species as opposed to *actually* (currently) suitable for the species (where "suitable" means that fecundity or survival is sufficiently high and reliable on average to prevent a population decline). Potential habitat is a more inclusive term—it includes habitat in the conventional sense, but also areas that are not currently suitable but that would normally be suitable under natural conditions (unmanaged or unimpaired conditions). As such it is a useful concept for recovery planning, where the intent is often not just to protect existing habitat but to restore degraded areas as well.

General Modelling Approach

Burnett *et al*. (2003) described a conceptual framework for mapping the potential freshwater habitat of salmonids, which we here adopt. They emphasized the importance of broad-scale geomorphic and hydrologic controls on the potential suitability of stream reaches. In particular, the potential suitability of stream reaches was seen as depending on three parameters: mean annual discharge of the reach, the channel gradient, and a parameter called the valley width index (the ratio of mean annual discharge to the width of the valley in which the stream occurs). The model was based on the idea that natural processes tend to spontaneously generate suitable habitat only in reaches where discharge, gradient, and topography fall within certain bounds. This framework is based on the hierarchical view of fish-habitat relationships advocated by Frissell *et al*. (1986) and Montgomery and Buffington (1998).

Burnett *et al*. (2003) focused on potential salmonid habitat in the Oregon Coast Range. To adapt the framework to Southern California, it is necessary for the habitat model to account for important differences between the ecology of Oregon and Southern California. In our view these key differences are as follows:

1) Oregon steelhead typically share streams with coho salmon, which have strong habitat preferences and also appear to exert asymmetric competition on steelhead (Young 2004). In Southern California, the steelhead may have a

broader realized niche due to lack of competition.

2) Summer stream temperature—omitted from the Oregon model—is an important limiting factor in Southern California (Douglas 1995, Matthews and Berg 1997).

3) Low summertime flows are probably an important limiting factor in Southern California, given the prevalence of intermittent streams in the region (Spina *et al*. 2005).

4) The steelhead in Oregon and Southern California may have slightly different tolerance limits for a given environmental parameter, due to local adaptation (Spina 2006).

5) Many rivers in Southern California run through wide, flat alluvial valleys, where their channels have only fine sediments. In these areas the sediment dynamics are likely to be dominated by deposition of fine sediments, and are not conducive to the formation of the gravel substrate and pool-riffle structure favored by juvenile steelhead.

To account for these differences, we modify the model of Burnett *et al.* (2003) in two ways. First, we add three additional predictors to the model: absence of alluvial substrate; mean August air temperature as an index of stream temperature; and mean August-September discharge as a substitute for mean annual discharge. Second, we re-parameterize the model using local data on *O. mykiss*.

Environmental Envelopes

The method used to re-parameterize the model was necessarily constrained by the available steelhead data, which in our area consisted mostly of observations of species occurrence tied to particular dates and localities (an example is collection data for *O. mykiss* specimens at the Los Angeles County Museum). A simple and robust method for fitting habitat models to such data is the environmental envelope method.

An environmental envelope is an interval on an environmental predictor that encompasses all known occurrences of a species (*e.g*., Carpenter *et al*. 1993). The two observations lying at the extremes—for example the warmest and coolest sites at which *O. mykiss* has been observed—define the zone of tolerance (or “envelope”) for the species, and all stream reaches having temperatures between these two limits are viewed as being potentially suitable. In practice an envelope-model usually has multiple environmental predictors; a stream segment has to fall within the zone of tolerance for every predictor to be considered suitable. Thus, an envelope model has a simple interpretation:

Under the envelope method, potential habitat is the set of stream segments falling within the same range of conditions that encapsulate the known occurrences of the species.

Limitations

An important limitation of the method has to do with structural problems in the available data, namely that they are non-random and censored. For the model to be unbiased and complete, the observers collecting steelhead data need to have been more-or-less spreading their effort systematically (or randomly) across the various stream environments in the region. Violations of this assumption will lead to false negatives, because the known occurrences of the species will cover a smaller range of conditions than all occurrences of the species. It will not lead to false positives.

Likewise, to fit a model of potential habitat, one must use observations from areas that are currently suitable, and the currently suitable areas must be more-or-less spread evenly across the full tolerance range of the species. Otherwise the model will have false negatives.

An appeal of the method is that one can succinctly describe violations of the above assumptions:

In the envelope method, if known occurrences of the species do not span the entire range of conditions that are potentially suitable for the species, the model will underpredict potential habitat.

Another limitation is that we assume the predictors to have no interaction effects—that is, the zone of tolerance on one predictor does not depend on the level of another predictor. If such interactions occur, they could lead to either false positives (in the case of negative interactions) or false negatives (in the case of positive interactions). If interactions occur, in general one would expect them to be negative, because an animal occupying a habitat near its limits of tolerance is stressed, and stress effects would be expected to be additive or synergistic. This suggests that interaction effects, if they occur, would tend to be negative and thus would tend to cause the model to overpredict.

A possible exception could be an interaction between the upper limits for summer flow and summer temperature. The predictor we used—mean August temperature—is an index for mean water temperature, but maximum daily water temperature is at least as important to fish survival as mean water temperature (Jobling 1994, Dunham *et al*. 2003). Maximum daily temperature depends on the mean water temperature, but it also depends on the level of discharge in the stream, because streams with higher discharges tend to have smaller daily fluctuations in temperature (Gu *et al*. 1998, Sinokrot and Gulliver 2000). This is a case where two predictors may have an important positive interaction that would cause false negatives with respect to large warm streams.

Finally, we note several issues of interpretation of the model and resulting maps:

1) In an envelope model, habitat is scored simply as yes or no.

2) Often when a map of a predictor is not available, one must make an astute choice of a proxy variable. In such cases, various mitigating factors can cloud the relationship between the predictor and the fish. An example is the use of summer air temperature to predict fish distribution, which makes an implicit assumption that water temperatures track air temperatures. This is largely true, but the relationship has scatter of about ±4° C (Mohseni and Stefan 1999).

3) Certain estimation problems apply. The range of a sample—used here to estimate the zone of tolerance--is usually smaller than the true range of the population.

4) Estimating ranges (envelopes) is extremely sensitive to errors in locality data (such as latitude or longitude). The reason is that such errors give an observation the appearance of an outlier, and the range is by definition determined by the two most extreme outliers in the dataset. We address this problem using resampling techniques.

5) There could be important predictors for which we have no convenient proxy variable; for example, the distribution of natural enemies.

Detailed Methods

Generating the Stream Networks

We constructed a model of the stream network using a 30m-resolution DEM (Digital Elevation Model) of the study area, obtained from the USGS. The reason we did not use existing digital stream networks is they omit small headwater streams, thought to be important steelhead habitat by Burnett *et al*. (2003). The DEM was converted to 10m resolution via spline interpolation. From this we generated a digital stream network using the programs Bld_grds and Netrace, obtained from Dan Miller (Earth Systems Institute, Seattle Washington) and described in more detail by Miller (2003). The result is a vector-based GIS of stream segments, or reaches, in which reach has a relatively uniform gradient and is on the order of 100m long. For more information on methods see Miller (2003); for parameter values of Bld_grds and Netrace used here see Appendix A.

Compiling Steelhead Data

The criteria for suitable steelhead observations were 1) they must be obtained from credible sources; 2) they must describe juveniles, identified to species; 3) observations were made during the summer (May – October inclusive) in the years 1961 – 2003; and 4) the locality information given in the account was sufficient to map the observation on USGS topographic maps (with less than 100m error) .

Suitable data were compiled from the sources listed in Table 1. This set of sources was not intended to be exhaustive, but rather to be representative of the study area as a whole. The rule to exclude accounts prior to 1961 was made to approximately match the period covered by the climate data used as a predictor (see below).

The data were mapped on digital versions of 7.5′ USGS topographic maps, using Topo! software (National Geographic Holdings, http://www.topo.com), and then overlaid on the digital stream network in a GIS. The observations were then "snapped" to the closest reach in the stream network.

Table 1. Sources for geo-referenced steelhead observations.

Barclay (1975), Boughton (2005), Casagrande at al. (2003), Engblom (2001), Hovey *et al*. (2003), LACM (2003), McEwan (1992), Nielsen (1997), Parmenter and McEwan (1999), Schuler (1973), Smith and Li (1983), Snider (1983), Stoecker and Stoecker (2003), Stoecker and CCP (2002), Payne and Associates (2001), USDA Forest Service (1979), Yedor (2002).

Estimating Stream Discharge

We used linear regression to estimate mean summer discharge for each reach in the stream network. The basic approach was to use USGS gauge data and precipitation maps for the period 1961 – 1990 to construct a relationship between precipitation and discharge, and then use the relationship to infer mean discharge in ungauged reaches.

The precipitation maps were obtained in digital form from the Climate Source (Corvallis, Oregon). They consisted of mean monthly and mean annual precipitation for the period 1961 – 1990 (at resolution of 1000m). See Daly *et al*. (1994) for the methods used to generate the maps.

From the USGS National Water Information System we identified stream gauges that had been operated during the period 1961 – 1990, that occurred in the study area, and that had no major water diversions above them that might alter the natural flow regime. After mapping the gauges in the GIS, we used the 10m DEM and algorithms from the software package ArcInfo (ESRI, Redlands California) to delineate the contributing watershed above each gauge. From this we estimated the area (ha) and mean precipitation (mm) for each contributing watershed. From the gauge data we estimated mean August-September discharge (m^3s^{-1}) for each site, again for the period 1961 – 1990. Symbols for these quantities are listed in Table 2.

Table 2. Quantities used in the regressions for estimating stream discharge.

	Description
CA_i	The area of the contributing watershed for stream segment *i*, in hectares
MAP_i	Mean annual precipitation in the contributing watershed of stream segment *i*, in millimeters
$Q89_i$	Mean discharge for months 8 and 9 (Aug & Sept), in m^3s^{-1}.

The data were used to fit a regression in which mean summer discharge ($Q89_i$) was a function of mean annual precipitation (MAP_i) and watershed size (CA_i):

$$\ln(Q89_i) = y_0 + a\ln(MAP_i) + b\ln(CA_i),$$

where y_0, a, and b are regression parameters. The fitted regression was then used to estimate values of $Q89_i$ for each segment *i* in the stream network.

Preparing the Other Predictors

Besides discharge, four other predictors were necessary for mapping potential habitat: channel gradient, valley width index (both as in Burnett *et al*. 2003), summer temperature and presence of alluvial substrate.

Channel gradient is the mean slope (in percent) of a stream channel measured parallel to its course. The estimator we used was the mean gradient for each reach (stream segment) in the digital stream network, estimated as in Burnett *et al*. (2003) and Miller (2003).

Valley width index is the ratio of valley width to mean annual discharge for a given stream segment; see Burnett *et al*. (2003) and Miller (2003) for methods.

The estimator for summer stream temperature was mean August air temperature for the period 1961 – 1990, obtained as a raster (1000m resolution) from the Climate Source (Corvallis, Oregon). See Daly *et al*. (1994) for methods used in generating this map. The key assumption is that air temperature is a suitable index of stream temperate, which seems reasonable given the results of Mohseni and Stefan (1999) and Mohseni *et al.* (1999). They found a predictable monotonic relationship between weekly stream and air temperatures for most of the United States.

Finally, a map of alluvium was derived from the geologic map of California (Jennings 1977), obtained in digital form from Saucedo *et al*. (2000).

Fitting the envelopes

To compute the environmental envelopes, we first used the GIS to overlay predictors on the map of steelhead observations, and thus obtained predictor values for each observation. From this dataset we then estimated four types of envelopes: complete envelopes, majority-rule envelopes, 95% envelopes, and consensus envelopes (ordered from least to most conservative).

A complete envelope is the interval defined by the maximum and minimum predictor values that are present in the steelhead observations (*i.e*., the range on that predictor). Because this sort of estimate is vulnerable to overprediction due to errors in the data (see introduction), we did resampling (bootstrapping) to obtain more robust estimates.

To do so, we resampled (with replacement) the steelhead data 50,000 times, computed complete envelopes for each resample, and then sorted the envelopes from most conservative (most restrictive) to most inclusive. The bootstrapped envelopes are defined as follows: A 95% envelope is the interval spanned by the 95% most conservative resamples. Majority-rule envelopes are the interval spanned by the 50% + 1 most conservative resamples; and consensus envelopes are the interval spanned by all 50,000 resamples.

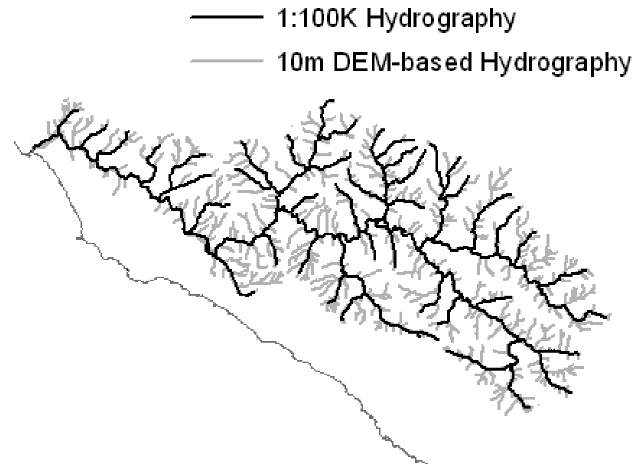


Figure 1. Comparison of the stream network derived in this memorandum to a commonly-used dataset. Depicted is the Big Sur River system

The study area is considered to include two evolutionarily significant units (ESUs) of steelhead—designated the south-central California coast ESU, which inhabits basins from the Pajaro River up to but not including the Santa Maria River system; and the Southern California Coast ESU, which inhabits basins from the Santa Maria River system south to the Tijuana River at the Mexican border. We fit a separate habitat model to each ESU.

In addition, we assumed that the envelope for temperature had only an upper boundary, or in other words, that no stream in the study area is too cold during the summer to be suitable for *O. mykiss*.

Products

Below we summarize key results and provide synoptic maps of potential habitat[1]. Specifically, we describe the preparation of the Aug-Sept Discharge model; depict the evidence that Aug-Sept Discharge and August Air Temperature are key limiting factors for the fish; describe the fitted environmental envelopes that form the core of the

[1] The GIS dataset describing the stream network and potential habitat can be obtained from the Branch Chief, Fisheries Investigation, SW Fisheries Science Center, 110 Shaffer Road, Santa Cruz, CA 95060.

habitat model; and provide 10 annotated synoptic maps of the study area.

The digital stream network we developed has greater detail than existing GIS hydrography models, including the National Hydrography Dataset (USGS 2003) and the 1:100K routed-stream network available from Calfish[2], which is derived from the National Hydrography Dataset. Specifically, the algorithm identified many small first-order channels in the upper watersheds that are not in the other coverages (an example is shown in Figure 1); these are commonly believed to comprise important steelhead habitat in the temperature rainforests further north (Oregon and Washington). Though many such reaches are probably dry channels in Southern California, we did not wish to make assumptions, preferring instead to let the model-fitting process make the determination of whether they comprise potential habitat.

Predictive Discharge Models

Twenty-nine USGS gauges met the criteria for inclusion in the regressions(Table 3). The regression model was statistically significant ($p < 0.005$); however the model only had moderate predictive ability ($R^2 = 0.380$). For other statistical details see Table 4. The regression equation used to assign values to individual stream segments was:

$$Q89_i = \exp[-34.02 + 3.400\ln(MAP_i) + 0.670\ln(CA_i)],$$

using the same notation as before. Standard error of prediction for a particular stream segment i can be estimated as

$$\hat{s}_{\ln Q89} = a\sqrt{p + qMAP_i + rCA_i + sMAP_i \cdot CA_i}$$

where $a = 1.736584$
$p = 3.141828$
$q = -0.43162$
$r = -0.312443$
$s = 0.054028$,

after Sokal and Rohlf (1981). Confidence intervals for a predicted $Q89_i$ can be obtained from the above equation as

Upper 95% c.i. = $Q89_i \exp(2.0555\hat{s}_{\ln Q89})$
Lower 95% c.i. = $Q89_i \exp(-2.0555\hat{s}_{\ln Q89})$.

[2] http://www.calfish.org

Table 3. USGS stream gauges used to fit the model of mean Aug-Sept discharge (1961 – 1990).

USGS ID	Name	Year Begin	Year End
11012500	Campo C nr Campo CA	Oct 1936	Sep 2000
11015000	Sweetwater R nr Descanso CA	Oct 1905	Sep 2000
11023340	Los Penasquitos C nr Poway CA	Oct 1964	Sep 2000
11031500	Agua Caliente C nr Warner Springs CA	Feb 1961	Sep 1987
11033000	WF San Luis Rey R nr Warner Springs CA	Apr 1913	Sep 1986
11054001	Mill C nr Yucaipa CA.+ canals CA	Oct 1918	Sep 1986
11055501	Plunge C nr East Highlands and Canals CA	Feb 1919	Sep 2000
11055801	City C nr Highland CA.+ canals CA	Oct 1919	Sep 2000
11058500	E Twin C nr Arrowhead Springs CA	Feb 1920	Sep 2000
11062001	Lytle C nr Fontana+brlne+cond+inf - W27 CA	Oct 1918	Sep 2000
11063500	Lone Pine C nr Keenbrook CA	Jan 1920	Sep 2000
11098000	Arroyo Seco nr Pasadena CA	Dec 1910	Sep 2000
11111500	Sespe Creek near Wheeler Springs CA	Oct 1947	Feb 1998
11113001	Sespe C + Fillmore Irr Co Cn nr Fillmore CA	Aug 1911	Sep 2000
11113500	Santa Paula C nr Santa Paula	Oct 1927	Sep 2000
11115500	Matilija C a Matilija Hot Springs	Oct 1927	Sep 1988
11116000	NF Matilija C a Matilija Hot Springs CA	Oct 1928	Sep 1983
11117600	Coyote Creek near Oak View CA	Oct 1958	Sep 1988
11117800	Santa Ana C nr Oak View	Oct 1958	Sep 1988
11124500	Santa Cruz C nr Santa Ynez CA	Oct 1941	Sep 2000
11137900	Huasna R nr Arroyo Grande CA	Jun 1959	Sep 1986
11138500	Sisquoc R nr Sisquoc CA	Oct 1929	Dec 1999
11141280	Lopez C nr Arroyo Grande CA	Jul 1967	Sep 2000
11143000	Big Sur R nr Big Sur CA	Apr 1950	Sep 2000
11147070	Santa Rita C nr Templeton CA	Oct 1961	Sep 1994
11149900	San Antonio R nr Lockwood CA	Oct 1965	Sep 2000
11151870	Arroyo Seco nr Greenfield CA	Oct 1961	Feb 1998
11152000	Arroyo Seco nr Soledad CA	Oct 1901	Sep 2000
11153900	Uvas C ab Uvas Res nr Morgan Hill CA	Aug 1961	Sep 1982

Table 4. Log-linear regression model for mean Aug-Sept discharge (Q89) during 1961 – 1990.

Predictive Ability:

$R^2 = 0.380$	Adj $R^2 = 0.332$		SE of Est. = 1.318	
Predictor[1]	**Coefficient**	**Std. Error**	**t**	**P**
Intercept	-34.0149	8.6203	-3.9459	0.0005
Mean annual precip. (ln)	3.4003	0.9905	3.4328	0.0020
Contributing area (ln)	0.6696	0.2541	2.6356	0.0140

Analysis of Variance:

	DF	SS	MS	F	P
Regression	2	27.6574	13.8287	7.9632	0.0020
Residual	26	45.1512	1.7366		
Total	28	72.8086	2.6003		

Assumptions:

Normality Test:	Passed (K-S Statistic = 0.166; p = 0.37)
Constant Variance Test:	Passed (P = 0.48)
Power (at $\alpha = 0.05$):	$\beta = 0.96$

[1] Units: Precipitation: mm; Contributing Area: ha; Discharge: m^3s^{-1}.

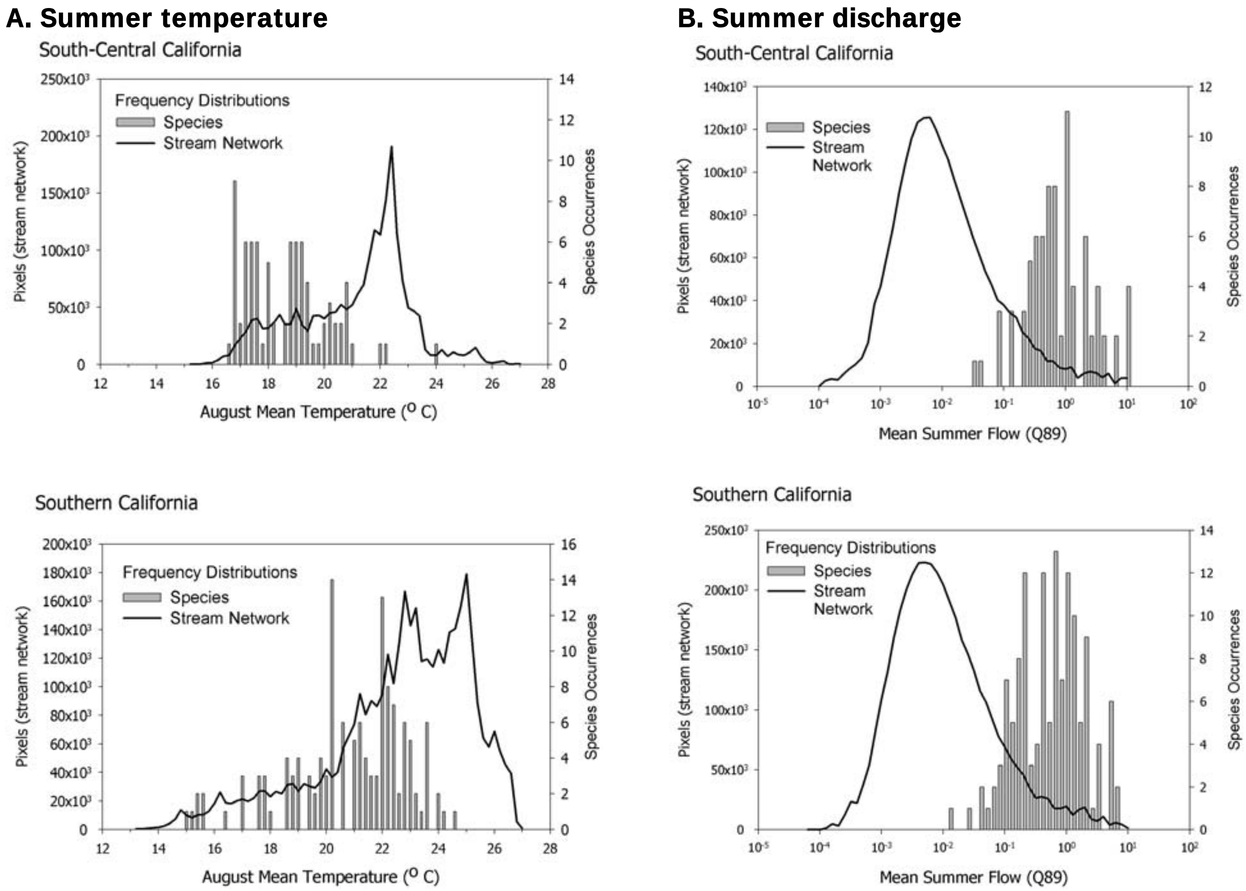


Figure 2. Distribution of fish observations across summer air temperatures (A), and summer discharge (B), relative to background availability in the entire stream network. Background availability is based on a pixelized version of the digital stream network described in the text.

Summer discharge and temperature

The data supported the hypothesis that mean summer discharge and temperature are key limiting factors for the fish. In the case of August mean temperature, the global distribution of stream reaches had a long tail on the left-hand (cool) side, and this was where *O. mykiss* were mostly observed (**Figure 2**A).

In the case of mean summer discharge, the fish tended to occur in the right-hand (high-discharge) tail of the global distribution of stream reaches (**Figure 2**B). In part, this is probably because many of the stream reaches assigned low values for summer discharge in reality have no surface discharge during the summer.

Environmental Envelopes

Table 5 shows the estimated parameters of each environmental envelope. In all cases the majority-rule and one-plus envelopes had the exact same parameters as complete envelopes, and hence are not shown. The parameters for the complete, 95%, and consensus envelopes were quite different. When mapped, the complete envelopes predicted 2½ times more potential habitat than the 95% envelopes, and 9 times more potential habitat than the consensus envelopes (Table 6). Of the three types of estimates, we recommend using the 95% envelopes as they most closely match our intuition for those areas with which we are personally familiar (see synoptic maps at end of section).

Table 5. Environmental envelopes estimated from observations of juvenile *O. mykiss* during the summers of 1961 – 2003.

South-Central California Coast ESU

	Lower boundary of envelope			Upper boundary of envelope		
	Complete*	95%	Consensus	Consensus	95%	Complete*
Summer Discharge (m^3s^{-1})	0.000763	0.002	0.0061	0.09257	0.26984	0.280266
Gradient (%)	0.03	0.03	0.23	6.2	9.31	10.72
Valley Width Index	2.8	3.44	5.84	26.28	37.53	64.96
Mean August Temp. (°C)	-	-	-	20.4	22	24.1
Mean Annual Temp. (°C)	-	-	-	15	15.2	16.1

Southern California Coast ESU

	Lower boundary of envelope			Upper boundary of envelope		
	Complete*	95%	Consensus	Consensus	95%	Complete*
Summer Discharge (m^3s^{-1})	0.000254	0.0008	0.00229	0.09842	0.15412	0.181588
Gradient (%)	0.03	0.03	0.51	8.26	10.57	16.26
Valley Width Index	2.54	2.69	3.76	18.68	29.56	51.24
Mean August Temp. (°C)	-	-	-	23.5	24.1	24.6
Mean Annual Temp. (°C)	-	-	-	16.2	17.4	17.5

* Majority-rule and one-plus envelopes were without exception identical to the complete envelopes.

Inspection of Table 5 indicates the two ESUs had similar tolerance limits for most of the predictors, but with a few notable exceptions. For the 95% envelopes, the lower limit for summer discharge was 2½ times smaller in the southern ESU as compared to the south-central ESU. Similarly, the upper limit for temperature (both mean annual and mean August) was about 2° C higher in the southern ESU compared to the south-central ESU.

We did not test if these differences were statistically significant. From a practical point of view, they are quite significant because they had very large effects on the amount of potential habitat predicted by the model. For example, substituting the August temperature envelope for the southern region into the habitat model for the south-central region would have caused the model to predict habitat in all of the eastern Salinas Valley and San Benito Valley. Field reconnaissance in these areas indicated that such a prediction was clearly a false positive. Conversely, substituting the south-central temperature limit into the southern habitat model would have eliminated potential habitat from many areas where steelhead are currently known to exist. Thus, the difference in limits does not seem spurious.

One possible explanation for the differences is that steelhead of the Southern California Coast ESU are locally adapted to hotter, drier conditions. Another is that the habitat used by steelhead has different relationships with mean air temperature in the two ESUs.

Table 6. Amount of potential over-summering habitat in each ESU, in stream kilometers.

	Potential habitat
South-Central ESU	
Complete envelope	7714 km
95% envelope	2867 km
Consensus envelope	548 km
Southern ESU	
Complete envelope	23,831 km
95% envelope	9399 km
Consensus envelope	2923 km

The data are far from sufficient to distinguish between the local-adaption hypotheses and the different-relationship hypothesis, but for a variety of reasons we tend to favor the latter. First, researchers have so far failed to find local genetic adaption in the thermal tolerances of *O. mykiss* (Myrick and Cech 2004; physiological adaptation has long been known, but is not pertinent here). On the other hand, researchers have indeed found fine-scale varation in stream temperatures, and have also found that salmonids routinely exploit this variation by retreating to the cold-water patches during the hottest period of the day (Matthews and Berg 1997, Torgerson *et al*. 1999, Ebersole *et al*. 2004). In the southern area, one would expect a larger proportion of steelhead to occur in these refugia, and this would tend to give them the appearance of being able to tolerate warmer air temperatures when in fact the real issue is that thermal refugia are proportionately more important to the populations there. In short, it is likely that at any given time a higher proportion of fish are in thermal refugia in the south vs. the south-central area. This in turn would cause a larger difference between mean temperature of water occupied by the fish, and mean temperature of the climate, showing up in the model as a larger upper tolerance limit for air temperature. A similar argument could be made for summer discharge and its relationship to wetted area of streams.

The main implications of this is that the model for the Southern California Coast ESU may have more false positives (warm areas with no potential for thermal refugia), but that these false positives may occur at a finer resolution than addressed by our model.

Synoptic Maps

The following pages depict 10 synoptic maps of potential habitat, using the 95% envelope model. The accompanying notes are based on the authors' personal observations and conversations with local experts, and are not meant to be definitive. Evidence for historic occurrence of steelhead at the basin level of resolution is based on Titus *et al*. (2003), Sleeper (2002), and Franklin (1999).

When interpreting these maps, please note that the algorithm for estimating the stream networks performed poorly in areas of low-relief. Thus, the channel positions on the floor of flat valleys such as the Salinas Valley or the Los Angeles Basin often do not correspond to their known positions. In general, channels in these areas have gradients too low to qualify as potential habitat under our model, or are disqualified due to alluvial substrate. However, the reader should be aware of a controversy. Historical evidence suggests these low gradient areas may once have been suitable for steelhead before alteration in the form of 1) widespread clearing of riparian cottonwoods and willows, 2) down-cutting of channels, and 3) loss of perennial flow. The historical data is described by C. Swift in the appendix of Boughton *et al*. in prep.

Similar considerations apply to areas now submerged under reservoirs. An attempt to reconstruct the submerged topography of such areas would be necessary to predict submerged potential habitat. Such an exercise was clearly beyond the scope of our study due to lack of digital data on the submerged topography. In general, the DEM represented reservoirs as flat surfaces and the channel-routing algorithm thus treated them as flat ground with too shallow a gradient to comprise potential habitat.

Finally, readers should be aware that lagoons serve as steelhead over-summering habitat. Bond (2006) has recently demonstrated that lagoons in fact can comprise very high-quality habitat supporting fast growth rates, early smolting of juveniles, and enhanced marine survival of steelhead. Thus they may have an importance out of proportion to their restricted distribution. However, the mapping of lagoons is outside the scope of this report.

Synoptic Maps

<u>Ordered north to south</u>

Map 1	Monterey Bay Area
Map 2	Central Coast Area
Map 3	San Luis Obispo Area
Map 4	Point Conception Area
Map 5	Santa Barbara to Point Dume
Map 6	Los Angeles Basin
Map 7	San Gabriel Basin and Orange County
Map 8	Santa Ana Basin
Map 9	North San Diego County
Map 10	South San Diego County

Map 1: Monterey Bay Area

In the Pajaro system, most of the potential habitat is predicted to be in the southern Santa Cruz Mountains: the redwood forests drained by Corralitos, Uvas, Llagas, and Pescadero Creeks (in the upper left quadrant of the map). The Pacheco Creek basin (upper right quadrant) was not predicted to contain any potential habitat, yet this watershed is a known steelhead area. One interpretation of the discrepancy is that the reservoir on the North Fork Pacheco may keep stream temperatures unnaturally low and stream flow unnaturally high during the summer.

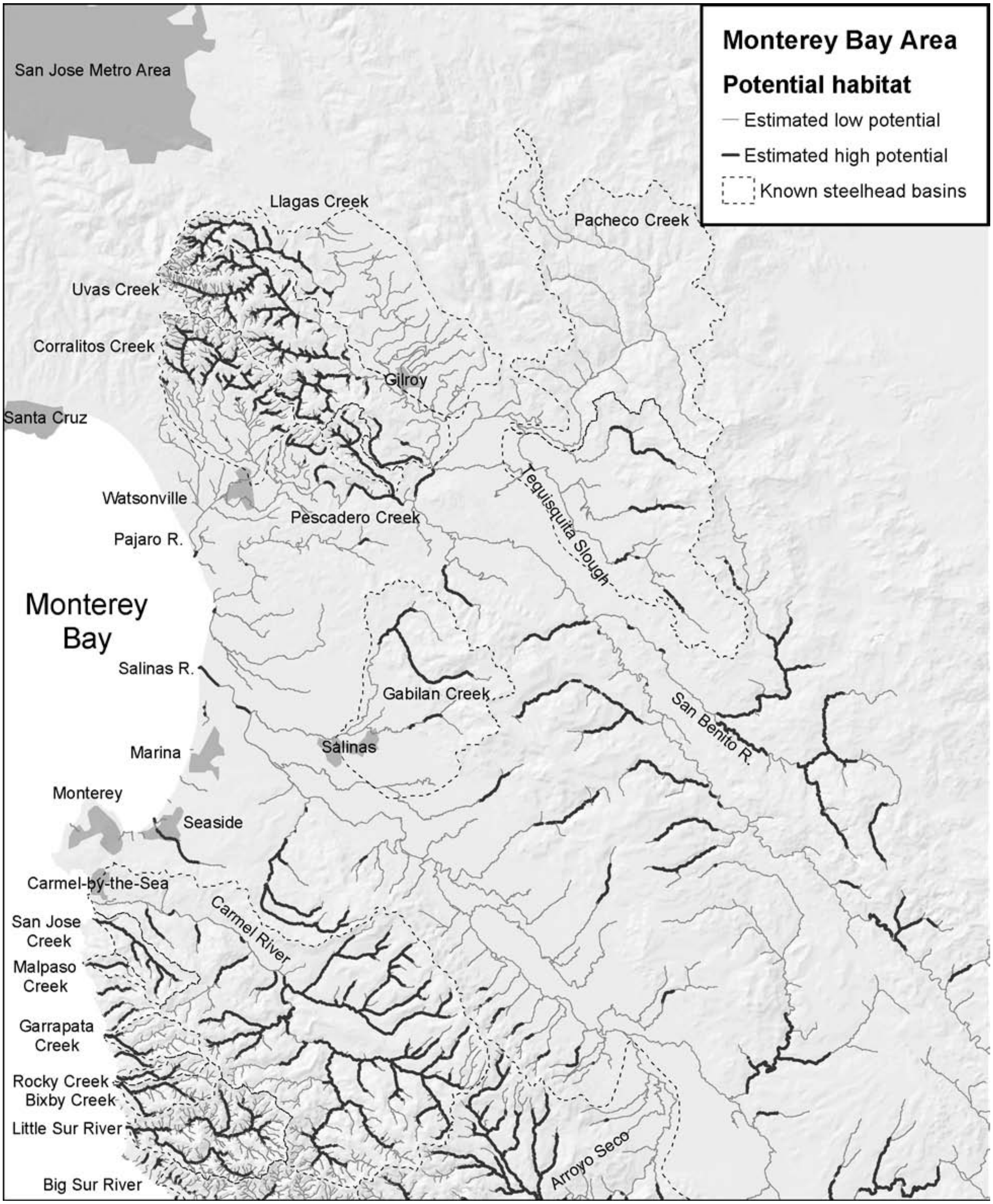
The Carmel River (lower left quadrant) had extensive potential habitat, consistent with its reputation for a historically large steelhead population.

The Big Sur Coast (lower left quadrant) was predicted to have the potential for numerous extremely small populations of *O. mykiss*. However, if interbasin movement were common, these would be more properly regarded as a few large trans-basin populations rather than numerous small ones. The basins with the most extensive potential habitat appeared to be the Big Sur and/or Little Sur basins, although the Big Sur is known to have a natural migration barrier that restricts access to habitat upstream of the state park boundary (J.J. Smith, personal communication, San Jose State University).

In the northern Salinas Valley and San Benito Valleys (center and lower right quadrants of the map), the model predicted numerous small patches of potential habitat on minor tributaries, where there was no record of past steelhead use. It was not certain whether this difference was a failing of the habitat model or a failing of the historical record. On the one hand, all these patches lie in a hot, extremely dry area, and it was not surprising that such areas have no record of *O. mykiss*. And yet, two similar subbasins *did* have records of steelhead occurrence, as seen on the map: they are Gabilan Creek (center of map) and the Tequisquita Slough watershed (upper right quadrant). In the latter, the specific stream in which steelhead have been recorded was Arroyo Dos Picachos.

Arroyo Dos Picachos and Gabilan Creek have exceptional characteristics beneficial for steelhead. Both are relatively shaded. Dos Picachos has consistent summer flows, probably due to volcanic geology; and Gabilan Creek probably has significant influence from coastal weather (i.e. cool fog in the summer). Most of the other streams in the San Benito and east-side Salinas watersheds are in arid areas with low streamflows and little stream shading (savannah and chaparral). Possibly the small west-side tributaries near Hollister would have had steelhead runs historically.

Map 1



Omitted for clarity are reservoirs and channels predicted to have Q89 < 0.5 cfs. Note that channel positions in low-relief areas are likely to be inaccurate, due to model assumptions.

Map 2: Central Coast Area

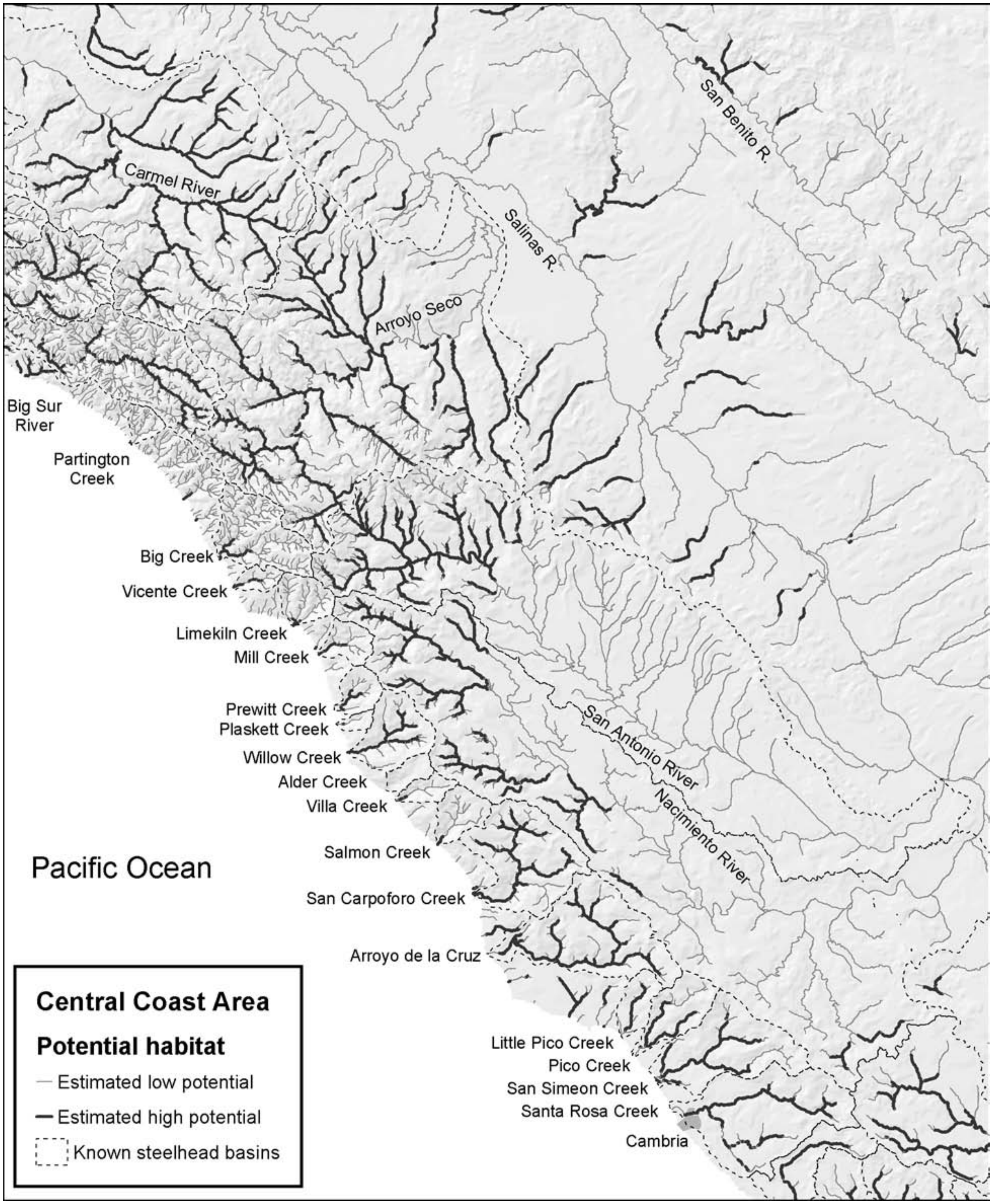
Arroyo Seco and tributaries (upper left quadrant) had more potential habitat than any other tributary system to the Salinas River.

The Nacimiento and San Antonio Rivers, also major tributaries of the Salinas River, had potential as steelhead streams. Map 2 suggested that the potential habitat was concentrated in the far northern reaches of each sub-basin (center of map).

The pattern of the north-eastern Salinas Valley (noted for Map 1) was continued in the south-eastern Salinas Valley: The map indicated patches of potential habitat in hot dry areas with no documented history of steelhead use (upper right quadrant). A few of these streams had records of migrating adults, but none of over-summering juveniles.

The southern Big Sur Coast (Big Sur River to Cambria) had numerous small basins with small amounts of potential habitat. Basins notable for relatively large amounts of habitat were Willow Creek, San Carpoforo Creek, Arroyo de la Cruz, San Simeon Creek, and Santa Rosa Creek, mostly in the southern area near the town of Cambria.

Map 2



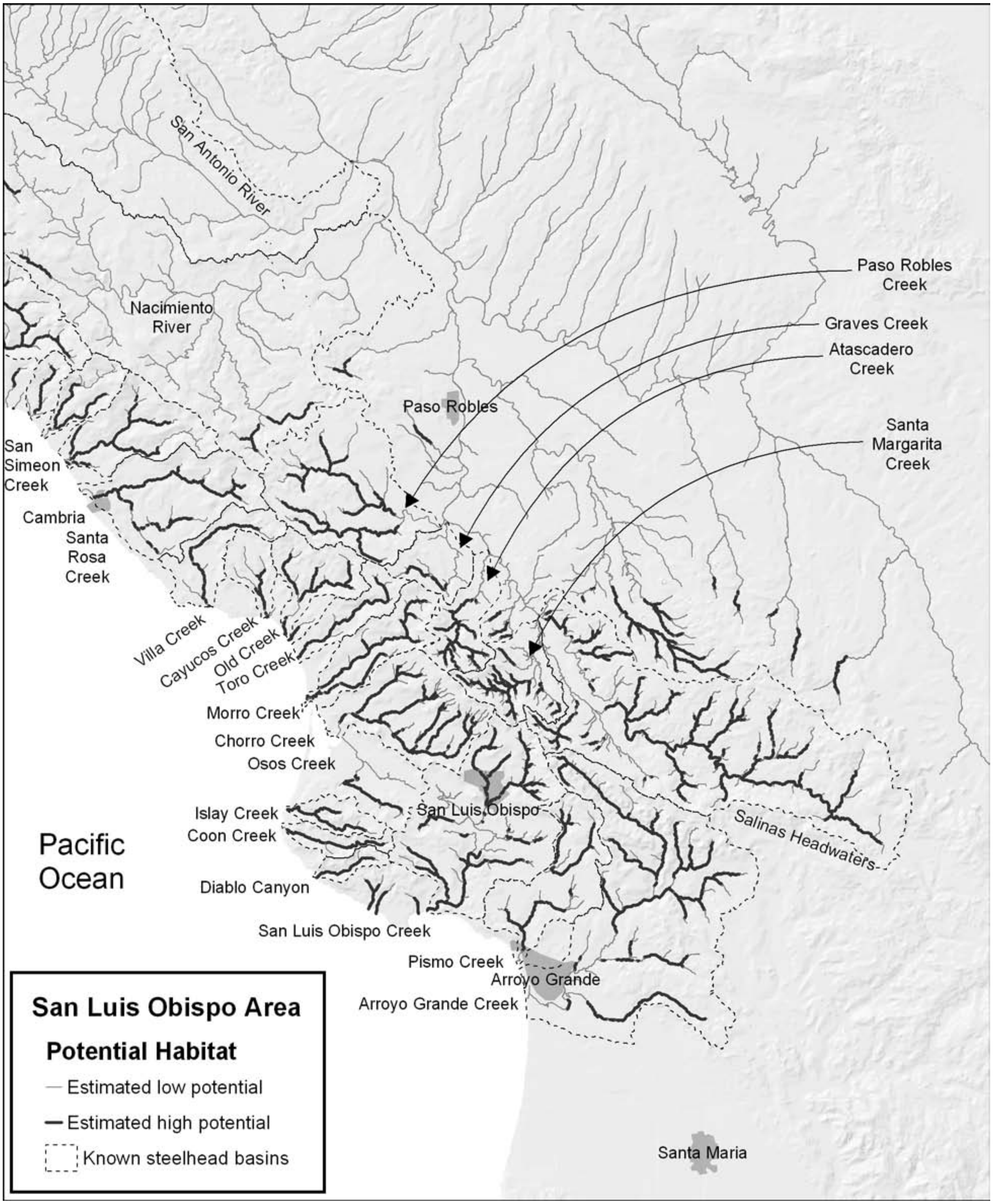
Omitted for clarity are reservoirs and channels predicted to have Q89 < 0.5 cfs. Note that channel positions in low-relief areas are likely to be inaccurate, due to model assumptions.

Map 3: San Luis Obispo Area

In the coastal basins along the San Luis Obispo Coast (Cambria to Arroyo Grande), a large fraction of stream reaches were predicted to be potential habitat. These basins were somewhat larger than those of the Big Sur Coast to the north, yet were still small enough to benefit from a marine-influenced climate during the summer. The Arroyo Grande basin appeared to have the most extensive potential habitat.

The extreme south-western end of the Salinas Valley (Center of map, south of Paso Robles) also had significant amounts of potential habitat. The most extensive potential habitat appeared to be in Paso Robles Creek and tributaries, Atascadero Creek and tributaries, and the Salinas River Headwaters area. However, these sub-basins probably did not have as much potential habitat as the Arroyo Seco, Nacimiento, or San Antonio systems further north in the Valley.

Map 3



Omitted for clarity are reservoirs and channels predicted to have Q89 < 0.5 cfs. Note that channel positions in low-relief areas are likely to be inaccurate, due to model assumptions.

Map 4: Point Conception Area

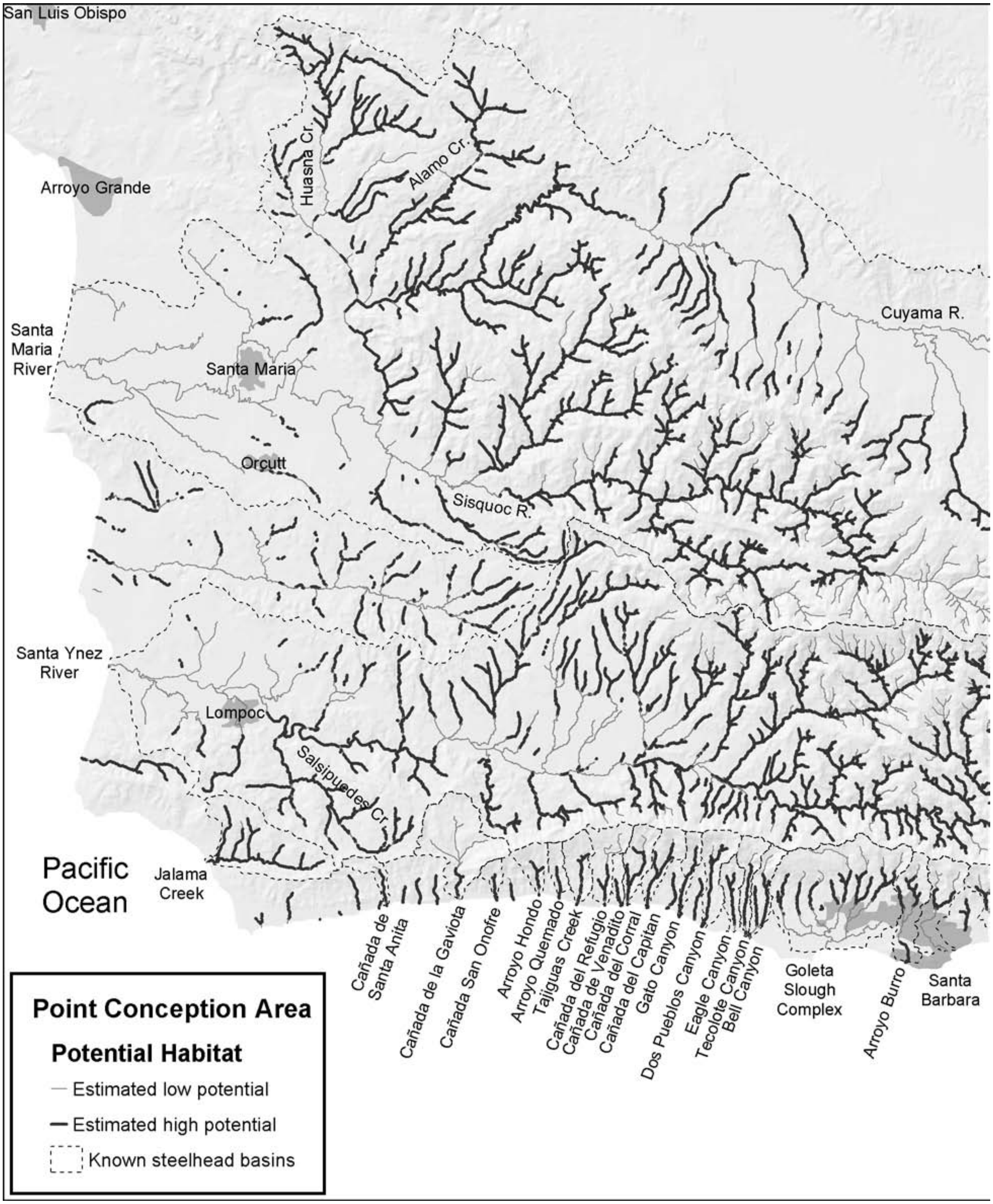
The map clearly depicts an extensive swath of potential habitat with a predicted distribution from the headwaters of Huasna and Alamo Creek (upper edge of the map), southeast through the San Rafael Wilderness (Sisquoc River, center of map), the eastern Santa Ynez basin, and finally to the upper Sespe and Piru watersheds (depicted on Map 5). This result largely conformed to expectations based on the historical record—namely that this area was the most important steelhead area in all of Southern California (Maps 4 – 10).

Potential habitat in the Santa Maria and Santa Ynez was notably more extensive than in any other basins, save the Santa Clara (Map 5). Most of the potential habitat in the Santa Maria system occurred in the Sisquoc River system (center of map) and in the lower part of the Cuyama River system (top-center).

Most of the potential habitat in the Santa Ynez system occurred in the east half of the basin (center-right of map; see also Map 5). However, the model predicted a distinct patch in Salsipuedes Creek and the adjoining mainstem of the Santa Ynez River (on the map, south-east and east of Lompoc, respectively).

Along the southern Santa Barbara Coast (bottom of map, Jalama Creek to Santa Barbara), the model generally agreed with the historical record: numerous small basins with historical records of steelhead were also predicted to have stream networks with large fractions of potential habitat.

Map 4



Omitted for clarity are reservoirs and channels predicted to have Q89 < 0.5 cfs. Note that channel positions in low-relief areas are likely to be inaccurate, due to model assumptions.

Map 5: Santa Barbara to Point Dume

The large swath of potential habitat depicted in Map 4 continued into the upper-left and center of Map 5. This swath included extensive areas in the eastern Santa Ynez basin (center-left on the map) and several large tributary systems of the Santa Clara Basin (center of map). These included Sespe Creek and Piru Creek; mostly in their western headwaters.

Contrary to expectations, lower Sespe Creek (east of Santa Paula) was generally not predicted to contain potential habitat.

There was a small but significant patch of habitat on another tributary of the Santa Clara River: Santa Paula Creek, north of the town of Santa Paula (center of map). This was a known steelhead creek. In contrast, none of the various small tributaries between Santa Paula and Saticoy had a record of steelhead occurrence, despite the model prediction of potential habitat in each one.

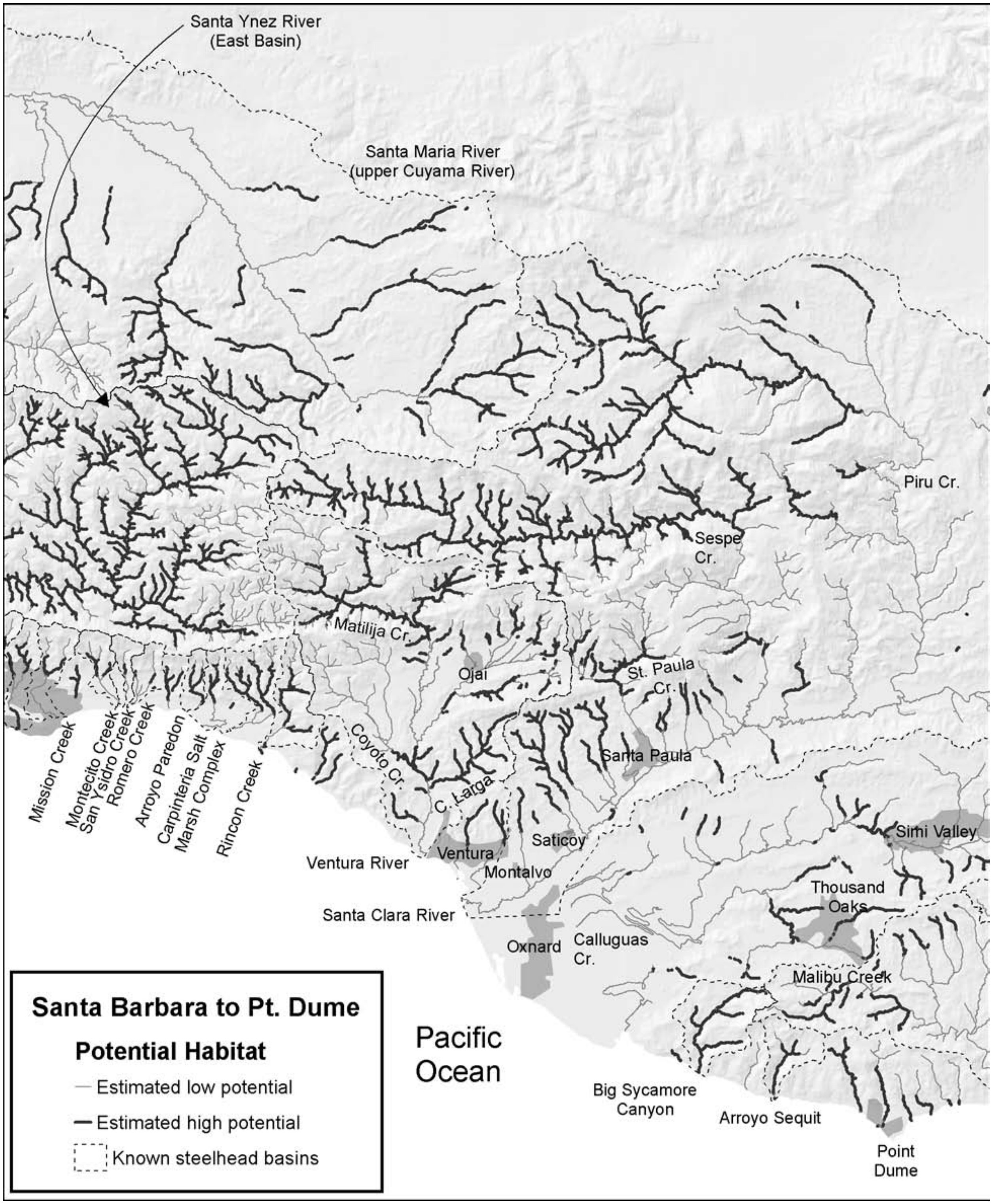
A number of other model predictions did not conform to widely-held expectations. For example, the model suggested that potential habitat in the Ventura River system was restricted to Cañada Larga (north of the town of Ventura) and the various forks of Matilija Creek (north-west end of the basin). Coyote Creek only had potential habitat in the lowest reach; whereas the expectation was for potential habitat in the headwaters due to records of its occurrence there.

Scattered patches of potential habitat appear in the vicinity of Thousand Oaks and Simi Valley (lower right quadrant of the map). This is in the watershed of Calleguas Creek, which is not a system for which we have historical records of steelhead occurrence.

Interestingly, most of the reaches in Big Sycamore Canyon are predicted to be potential habitat. The reaches are reported to be nearly all dry during the summer, so in this case the model predictions do not conform to expectations.

See Map 6 for notes on the Arroyo Sequit and Malibu Creek systems.

Map 5



Omitted for clarity are reservoirs and channels predicted to have Q89 < 0.5 cfs. Note that channel positions in low-relief areas are likely to be inaccurate, due to model assumptions.

Map 6: Los Angeles Basin

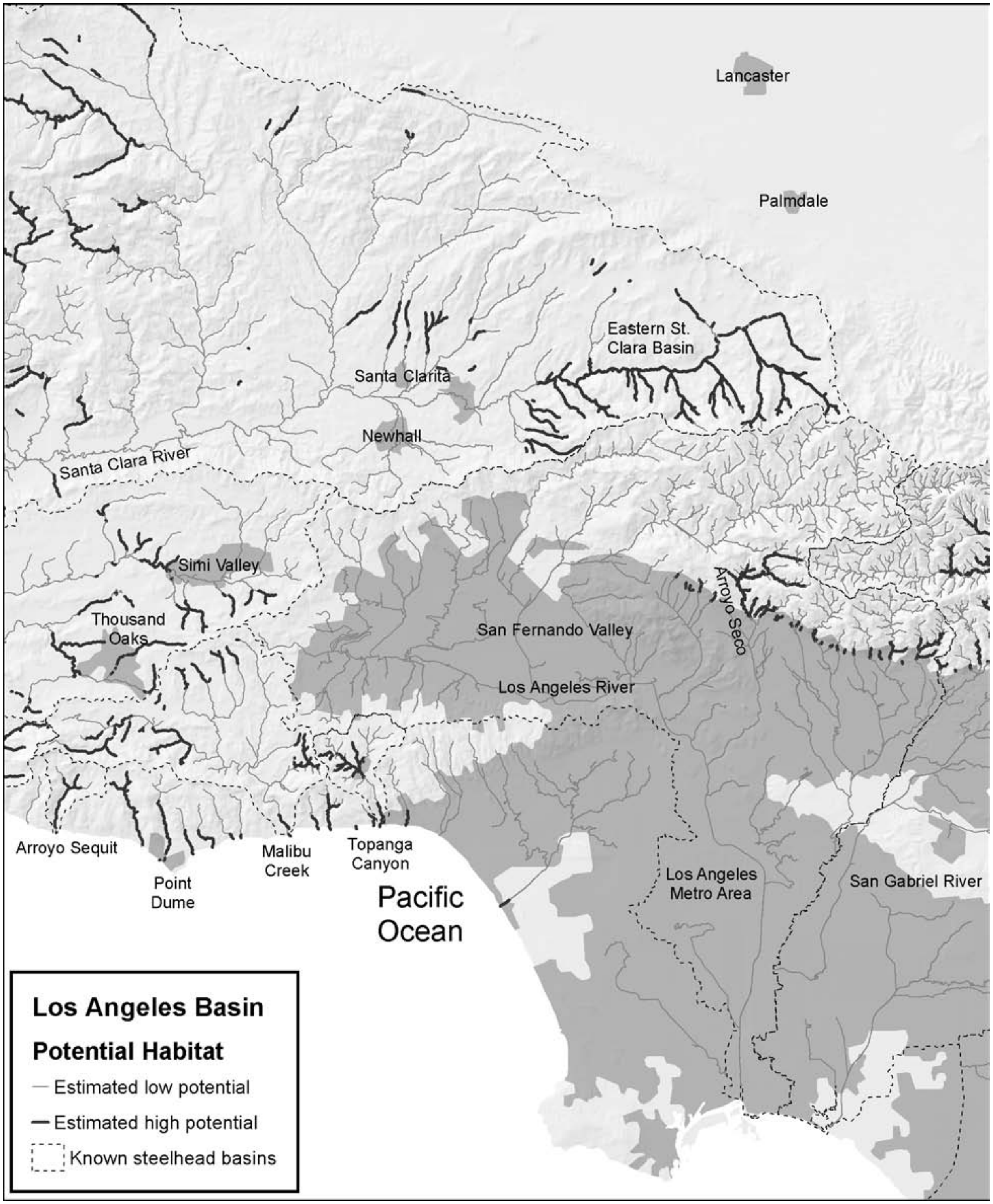
In the Santa Monica Mountains, (lower left quadrant of the map), the four historic steelhead basins were all predicted to have small but significant areas of potential habitat (these steelhead basins were Arroyo Sequit, Malibu Creek, Topanga Canyon, and on Map 5, Big Sycamore Canyon). A surprise was the modest amount of potential habitat predicted for the Malibu Creek system. It appeared to be restricted to the far west end and extreme upper tributaries elsewhere (as well as a small patch at the mouth).

Also in the Santa Monica Mountains were two small systems with predicted habitat but no past record of steelhead occurrence. These were the two creeks between Point Dume and Arroyo Sequit, namely Zuma and Trancas Canyons.

The model predicted a distinct patch of potential habitat in the far eastern end of the Santa Clara basin (upper right quadrant, east of Newhall). This did not conform to expectations. Reports from the area suggested that steelhead were confined to the western end of the Santa Clara system (Map 5). Visits to the eastern area between Newhall and Palmdale indicated that this area is drier than implied by the model, due to a rain-shadow effect from the San Gabriel Mountains (C. Swift, personal communication, Entrix). It probably did not contain potential habitat in reality.

The Los Angeles River system was predicted to have almost no potential habitat, with the possible exception of the headwaters of Arroyo Seco (center-right on the map, east of the San Fernando Valley).

Map 6



Omitted for clarity are reservoirs and channels predicted to have Q89 < 0.5 cfs. Note that channel positions in low-relief areas are likely to be inaccurate, due to model assumptions.

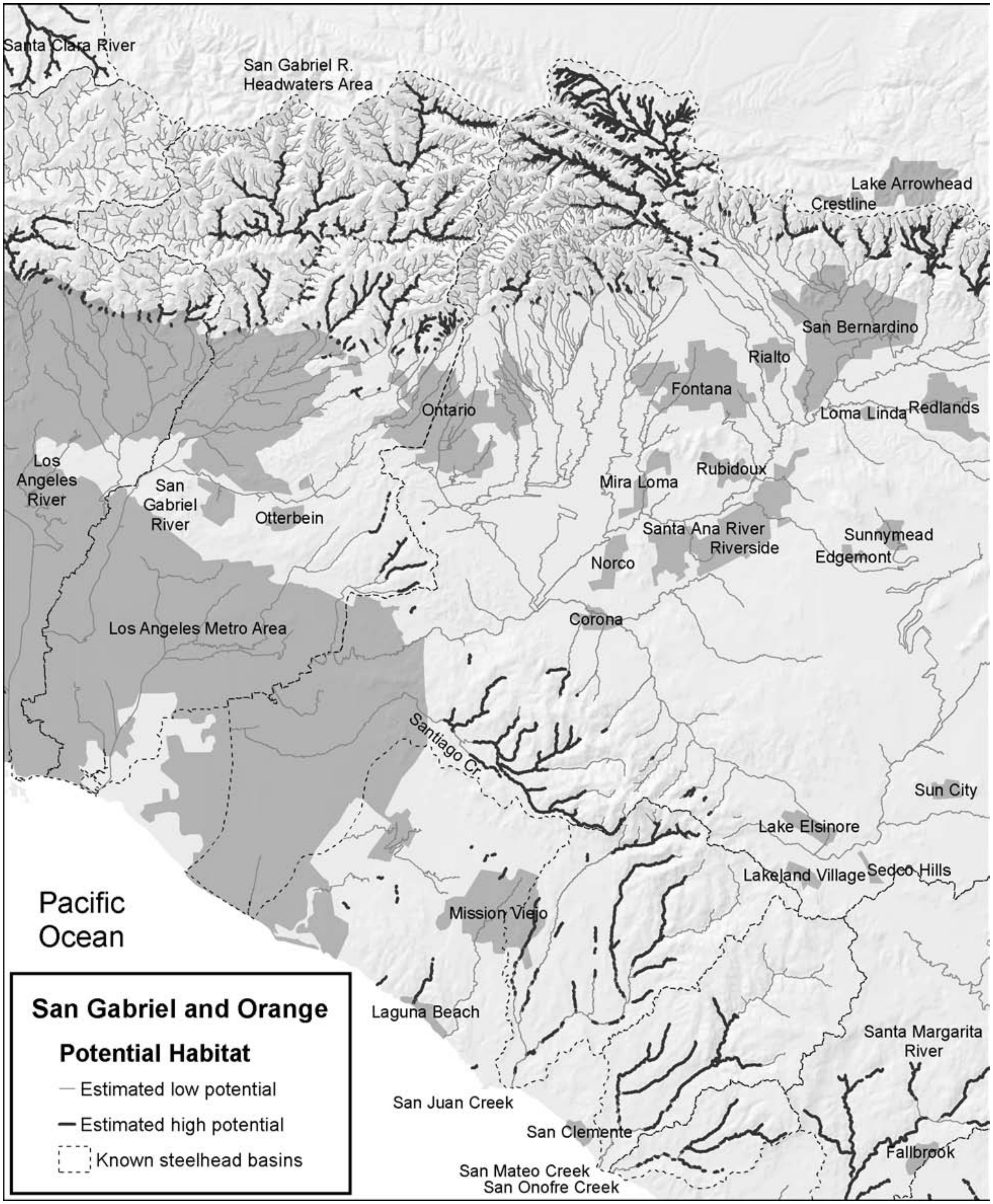
Map 7: San Gabriel Basin and Orange County

The San Gabriel River system appeared to have several significant patches of potential habitat in its northern headwaters, north and northwest of Ontario (top left quadrant of the map). Most significant of these were the various forks of the San Gabriel River itself. Other tributaries with potential habitat, such as the ones immediately northwest of Ontario, were separated from the main patches of habitat by reaches in the flat lowlands south of the San Gabriel Mountains.

In the Orange County area (south-east quadrant of the map), several coastal creeks appeared to have both significant amounts of potential habitat, and a historical record of steelhead occurrence. These were San Juan Creek, San Mateo Creek, and San Onofre Creek (the latter two cross the border into San Diego County). San Mateo Creek currently harbors a small steelhead population. San Juan Creek had a well-documented history of steelhead occurrence.

Of interest was the large patch of potential habitat between Mission Viejo and Corona. This is Santiago Creek and its tributaries, part of the Santa Ana System, and was proximal to the ocean relative to the other potential habitat in the Santa Ana System (Map 8). We have not found any specific historical records of steelhead in this creek, but the large patch of potential habitat raises the question.

Map 7



Omitted for clarity are reservoirs and channels predicted to have Q89 < 0.5 cfs. Note that channel positions in low-relief areas are likely to be inaccurate, due to model assumptions.

Map 8: Santa Ana Basin

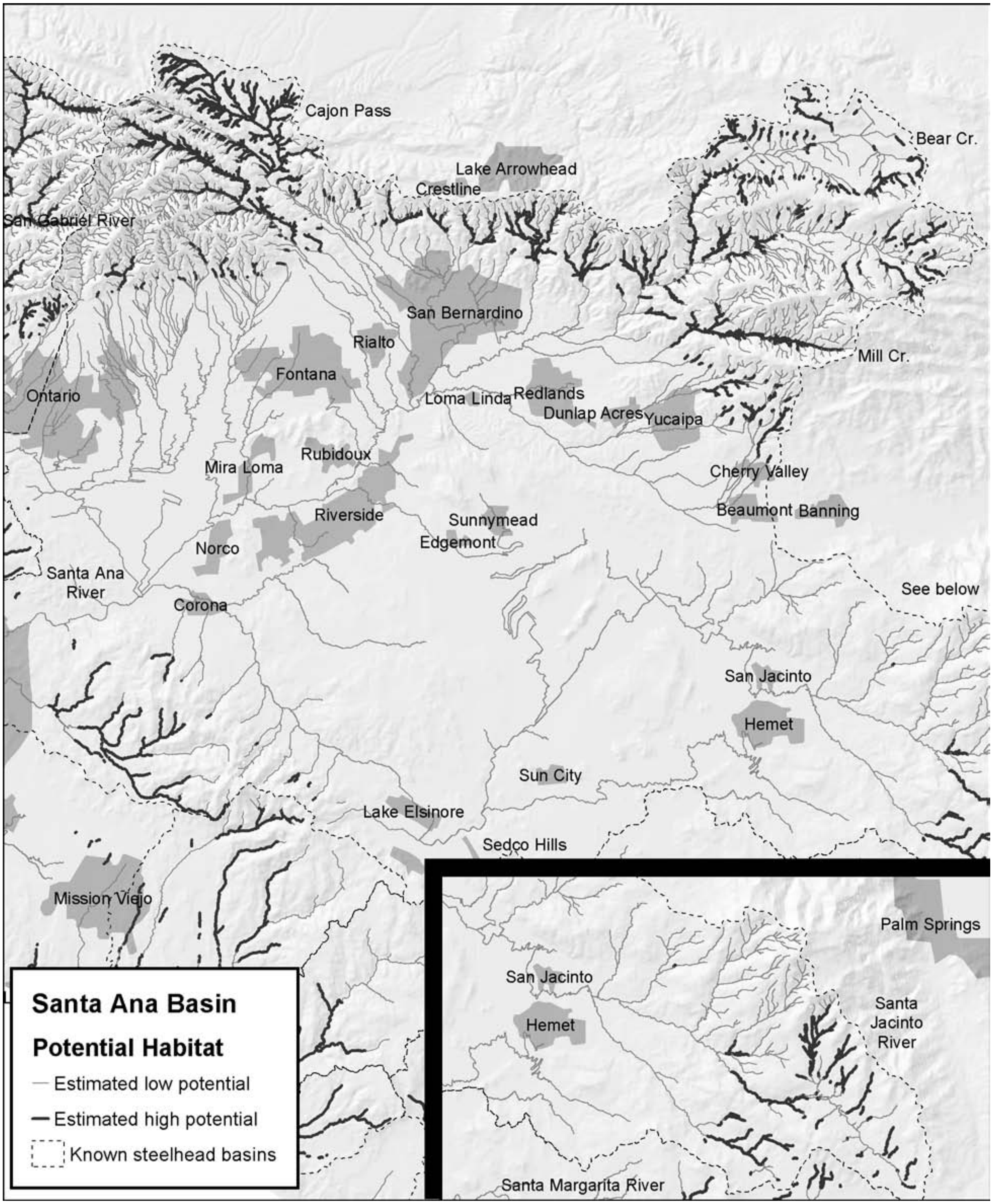
The Santa Ana basin had small patches of potential habitat scattered throughout three headwaters areas.

The most extensive of these appeared to be the area west of Cajon Pass (northwest of San Bernardino on the map). The second headwaters area was Bear Creek and Mill Creek in the mountains north-east of Redlands, with numerous small patches between San Barnardino and Crestline. Most of the individual streams in these two areas were separated from one another (as the fish swims) by reaches in the flat lowlands .

The third headwaters area was in the far south-east, in the headwaters of the San Jacinto River (inset map). Historically, the San Jacinto River infrequently discharged into the Santa Ana River via Lake Elsinore. Thus in terms of steelhead migration, the headwaters area of the San Jacinto has always been very isolated.

For the patch between Mission Viejo and Corona (lower left quadrant of map), see notes for Map 7.

Map 8



Omitted for clarity are reservoirs and channels predicted to have Q89 < 0.5 cfs. Note that channel positions in low-relief areas are likely to be inaccurate, due to model assumptions.

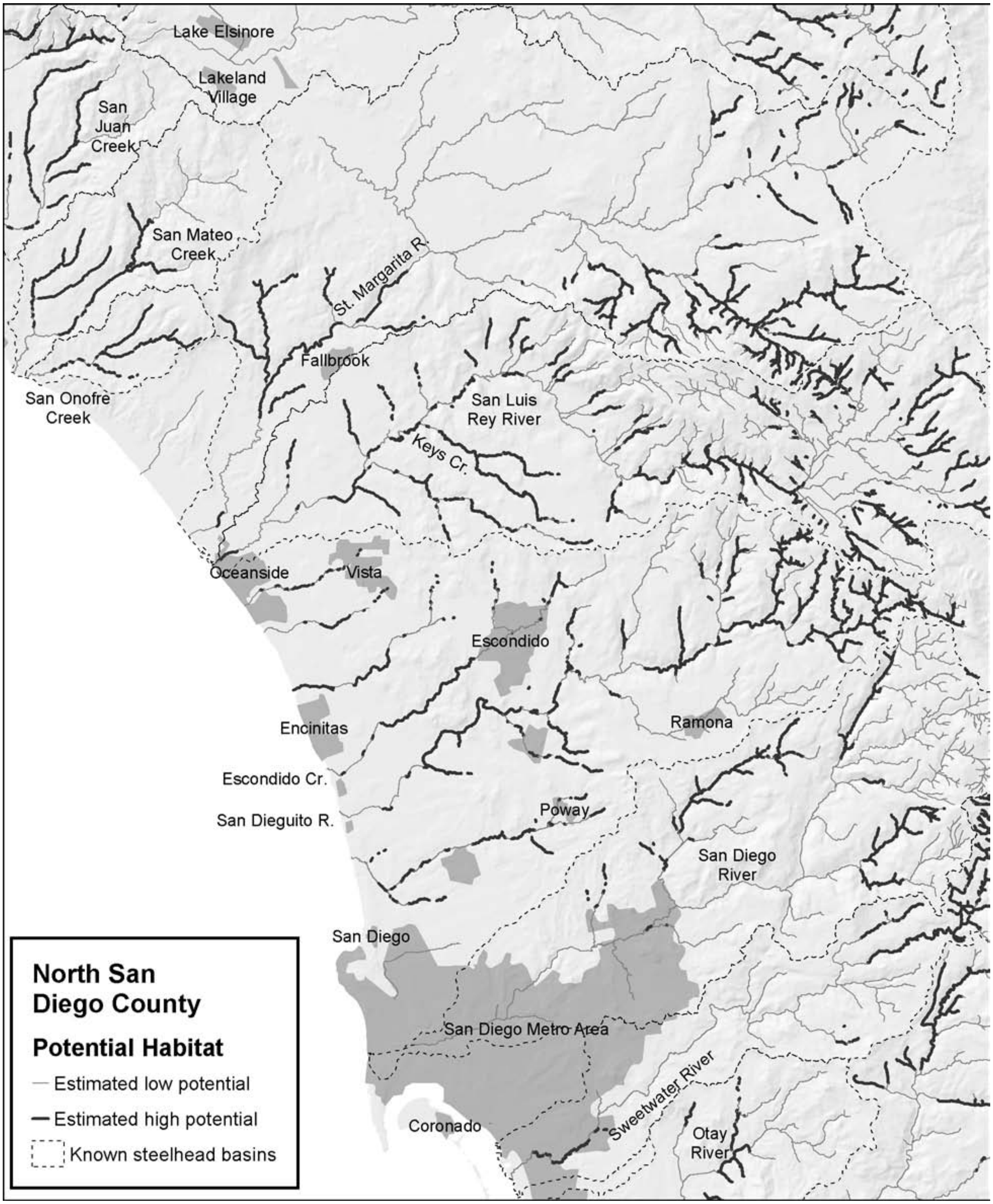
Map 9: North San Diego County

The Santa Margarita basin (top center) had two clusters of potential habitat—one in the vicinity of Fallbrook and a second in the eastern headwaters region. Nothing was known from the historical record about steelhead in either of these areas.

In other basins south of Fallbrook, the model suggested numerous small patches of potential habitat, none particularly large. The most extensive appeared to be Keys Creek, a tributary of the San Luis Rey River (north of Escondido); the mainstem San Luis Rey itself in the canyon below Lake Henshaw; Escondido Creek and San Dieguito River just southwest of the town of Escondido; and the headwaters of the San Dieguito River northeast of Ramona. Escondido Creek and San Dieguito River did not have historical records of steelhead occurrence, and it must be said that the historical record for the other systems on this map was quite vague.

See Map 10 for notes on creeks south of Ramona.

Map 9



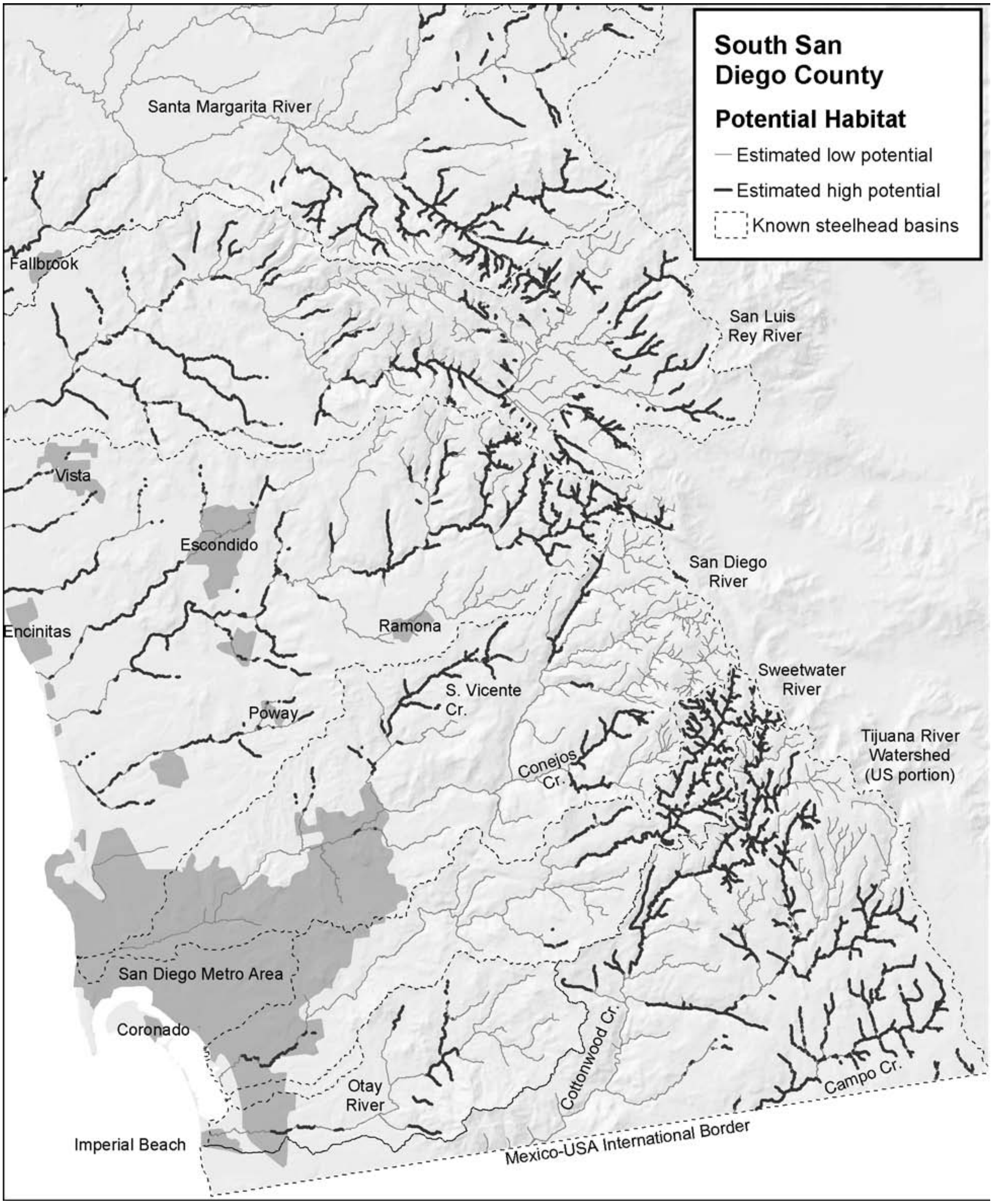
Omitted for clarity are reservoirs and channels predicted to have Q89 < 0.5 cfs. Note that channel positions in low-relief areas are likely to be inaccurate, due to model assumptions.

Map 10: South San Diego County

This map depicts the southern geographic limits of historic steelhead distribution (with the exception of a single population much further south in Baja California del Norte). Although the record indicated steelhead were present, their detailed historic distribution here was virtually unknown.

The habitat model suggested numerous areas with the potential for over-summering habitat. Overall the system of patches appeared somewhat fragmented. The most significant patches included the headwaters of San Vicente Creek just south of Ramona; and headwaters of the San Diego River and Conejos Creek east and southeast of Ramona (above current-day El Capitan Reservoir). In the extreme far south, both the Sweetwater River and Cottonwood Creek (a tributary of Tijuana River) appeared to have surprisingly extensive networks of potential habitat in their eastern headwaters. The Otay River occurred in a smaller watershed, but had a significant patch of potential habitat as well as historic accounts of steelhead use.

Map 10



Omitted for clarity are reservoirs and channels predicted to have Q89 < 0.5 cfs. Note that channel positions in low-relief areas are likely to be inaccurate, due to model assumptions.

Acknowledgements

We wish to thank Fred Watson for useful insights and analyses; Rob Schick and Aditya Agrawal for much effort in generating the 10m DEM and derived stream network; Morgan Kilgour and Jon Goin for help georeferencing the fish observations; and Ethan Mora for preparing the metadata and the final release of the digital stream network.

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Appendix A. Input parameters used for generating stream networks using Bld_grds.exe and Netrace.exe (see Miller 2003).

Input Parameters for Bld_grds and Trace	
1	flow direction algorithm (1 for Tarboton, 2 for Tarboton + convergence)
2	sl, number of pixels over which slope is calculated (> 1 to address "pocket terracing")
2.0	dig; depth of DEM incision for drainage enforcement
1	Channel threshold criteria:(1) Drainage area (2) Specific drainage area.
7500.	channel_area_threshold ! maximum area for zero-order channel
1500.	C_min, square meters ! (1500./1000000. for Oregon)
2.0	c_exp, slope exponent
0.25	S_max ! minimum slope for landslide potential, calibrated to DEM with landslide inventory
1.5	P_min, minimum number of inflowing cells for channel head
50.	lstop_max ! maximum length for unchannelized, low-gradient debris flow runout, DEM-resolution dependent
30.	Xmin, minimum window length for channel gradient estimation
300.	Xmax, maximum window length
0.001	Smin, gradient at and below which Xmax applies
0.2	Smax, gradient at and above which Xmin applies
2	Fit Order, integer, polynomial order for fit
50.	junction_length ! channel length used to estimate junction angles
2.19108	width_coefficient_1, channel width function,
1.32366	width_coefficient_2, channel width function
2.19108	width_coefficient_3
1.32366	width_coefficient_4
180.	width_cross_over (sq. km)
0.3933	depth_coefficient_1, bank-full depth = depth_coefficient_1*(area**depth_coefficient_2)
0.1484	depth_coefficient_2
1	reach method: 1) channel widths, 2) specified length !
20	# of channel widths for a reach, for reach-method 1
10.	minimum reach length in meters, for reach-method 2
10.	maximum reach length in meters, reach-method 2
0.04	area (km2) at and below which minimum reach length is enforced, reach-method 2
50.0	area (km2) at and above which maximum reach length is enforced, reach-method 2
150.	minimum reach length for increasing max_grad_down
200.	maximum reach length for increasing max_grad_down
0.04	Drainage area (sq km) at and below which minimum reach length applies
50.	Drainage area (sq km) at and above which maximum reach length applies
1.0	Area weighting for reach breaks (larger values increase effect of tributary inputs)
5	vh, number of bank-full depths above channel to qualify as floodplain
0.15	ds_v, increase over channel gradient to qualify as floodplain
6.3187e-6	Mean annual flow, coefficient 1, AF = c1*(Area^c2)*(Precip^c3)
0.990	Mean annual flow, coefficient 2, Area in acres, Precip in inches
1.593	Mean annual flow, coefficient 3
UTM grid information	
27	datum, 83 for NAD83, 27 for NAD27
10	UTM zone number

SOIL parameters (assuming metric units) used by SHALSTAB	
2000.	Soil Saturated Bulk Density (kilograms per cubic meter)
45.	Soil Friction Angle (degrees)
0.0	Soil Cohesion (Pascals)
65.0	Saturated Soil Conductivity (meters per day)
1.0	Soil Depth (meters)
0.05	Soil Porosity

RASTER file generation for probability of debris-flow delivery	
5	number of fish-barring gradients
10	Downstream gradient to bar fish passage(all)
0.20	Downstream gradient to bar fish passage(cutthroat?)
0.14	Downstream gradient to bar fish passage(steelhead)
0.10	Downstream gradient to bar fish passage(coho)
0.07	Downstream gradient to bar fish passage(chinook)

SHAPEFILE options	
y	ARCVIEW shape file output for channel reaches (y/n)
n	Force reach breaks at channel junctions (y/n)
2	1) Fixed-length reaches, or 2) homogenous reaches
y	Stream order (y/n)
y	Channel_gradient (y/n)
2	Gradient calculation method: 1) via contours, 2) poly fit over centered window
n	Debris flow delivery (y/n)
y	Valley width (y/n)
n	Valley side slopes (y/n)
y	Mean annual discharge (cfs) calculation for western Oregon (y/n)
n	Include lake attribute (even if no lake mask) (y/n)
n	ARCVIEW shape file output for tributary junctions (y/n)
n	Link shape file (channel links only, used to create routed channel coverage) (y/n)
n	Specified reach endpoints (requires input file with endpoint locations) (y/n)

RASTER output options	
n	Hillslope pixel distance to nearest stream channel, raster file (y/n)
n	Hillslope pixel delivered-to-channel-reach ID, raster file (y/n) (requires reach shapefile)
n	Create valley floor raster image vmask_ID.flt (.hdr) (y/n) (requires reach shapefile)
n	Debris flow inundation hazard (y/n)

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