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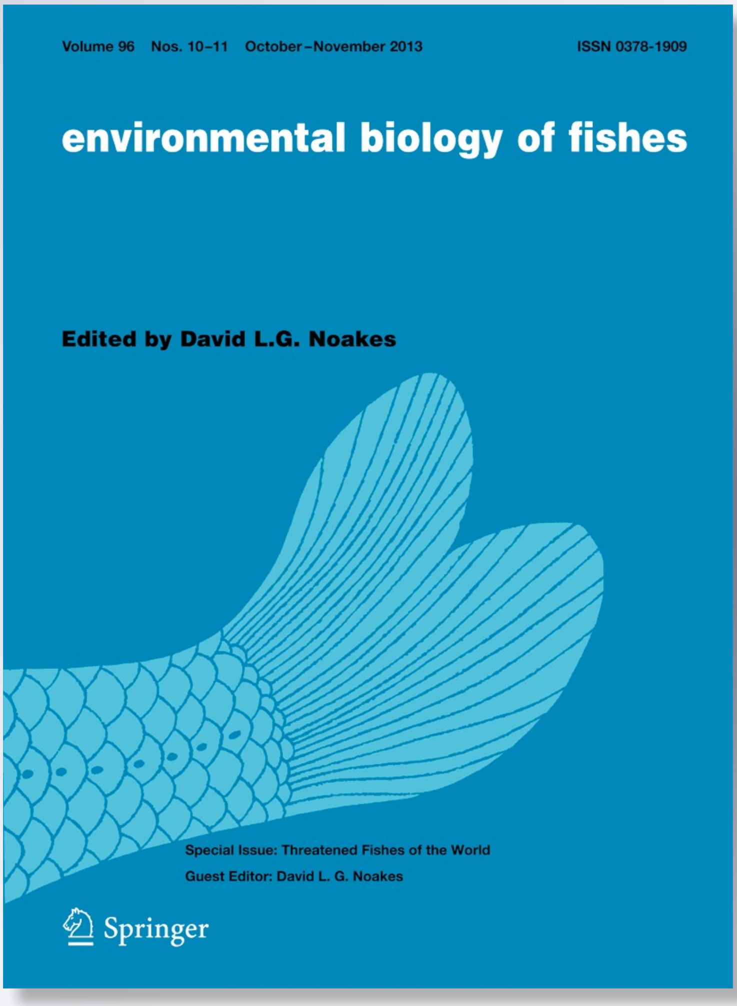

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Impending extinction of salmon, steelhead, and trout (Salmonidae) in California

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Abstract California contains the southernmost native populations of most Pacific Coast salmon and trout, many of which appear to be rapidly headed toward extinction. A quantitative protocol was developed to determine conservation status of all salmonids native to the state. Results indicate that if present trends continue, 25 (78%) of the 32 taxa native to California will likely be extinct or extirpated within the next century, following the bull trout (*Salvelinus confluentus*), which was extirpated in the 1970s. California's salmonids are adapted to living in a topographically diverse region with a Mediterranean climate, characterized by extreme seasonal and inter-annual variability in streamflow. Consequently, California salmonids have evolved extraordinary life history diversity to persist in the face of stressful conditions that often approach physiological limits. The spatial distributions of California salmonids vary from wide-ranging anadromous forms to endemic inland forms persisting in only a few kilometers of stream. Eighty-one percent of anadromous taxa are threatened with extinction and 73% inland taxa are either threatened or already extinct. Although specific drivers of decline differ across species, major causes of decline are related to increasing competition with humans for water, human degradation of watersheds, and adverse effects of hatchery propagation. Climate change, interacting with the other causes of decline, is increasing the trajectory towards extinction for most populations. Bringing all of California's salmonid fishes back from the brink of extinction may not be possible. If there are bold changes to management policy, however, self-sustaining populations of many species may be possible due to their inherent ability to adapt to changing conditions.

Keywords Status assessment · Aquatic conservation · Climate · Hatchery · Mediterranean

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Introduction

> "…political compromise can't halt the forces that lead to extinction. Political compromises resolve human contests, but they seem to exert little or no influence over complex ecosystems. Without drastic action, the relentless ticking of the extinction clock continues."
>
> Paul VanDevelder, High Country News, March 4, 2011

Salmon, trout, and their relatives (Salmonidae) are iconic fishes of the Northern Hemisphere. They have adapted to cold productive oceans, rushing streams, and deep cold lakes, supporting fisheries wherever they occur. Salmonids have evolved diverse life history strategies in response to living in landscapes shaped by glaciers, volcanoes, earthquakes, and climatic extremes (Waples et al. 2008). Many undertake long oceanic and freshwater migrations while others evolved in isolation under extreme local conditions (Moyle 2002). Mobility coupled with natal homing and remarkable behavioral plasticity has resulted in a handful of species producing hundreds of genetically distinct runs, regional populations, and subspecies, representing distinctive color patterns, behaviors, and ecological attributes, tuned to local environmental conditions (Allendorf and Waples 1996; Behnke 2002). Many are top predators in the ocean and freshwater systems they inhabit. Their adaptability has also made some species extremely abundant, resulting in valuable fisheries throughout the northern hemisphere and, through introductions, the southern hemisphere as well (Montgomery 2003).

Despite their ecological, cultural, aesthetic, and economic importance, salmonid fishes are in severe decline in many, if not most, of their native habitats. Many populations have been extirpated, especially in heavily industrialized areas (Montgomery 2003). Perhaps nowhere in the world is the diversity of salmonids and their problems more evident than in California where a highly endemic fish fauna is interacting with intense human population pressure (Lackey et al. 2006; Moyle et al. 2008). The state's dynamic geology and climate have resulted in evolution of many distinctive forms, all characterized by distinctive zoogeographic, genetic, and life history patterns, such as three subspecies of golden trout in the Sierra Nevada and eight distinct types of Chinook salmon (Table 1). The diversity of salmonids is also the result of California's large size (411 000 km^2), varied topography, and long coast line (spanning 10° of latitude) which is adjacent to the California current region of the Pacific Ocean (Moyle 2002), one of the most productive oceanic ecosystems in the world (Carr 2001). Based on genetic and ecological distinctiveness we recognize 32 salmonid taxa native to California (21 of them anadromous, 11 of them non-anadromous), although just eight are considered "full species" (Table 1). Twenty-five of these taxa support or once supported major commercial and sport fisheries, while the rest historically supported at least small recreational fisheries. Today, most of these fisheries are either shut down or severely limited. In addition, the anadromous forms represent the southernmost native populations of the full species to which they belong.

The thirty-two taxa in this paper fit the definition of species under the federal Endangered Species Act of 1973, as 'full' species, subspecies, Evolutionary Significant Units (ESUs) or Distinct Population Segments (DPSs) although four are not yet officially recognized as such. Fifteen (47%) of them are already listed under state and federal Endangered Species Acts (Table 1) and one, the bull trout, last observed in the state in 1974, is extirpated. Even with half the native salmonids officially imperiled, no overview of salmonid status exists for California. In this paper, such an overview is presented based on standardized status assessments made independently of assessments of state and federal agencies. Because the decline of California's native salmonids may foreshadow similar declines to the north, our study can be viewed as a foundation for understanding synergistic impacts of human population growth and climate change on salmonid-bearing aquatic systems. As such, we discuss vulnerability of California salmonids to climate change and other significant anthropogenic threats, especially hatchery propagation.

Our appraisal of the conservation status of the salmonid fishes of California was designed to answer the following questions:

1. What is the conservation status of all California salmonids, both individually and in aggregate?
2. How does this status assessment compare to official Endangered Species Act assessments?
3. What are the major factors affecting status?

Table 1 List of all native salmonid fishes known to breed in California, ranked by level of extinction threat. Conservation status is for California only and approximates the IUCN classification system. For definitions of status scores and categories see Table 4

Species	Distribution	Status score	Conservation status
Bull trout, *Salvelinus confluentus*	Pacific Northwest	0.0	Extirpated in CA
Central coast coho salmon, *Oncorhynchus kisutch*[b]	California[d]	1.1	Endangered[a]
Pink salmon, *O. gorbuscha*	Pacific Coast[d]	1.3	Endangered
Upper Klamath-Trinity spring Chinook salmon, *O. tshawytscha*[b]	California[d]	1.6	Endangered
Southern Oregon Northern California coast coho salmon, *O. kisutch*[b]	California & Oregon[d]	1.6	Endangered[a]
Chum salmon, *O. keta*	Pacific Coast[d]	1.6	Endangered
Central Valley late fall Chinook salmon, *O. tshawytscha*[b]	California[d]	1.7	Endangered
Klamath Mountains Province summer steelhead, *O. mykiss*[c]	California[d]	1.7	Endangered
Southern California steelhead, *O. mykiss*[c]	California[d]	1.7	Endangered[a]
Paiute cutthroat trout, *O. c. seleneris*	California	1.7	Endangered[a]
Northern California coast summer steelhead, *O. mykiss*[c]	California[d]	1.9	Endangered[a]
McCloud River redband trout, *O. m. stonei*	California	1.9	Endangered
Kern River rainbow trout, *O. m. gilberti*	California	1.9	Endangered
Central Valley winter Chinook salmon, *O. tshawytscha*[b]	California[d]	2.0	Vulnerable[a]
Central Valley spring Chinook salmon, *O. tshawytscha*[b]	California[d]	2.0	Vulnerable[a]
Central Valley fall Chinook salmon, *O. tshawytscha*[b]	California[d]	2.0	Vulnerable
California golden trout, *O. m. aguabonita*	California	2.0	Vulnerable
Little Kern golden trout, *O. m. whitei*	California	2.0	Vulnerable[a]
Eagle Lake rainbow trout, *O. m. aquilarum*	California	2.1	Vulnerable
Lahontan cutthroat trout, *O. c. henshawi*	Western USA	2.1	Vulnerable[a]
Upper Klamath-Trinity fall Chinook salmon, *O. tshawytscha*[b]	California[d]	2.4	Vulnerable
California Coast fall Chinook salmon, *O. tshawytscha*[b]	California[d]	2.4	Vulnerable[a]
Central Valley steelhead, *O. mykiss*[c]	California[d]	2.4	Vulnerable[a]
South Central California coast steelhead, *O. mykiss*[c]	California[d]	2.4	Vulnerable[a]
Central California coast winter steelhead, *O. mykiss*[c]	California[d]	2.7	Vulnerable[a]
Northern California coast winter steelhead, *O. mykiss*[c]	California[d]	3.3	Near Threatened[a]
Goose Lake redband trout, *O. m. subsp.*	California	3.3	Near Threatened
Coastal cutthroat trout, *O. clarki clarki*	Pacific Coast	3.4	Near Threatened
Southern Oregon Northern California coast fall Chinook salmon, *O. tshawytscha*[b]	California & Oregon[d]	3.7	Near Threatened
Mountain whitefish, *Prosopium williamsoni*	Pacific Northwest	3.9	Near Threatened
Klamath Mountains Province winter steelhead, *O. mykiss*[c]	California & Oregon[d]	3.9	Near Threatened
Coastal rainbow trout, *O. m. irideus*	Pacific Coast	4.7	Least Concern

[a] Taxon listed by federal and/or state Endangered Species Acts

[b] Taxon is an evolutionary significant unit (ESU)

[c] Taxon is a distinct population segment (DPS)

[d] Taxon is anadromous

4. How do factors causing declines differ for anadromous and resident taxa?
5. What conservation strategies are likely to be most effective in maintaining salmonid populations in California?

Materials and methods

Evaluation of status In order to answer the above questions we compiled existing information for each salmonid taxon in California (including peer-reviewed literature, agency reports, gray literature, and observations of the professional biologists). For listed species, we also reviewed the official listing and status reports as important sources of information. All sources were condensed into comprehensive species accounts with standard format, found in Moyle et al. (2011, in press). For the majority of California taxa these accounts represent the most complete and exhaustive review of biological and management data assembled to date. Status assessments were produced using information contained in each species account using a standardized protocol designed to quantify extinction risk for California salmonids (Tables 2, 3, 4, 5).

The status scores were the numeric average of seven extinction threat metrics: 1) area occupied, 2) estimated adult abundance, 3) intervention dependence, 4) tolerance, 5) genetic risk, 6) climate change, and 7) anthropogenic effects (Table 2). Each of these metrics was rated on a 1–5 scale, where a score of '1' indicated a highly negative effect on species viability and '5' indicated a neutral or positive effect, and '2' through '4' were intermediate (Table 2). Collectively, the metrics were designed to analyze major factors affecting salmonid viability in California with minimal redundancy among them. The results of the seven metrics were then averaged to produce an overall numeric threat score for each species ranging from 1 to 5, one being at highest risk of extinction and five being reasonably secure at this time.

Anthropogenic threats analysis Scoring the anthropogenic threats metric required a secondary analysis of 15 anthropogenic factors associated with salmonid decline in California (Tables 3, 4; full descriptions of categories can be found in Appendix A). The 15 anthropogenic threats addressed include: 1) major dams, 2) agriculture, 3) grazing, 4) rural residential development, 5) urbanization, 6) instream mining, 7) mining, 8) transportation, 9) logging, 10) fire, 11) estuary alteration, 12) recreation, 13) harvest, 14) hatcheries, 15) alien species.

Each of these human-caused limiting factors was rated on a five-level ordinal scale rated "critical," "high," "medium," "low," or "no" threat level (Table 3). Each taxon's anthropogenic threat score was then assigned a 1–5 value via the scoring rubric (Table 2, metric 7).

In order to facilitate broader understanding of our status ratings, we calibrated our numeric scoring rubric so that our ratings would approximate the five

Table 2 Scoring rubric used to assess status of native salmonid fishes in California. Each metric scored 1 through 5. Final status score is the average of all seven metrics scores. Note that there are separate "area occupied" metrics (1A and 1B) for resident vs. anadromous species. All metrics as of December 31, 2010

1A. Area occupied: resident salmonids
  1. One watershed/stream system in California only, based on watershed designations in Moyle and Marchetti (2006)
  2. 2–3 watersheds/stream systems without fluvial connection
  3. 3–5 watersheds/stream systems with or without fluvial connection
  4. 6–10 watersheds/stream systems
  5. More than 10 watersheds/stream systems

1B. Area occupied: anadromous salmonids
  1. 0–1 apparent self-sustaining populations
  2. 2–4 apparent self-sustaining populations
  3. 5–7 apparent self-sustaining populations
  4. 8–10 apparent self-sustaining populations
  5. More than 10 apparent self-sustaining populations

2. Estimated average adult abundance
  1. ≤500
  2. 501–5000
  3. 5001–50,000
  4. 50,001–500,000
  5. 500,000 +

3. Dependence on human intervention for persistence
  1. Captive broodstock program or similar intensive measures required to prevent extinction
  2. Continuous active management of habitats (e.g., water addition to streams, establishment of refuge populations, or similar measures) required
  3. Frequent (usually annual) management actions needed (e.g., management of barriers, special flows, removal of alien species)
  4. Long-term habitat protection or improvements (e.g., habitat restoration) needed but no immediate threats need to be dealt with
  5. Species has self-sustaining populations that require minimal intervention

4. Environmental tolerance under natural conditions
  1. Extremely narrow physiological tolerance (thermal maxima or minima, sensitivity to dissolved oxygen levels, swimming ability, etc.) in all habitats
  2. Narrow physiological tolerance to conditions in all existing habitats or broad physiological limits but species may exist at extreme edge of tolerances
  3. Moderate physiological tolerance in all existing habitats
  4. Broad physiological tolerance under most conditions likely to be encountered
  5. Physiological tolerance rarely an issue for persistence

Table 2 (continued)

5. Genetic risks
   1. Fragmentation, genetic drift, and isolation by distance, owing to very low levels of migration, and/or frequent hybridization with related fish are major forces reducing genetic viability
   2. As above, but limited gene flow among populations, although hybridization can be a threat
   3. Moderately diverse genetically, some gene flow among populations; hybridization risks low but present
   4. Genetically diverse but limited gene flow to other populations, often due to recent reductions in connectivity
   5. Genetically diverse with gene flow to other populations (good metapopulation structure)
6. Vulnerability to climate change
   1. Vulnerable to extinction in all watersheds inhabited
   2. Vulnerable in most watersheds inhabited (possible refuges present)
   3. Vulnerable in portions of watersheds inhabited (e.g., headwaters, lowermost reaches of coastal streams)
   4. Low vulnerability due to location, cold water sources and/or active management
   5. Not vulnerable, most habitats will remain within tolerance ranges
7. Anthropogenic threats analysis
   1. One or more threats rated *critical* or 3 or more threats rated *high* – indicating species could be pushed to extinction by one or more threats in the immediate future (within 10 years or 3 generations)
   2. 1 or 2 threats rated *high* – species could be pushed to extinction in the foreseeable future (within 50 years or 10 generations)
   3. No *high* threats but 5 or more threats rated *medium* – no single threat likely to cause extinction but all threats in aggregate could push species to extinction in the next century
   4. 2–4 threats rated *medium* – no immediate extinction risk but taken in aggregate threats reduce population viability
   5. 1 threat rated *medium* all others *low* – known threats do not imperil the species

status categories used by the International Union for the Conservation of Nature (IUCN) (Table 4). The scores only apply to salmonids in California, so species with wide distribution outside the state (e.g., chum or pink salmon) could receive low scores within the state, reflecting California's geographic position at the edge of their range. Examples of the conservation status assessment and anthropogenic threats analysis can be found as Appendix C.

Information quality Because the quality and quantity of information varied among species, each species account was rated, on a 1–4 scale, for certainty of status determination. A score of "1" relied solely on professional judgment while a score of "4" indicated that information was based primarily on published literature (Tables 5).

Results

Of the 32 salmonid taxa native to California, only bull trout have been extirpated, although 12 (38%) taxa are in danger of extinction in the near future if present trends continue (endangered, scores of 1.0–1.9). Another 12 (38%) species are sufficiently threatened to be on a trajectory towards extinction (vulnerable, scores of 2.0–2.9), while six (19%) are in long-term decline or have small isolated populations but currently do not face extinction (near-threatened, scores of 3.0–3.9). A single (3%) taxon, coastal rainbow trout, was found to be of least concern (≥4.0; Fig. 1). The average status score of all extant taxa was 2.3. The certainty ratings of status evaluations averaged 3.1 out of 4.0 (SD 0.8), with 78% of accounts based on extensive peer-reviewed and/or agency literature and only 3% based mainly on our professional judgment.

Of the 15 salmonids listed by the state and/or federal Endangered Species Acts (ESA), our analysis found one to have been extirpated, five to be endangered, eight to be vulnerable and one to be near-threatened (Table 1). Conversely, of the 12 fishes that we rated as endangered 5 (38%) were already formally listed under the ESA, as were 8 (67%) of the 12 fishes we rated vulnerable and 1 (17%) of the 6 we rated near threatened.

All seven status metrics were positively correlated with one another ($P<.05$) indicating that declines of most species were caused by multiple factors. Similarly, a Principal Components Analysis (JMP 9 2011) showed that all seven eigenvectors for the first component weighted approximately equally (Appendix B). Each species, however, had its own distinctive combination of metrics contributing to its score. The metrics contributing most often to a taxon's endangered or vulnerable status were climate change (74% of species received scores of 1 or 2), genetic risk (71%) and anthropogenic threats (71%). Only the coastal

Table 3 Criteria for ordinal ranks assigned to anthropogenic threat factors with expected timelines for decline

Factor threat level	Criteria	Temporal impact
Critical	Could push species to extinction	3 generations *or* 10 years, whichever is less
High	Could push species to extinction	10 generations *or* 11–50 years, whichever is less
Medium	Unlikely to drive a species to extinction by itself but contributes to increased extinction risk	Next 100 years
Low	May reduce populations but extinction unlikely as a result	Indefinite
No	No known impact to the taxon under consideration	–

rainbow trout was rated as least concern (score ≥4.0) because of its large populations, wide distribution, high tolerance of environmental change and genetically diverse populations.

Of the 15 causes of decline included in scoring of the anthropogenic threats the ones most often rated “critical” or “high” were hatcheries (45%), major dams (29%), estuary alteration (29%), harvest (26%), logging (23%) and alien species (23%). Thirteen species (42%) had at least one “critical” rating, indicating the factor had a high likelihood of causing extinction in the near future, while 19 species (61%) received at least one “high” rating. The largest number of “high” ratings awarded to a single species was six. All species had different combinations of causes of decline by kind and severity (Table 6).

Discussion

1. *What is the conservation status of California salmonids, both individually and in aggregate?*

The majority of salmonid species are declining rapidly and, if present trends continue, 78% (25 of 32 extant forms) are likely to be extirpated from the state in coming decades. Over three-quarters of these taxa are regional endemic species, so their loss would likely represent global extinction (Moyle et al. 2008). This pattern reflects the decline of the inland fishes in general (Moyle et al. 2011) but is much more severe and involves species that once supported large fisheries. Timelines of extinction trajectories depend on human activities, but the rapid decline of two ESUs of coho salmon (Fig. 2) provides documentation of the speed with which once-abundant fish taxa can diminish to near extinction. Coho salmon numbered in the hundreds of thousands only 50–60 years ago and were significant members of the state’s coastal stream and ocean ecosystems (Brown et al. 1994); today they number in the hundreds (National Marine Fisheries Service 2010) making the recently completed recovery plan for California coho salmon (NMFS 2010) a strategy to prevent imminent extinction.

Likewise, the combined abundance of Chinook salmon ESUs in the Central Valley once averaged around 2 million fish annually (Yoshiyama et al. 1998); today three of the runs (spring, winter, late-fall) average only a few thousand fish each. The fall-run has recently been experiencing extreme annual

Table 4 Conversion of numeric status scores to verbal status category definitions. To facilitate understanding the conservation implications of the ratings, the scoring rubric was calibrated to correspond to IUCN status categories at each integer break. ‘ESA’ is federal Endangered Species Act of 1973 and/or the California Endangered Species Act

Status category	Definition	Scores
Extinct	Globally extinct or extirpated from inland waters of California	0
Endangered	High risk of extinction in the wild, in short-term (<10 generations). Qualify for listing as endangered under ESA	1.0–1.9
Vulnerable	High risk of endangerment in the wild, but less so than endangered species. Most qualify for threatened listing under ESA	2.0–2.9
Near-threatened	Declining, fragmented and or small populations that can be subject to rapid or unexpected status change. Qualify as Species of Special Concern in California	3.0–3.9
Least Concern	California populations do not appear to be in overall decline; abundant and widespread	4.0–5.0

Table 5 Certainty of status assessment, rated from low (1) to high (4)

1. Status is based on professional judgment, with little or no published information
2. Status is based on professional judgment augmented by moderate amounts of published or gray literature
3. Status is based on reports found mainly in the in gray literature with some information in peer-reviewed sources but where data gaps exist in some important areas
4. Status is based on highly reliable information, with numerous accounts in the peer-reviewed and agency literature

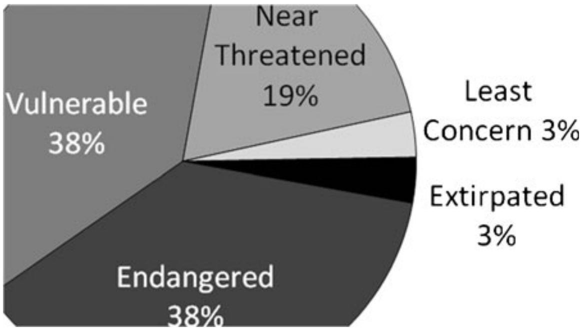

Fig. 1 2011 Conservation status of native salmonid fishes of California (N=32). See Table 5 for category definitions

fluctuations in abundance, reaching an all-time low of 66000 in 2008 (Anadromous Fish Restoration Program website) and appears to be heavily influenced by hatchery production (Williamson and May 2005; Williams 2006; Lindley et al. 2009).

Depending on the rate at which climate change and human impacts continue to alter California's aquatic environments, it is possible that a majority of California's endemic salmon, trout and steelhead could follow coho salmon to extinction within 50 to 100 years. Two of the species with high likelihood of being extirpated from the state are pink salmon and chum salmon (Table 1), species that have never been particularly common in California although they were a recognized part of fish fauna in the 19th and 20th centuries and contributed to salmon harvest (Moyle et al. 2008).

Table 6 Proportion of the 31 extant California salmonid taxa affected by 15 categories of anthropogenic causes of decline. See text and Table 2 for descriptions of causes and definitions of critical, high, medium, and low rating levels

	Threat level (% taxa)				
Cause of decline	Critical	High	Medium	Low	No effect
Major dams	6	23	42	13	16
Agriculture	0	16	55	10	19
Grazing	0	6	68	26	0
Rural residential	0	0	32	55	13
Urbanization	0	3	35	39	23
Instream mining	0	6	52	19	23
Mining	0	6	10	81	3
Transportation	0	6	52	39	3
Logging	6	16	52	26	3
Fire	0	10	58	32	0
Estuary alteration	3	26	39	0	32
Recreation	0	0	26	74	0
Harvest	3	23	39	35	0
Hatcheries	10	35	23	19	13
Alien species	13	10	39	39	0

2. *How does this status assessment compare to official Endangered Species Act assessments?*

For ESA-listed salmonid species we relied on the same information used by state and federal agencies for status assessment, but we applied a standardized protocol to all species. This approach allowed direct comparison of the status of both listed and unlisted species. With several notable exceptions, our results largely supported ESA listings of species that face high levels of extinction threat. However, our results also suggest that less than half of California salmonids that face similar high levels of extinction threat are listed. Thus, of the 12 most endangered salmonids in our analysis, only five are listed under the state or federal ESAs (Table 1). The incongruity between official lists and our assessment likely stem from differences in methods and scope but may also reflect the peculiarities of the ESA listing processes, as well

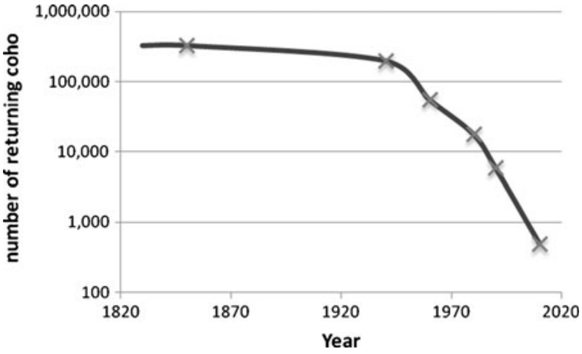

Fig. 2 Annual abundance estimates of adult coho salmon returning to California rivers to spawn. Data from NOAA (2010) and Brown et al. (1994)

differing evaluations of what constitutes an ESU or DPS. Regardless of cause, our status assessment suggests that state and federal ESAs are not sufficiently protecting California's salmonid fishes against extinction.

3. *What are the major factors affecting status?*

Although causes of decline are multiple and interacting, climate change and hatchery propagation appear to be the two most pressing extinction threats to California's salmonids. In California, 150 years of water capture and diversion have fundamentally changed the nature of aquatic ecosystems, especially in the state's Central Valley. Historically, aquatic habitats were complex and spatially heterogeneous with streamflow that varied both seasonally and interannually. The legacy of land use and water development has both simplified and stabilized California's waterways. Not only has recent anthropogenic action radically altered quality, extent and spatial patterns of fish habitat, but selection regimes under which the state's native fishes evolved have also been irrevocably altered. Species can track this change via phenotypic plasticity or by populations adapting to changing local conditions (Waples et al. 2008), both of which are ultimately dependent on genetic diversity. In light of the wholesale changes to California's aquatic habitats and the dependency of salmonid fishes on cold, clean and abundant water it is remarkable that we have lost only one salmonid taxon to extinction. This is particularly true when the long history of dependence on hatchery production to mitigate for habitat loss is considered in light of recent insights into the deleterious genetic effects of hatchery propagation on wild stocks (Goodman 2005; Akari et al. 2008; Chilcote et al. 2011). The capacity for hatchery introgression to genetically interrupt local adaptation in naturally reproducing populations is particularly troubling because it likely reduces the capacity of "wild" stocks to track changes to physical habitats. Our analysis suggests a lag effect, whereby the cumulative impact of past actions are now pushing salmonids towards extinction at a rate amplified by changing climatic conditions.

Increasing human population pressure, coupled with naturally stressful environments at the southern limit of the family's distribution, make California's salmonid fauna particularly vulnerable to climate change. The multiple stressors documented here are likely to be amplified by ongoing increases in temperature, changes in precipitation patterns, and decreases in snowpack (Mote et al. 2003). Accordingly, vulnerability to climate change was the metric with the largest negative effect on salmonid status. Put simply, all California populations are being adversely impacted by the shrinking availability of coldwater habitats.

Summer and fall are expected to be warmer and drier in the next century (Scavia et al. 2002), conditions associated with low salmonid survival (Lehodey et al. 2006; Wells et al. 2008). Anadromous salmonids can tolerate water temperatures from 0 to 25° C; however, survival and reproduction for most species are impaired at temperatures higher than 18°C (Brett 1971; Richter and Kolmes 2005). At the southern edge of their range, salmonids in California often already experience environmental conditions near the limit of their tolerance (Moyle et al. 2008). For instance, summer temperatures in many California rivers already exceed 22°C (McCullough 1999; California Data Exchange Center 2009). Thus, small thermal increases in summer water temperatures can result in suboptimal or lethal conditions and consequent reductions in salmonid distribution and abundance (Ebersole et al. 2001; Roessig et al. 2004).

Changes in how, when, and where precipitation falls in California also significantly alter salmonid habitats. During summer and fall, rising water temperatures are being exacerbated due to lower base flows resulting from reduced snowpack (Stewart et al. 2004; Hamlet et al. 2005; Stewart et al. 2005). Snowpack losses are expected to be increasingly significant at lower elevations, with elevations below 3000 m suffering reductions of as much as 80% (Hayhoe et al. 2004). Consequently, in the long run, changes in stream flow and temperature are expected to be most significant in streams fed by the relatively lower Cascades and northern Sierra Nevada, while the southern Sierra Nevada with its much higher elevations is predicted to retain a higher proportion of its snowpack (Mote et al. 2005).

Connectivity among habitats is becoming increasingly important as temperatures climb. In particular, seasonal access to cold water areas, especially smaller streams at higher elevations, is becoming more important to salmonids seeking coldwater refuges (Crozier et al. 2008). Under these conditions, mainstem rivers such as the Klamath River will be available primarily as seasonal migration corridors (Quiñones and Moyle in press). Habitat connectivity becomes as important as habitat quantity and quality when populations decrease and habitat is fragmented (Isaak et al. 2007). Consequently, removing physical (e.g., dams, shallow water) and physiological (e.g., warm water temperatures) barriers to upstream migration and behavioral thermoregulation will become an increasingly important conservation strategy.

The amount of habitat for warm water species, such as alien bass (*Micropterus* spp.) and sunfishes (*Lepomis* spp.) of the family Centrarchidae, will increase concurrently with decreases in coldwater habitat (Mohseni et al. 2003). Consequently, local declines in salmonid abundance will likely be coupled with increases in abundance of nonnative fishes, many of them predators on salmonids (Marchetti et al. 2001, 2004).

Climate-driven changes to estuarine and ocean systems also have potential to significantly impact anadromous populations (Quiñones and Moyle in press). A combination of melting ice sheets and glaciers, and thermal expansion of oceans contributed to a global sea level rise of 17 cm from 1961 to 2003 and changed the size and characteristics of estuaries (Intergovernmental Panel for Climate Change 2007). In California a roughly 20 cm increase in sea level during the 20th century has been intensified by land subsidence (Knowles and Cayan 2002; Cayan et al. 2008) and has reduced the amount and quality of tidal habitat through physical inundation, associated erosion, and increases in salinity (Scavia et al. 2002). With sea level changes associated with a 2°C temperature increase, Humboldt Bay and San Francisco Bay will likely lose 29–55% of their tidal flats and salt marshes (Galbraith et al. 2002), although increased pressure on levees may result in the sea reclaiming urbanized edge areas or large diked freshwater marshlands such as Suisun Marsh (Lund et al. 2007).

Although the effect of changing climatic conditions on marine salmon production will be patchy and hard to predict (Coronado and Hilborn 1998), some regional trends appear likely. For instance, marine survival rates in California salmon have been closely linked to several cyclical patterns of regional sea surface temperature such as the Pacific Decadal Oscillation, El Niño Southern Oscillation (Beamish 1993; Hare and Francis 1995; Mantua et al. 1997; Mueter et al. 2002), and the North Pacific Gyre Oscillation (Di Lorenzo et al. 2008). With increasing temperatures, concentrations of zooplankton, the primary prey of juvenile salmonids entering the ocean, may decrease, resulting in lower salmon survival (McGowan et al. 1998; Hays et al. 2005). Smolt-to-adult survival is also strongly correlated with upwelling driven by strong winds during the spring and fall (Scheuerell and Williams 2005). In addition to causing increases in surface temperatures similar to El Niño events (Schwing et al. 2010; Wang et al. 2010), climate change is predicted to alter wind patterns, negatively affecting upwelling. Increased acidity (Hauri et al. 2009) also may reduce ocean productivity in California's coastal waters. In response, salmonid distributions in the northern Pacific Ocean are predicted to shift poleward (Pierce 2004).

The southernmost steelhead populations are characterized by a relatively high genetic diversity compared to populations farther north (McCusker et al. 2000). It is likely that southern salmonid gene pools reflect a history of resilience as well as adaptations to watersheds characterized by aridity and extreme seasonal variation (Nielsen et al. 1999). Extinction of these highly endangered southern populations will likely result in loss of traits adapted to the very environmental characters that embody predicted climatic changes to watersheds further north.

Hatchery propagation of fish species is generally designed to increase overall abundance, mostly to support commercial and sport fisheries, although hatcheries have also been created as mitigation for human actions that have negative effects on salmonid populations. Consequently, while hatchery propagation of salmonids in California began in the 1870s, it was during the period of 1940 to 1960, coincident with the creation of the major dams, that hatchery construction boomed (Moyle 2002; Williams 2006). As a result, Many Central Valley streams with significant natural spawning runs also have a production hatchery on or near them (Yoshiyama et al. 2000). While hatcheries produce large numbers of fish, this production has often masked continued declines of wild stocks (Chilcote et al. 2011). The negative effects of hatchery production on wild stocks can be divided into ecological and genetic impacts, although the two interact considerably. Ecological effects include competition, predation, and disease transfer from hatchery stocks to wild populations (Allendorf and Ryman 1987; Krkosek et al. 2005). Competition between hatchery and wild fish can reduce abundance (Pearsons and Temple 2010) and survival of wild juveniles in river, estuarine and marine habitats

(Nickelson et al. 1986; Levin et al. 2001; Levin and Williams 2002; Nickelson 2003). Hatchery supplementation may even exceed the carrying capacity of the marine habitats, particularly in times of low ocean productivity (Beamish et al. 1997; Levin et al. 2001), resulting in high ocean mortality rates and consequently, lower adult returns (Beamish et al. 1997; Heard 1998; Kaeriyama et al. 2004). Augmentation of populations to support fisheries can increase harvest rates of wild fish to unsustainable levels while saturating the environment with hatchery fish (Naish and Hard 2008).

The natural ability of salmonids to adapt to changing conditions has made them relatively easy to culture. Not surprisingly, propagation also leads to rapid behavioral and morphologic changes in response to selection in the hatchery environment "with attendant deterioration of performance under natural conditions" (Goodman 2005 pg 374). For half a century there has been evidence of decreased performance of hatchery-derived populations of resident trout when compared to analogous wild populations under natural conditions (Greene 1952; Flick andWebster 1964; Moyle 1969) but domestication selection issues are not confined to resident salmonids (Ford 2002). Both genetic models and empirical studies have shown that after just a few generations, domestication yields individual fish with lower reproductive success which can reduce fitness of proximate wild populations (Chilcote et al. 1986; Unwin and Glova 1997; Bisson et al. 2002; Goodman 2005), presumably resulting in unsustainable natural populations (Lynch and Healy 2001). Continuous introgressive hybridization between fish of hatchery ancestry and naturally produced individuals will progressively diminish productivity of naturally spawning populations (Reisenbichler and Rubin 1999; Goodman 2005), presumably resulting in unsustainable natural populations (Lynch and Healy 2001). Recent multi-generational genetic studies (Akari et al. 2007a, b, 2008, 2009) and meta-analysis (Chilcote et al. 2011) have corroborated earlier findings that when fish with hatchery ancestry spawn in the river they produce substantially fewer successfully reproducing offspring than do wild fish from the same genetic stock.

Because hatchery stocks are not dependent on natural reproduction, fitness under natural conditions (or lack thereof) has little effect on the annual production of hatchery smolts. Currently more than 30 million Chinook smolts are produced annually in the Central Valley irrespective of the return rate of hatchery fish. Hatchery juveniles compete directly with naturally reproduced fish in both the river and marine environments. Meanwhile, hatchery genetics continue to penetrate the "wild" genepool as hatchery adults stray and spawn in river, decreasing the fitness and reducing the reproductive capacity of the naturally produced population. In California's Central Valley, fall-run Chinook salmon which spawn in-river are genetically indistinguishable from hatchery stocks (Williamson and May 2005; Lindley et al. 2009). Otolith microchemistry (J. Hobbs, UC Davis, unpubl. data), and recent fractional marking studies (California Department of Fish and Game, unpublished data) also suggest that in-river-spawning fall-run Chinook salmon are predominantly hatchery fish or of recent hatchery origin.

4. *How do factors causing declines differ between anadromous and resident taxa?*

Seventeen (81%) of the anadromous salmonids are in serious decline (scoring <2.9), while 8 (73%) of inland salmonids had similarly low scores. However, different combinations of threat factors drive decline in the two groups. Many resident taxa are endemic to single watersheds in very small areas, such as the golden trouts of the Upper Kern River Basin (Moyle et al. 2008). For such fish localized factors, such as a single introduction of an alien trout species, can have major negative effects. Accordingly, alien species were rated as a major threat (scored 1 or 2) for 64% of resident taxa but not for a single anadromous taxon. In contrast, major dams (43%), estuary alteration (43%), harvest (38%) and agriculture (24%) were rated critical or high for anadromous taxa but not for any resident fishes. Hatchery propagation, on the other hand, has major negative impacts on both groups, although in somewhat different ways. Genetic impact of hybridization with hatchery fish is a major threat for both groups but in anadromous fishes the primary threat comes from intra-taxon hybridization (e.g., interbreeding of hatchery Chinook salmon with naturally reproducing fish) while in most resident taxa the danger is from inter-taxa hybridization,usually rainbow trout interbreeding with golden or cutthroat trout (Moyle et al. 2008). Ecological impacts such as competition, predation and disease transfer between hatchery and wild stocks also have negative effects on both groups although direct competition may be a greater threat overall threat to resident species, such as competition with stocked nonnative trout in Sierra Nevada golden and cutthroat populations (Dunham et al. 2004). The Eagle Lake rainbow trout is a curious mix of these impacts, having been largely maintained by hatchery production for over 60 years (Carmona-Catot et al. 2011), a situation exacerbated by the fact that alien brook trout dominate their principal spawning and rearing stream.

5. *What conservation strategies are likely to be most effective in maintaining salmonid populations in California?*

A species' ability to respond to changing environmental conditions is closely correlated to the magnitude of its genetic variability and consequently life history variation (Reusch et al. 2005; Schindler et al. 2008). Because diverse habitats are necessary for expression of life history variation, decreases in habitat diversity can lead to reductions in life history diversity and to diminished resilience of salmon populations (Waples et al. 2009). Therefore, restoration and protection of physical habitat diversity is essential to maintaining genetic diversity and fostering resilience to both climate change and human population pressure in salmonid stocks (Hilborn et al. 2003; Rogers and Schindler 2008; Schindler et al. 2008; Carlson et al. 2011).

Because habitat diversity is essential to maintaining life history diversity, conservation strategies that restore and improve physical habitat quality, extent, and connectivity are essential tools in improving the odds of salmonid persistence (Greene et al. 2010). This general action must go hand in hand with changing hatchery operations, that reduce the adaptive potential of wild populations via introgression with domesticated hatchery genomes. The following conservation actions address both physical and biological processes and if implemented will increase the likelihood of salmonid recovery and persistence in California in the face of climate change.

General conservation actions

- Develop and implement individualized conservation strategies for all 31 extant taxa with the goal of maintaining self-sustaining populations throughout their range. The strategies must take into account climate change (Quiñones and Moyle in press) as well as increasing water demand, changing land use and recent insight into the negative impacts of hatcheries. An initial management step in the strategy would be to evaluate all species that scored between 1.0 and 2.9 in this report for formal listing as threatened or endangered species under the ESA. For an example, see Carmona-Catot et al. (2011).
- Enforce and strengthen existing laws and regulations, tied to the Clean Water Act, the Endangered Species Act, State Forestry Practice Rules, the Fish and Game Code, and similar measures, to increase protection for salmonids and their rivers.

Hatcheries

- Reform statewide hatchery policy so that the overarching goal of hatcheries is protection of wild populations of fish, rather than enhancing fisheries.
- End gene flow between hatchery strays and naturally reproducing spawning groups. This is essential for recovery of naturally reproducing stocks. Segregation of hatchery and naturally reproducing gene pools may be achieved in two ways: 1) physical segregation via active sorting at weirs or dams whereby only non-hatchery fish are passed upstream above the barrier, 2) use of hatchery brood stocks that are divergent from local genomes so that when hybridization between naturally produced individuals and hatchery strays inevitably occurs the hybrid progeny inherit a genome unfit for local conditions, experience high mortality in the wild and are rapidly culled from the naturally produced gene pool.
- Mark all hatchery fish with external marks so targeted management is possible.
- Relocate salmon and steelhead production hatcheries closer to river mouths in order to reduce mixing of wild and hatchery stocks.
- Relocate at least some harvest from the ocean to rivers and estuaries to allow targeting populations best able to sustain fishing pressure, especially hatchery stocks, while protecting imperiled naturally reproduced anadromous runs from overfishing.
- Close hatcheries where adverse impacts outweigh benefits.

Habitat

- Provide immediate additional protection to 'salmon strongholds' where salmonid diversity is high and habitat conditions are still reasonably good, such as the Smith River and the Blue Creek watershed of the Klamath Basin. This means reducing the human footprint on stronghold watersheds as much as possible by managing the watersheds first and foremost for native fish.
- Restore connectivity between river channels and seasonal habitat such as oxbows, riparian terraces, and floodplains wherever possible.
- Protect and restore cold water habitats, especially streams with groundwater inputs, the mouths of tributaries where hyporheic flows may provide thermal refuges, and watersheds that lie within the coastal fog belt. In regulated streams, reserve as much cold water in reservoirs as possible for providing suitable flows for native salmonids.
- Remove artificial migration barriers (including small and large dams, low flow and warm water barriers) to provide salmonids access to a wider range of habitats, comparable to historic ranges.
- Protect and restore riparian buffers alongside lower order streams (1st–3rd) where riparian vegetation can provide significant protection from solar radiation and maintain cooler water temperatures, as well as reduce sediment input.
- Reduce fine sediment delivery to streams to prevent streams from becoming shallower and thus more likely to become warmer, by improved watershed management (e.g., reducing effects from high road density, logging, and mining).

In summary, the salmonid fauna of California is on the verge of losing much of its diversity, among both anadromous and resident forms. These taxa have distinctive adaptations to stresses imposed by an arid Mediterranean climate. As the human population grows and the climate becomes harsher, conserving salmonids *in situ* as wild self-sustaining populations will require a level of commitment to aquatic conservation so far not seen in this state, including major shifts in water policy (Hanak et al. 2011). In order to prevent a wave of extinctions, new conservation strategies must address the most pressing drivers of salmonid decline in California. To that end, we have presented a partial list of conservation strategies tailored to alleviate the most egregious causes of decline identified by our analysis, climate change and genetic risks posed by hatchery propagation. We feel that this approach can be effective in maintaining salmonid populations in California for the near term. However, as Lackey et al. (2006) pointed out, maintaining self-sustaining runs of each anadromous species for future generations will take nothing short of a fundamental re-evaluation and radical restructuring of California's society.

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Appendix A

Descriptions of factors causing decline used in Anthropogenic Threats Analysis

Major dams Dams were recorded as having a high impact on a species if they cut off a species from a large amount of its range, if they caused major changes to habitat, or if they significantly changed water quality and quantity downstream of the dam. The effects of the reservoirs created by dams were also evaluated. Dams were regarded as having a low impact if they were present within the range of the species but their effects were either very small or poorly known.

Agriculture The effects of agriculture were regarded as being high if agricultural return water or farm effluent heavily polluted streams, if diversions severely reduced flow, if large amounts of silt flowed into streams from farmland, if pesticides had significant impacts or were suspected of having them, and if other factors directly affected the streams in which a species lived. Agriculture was regarded as having a low impact if it was not pervasive in the watersheds in which the species lived or was not causing significant changes to aquatic environments.

Grazing Livestock grazing was separated from other forms of agriculture because its effects are widespread on range and forest lands throughout California, especially the effects of cattle. Impacts are high where stream banks are trampled and riparian vegetation removed, resulting in streams becoming incised and the drying of adjacent wetlands. Removal of vegetation can also result in large amounts of silt being washed into streams, increased summer temperatures, and decreased summer flows. Impacts are low where grazing occurs in watersheds but changes described above are minimal.

Rural residential As California's human population grows, people spread across the landscape, often settling in diffuse patterns along or near streams. This results in water removal, streambed alteration (to protect houses, create swimming holes, construct road crossings, etc.), and pollution (especially from septic tanks). Where such housing is abundant and unregulated, it causes major changes to streams and their fishes and is rated as a high impact. Where such housing is present but scarce, the effects are usually low.

Urbanization When humans concentrate in towns and cities, they alter the streams that flow through them to reduce flooding and acquire the water. Pollution is rampant, both through sewage discharges and through less obvious means such as storm drains. Generally, the bigger the city, the bigger its effects on local streams and fish populations.

Instream mining The most severe instream mining took place during the 19th and early 20th century when miners excavated and dredged river beds for gold, turning them over multiple times. These severe legacy effects are still with us in many rivers. Nearly as severe, at least locally, have been instream gravel mining operations, in which large pits were dug into streambeds and banks altered. Such mining is largely banned (in favor of mining off-channel areas) but also has legacy effects. This was usually rated intermediate when present, although severe legacy affects resulted in high ratings for some species. The impacts of contemporary recreational and professional suction dredge mining for gold can also result in a high rating.

Mining This refers to hard rock mining, in which tailings can be dumped into streams and pollutants result from mine drainage, mostly of abandoned mines. The effects of mercury, used in processing gold in placer and dredge mining is also included here. High ratings come from situation where mines, even if abandoned, form a major threat because their wastes are poised on the edges of rivers (e.g. Iron Mountain Mine near Redding). Low ratings for species usually come from situations where old mines are present but their effects on nearby streams are not known or not obvious.

Transportation Historically, river banks were favorite places to construct roads and railroads, so many rivers and creeks have roads and railroads running along one or both sides, often confining the stream channel and subjecting the streams to pollution from vehicle emissions, waste disposal, and accidents. Also culverts and other drainage modifications associated with roads often block fish migration or restrict fish movements. Dirt roads can become hydrologically connected to streams, increasing siltation and changing local flow regimes and seriously impacting aquatic habitat. The ratings were made based on how pervasive roadside streams are in the areas occupied by the species

Logging Timber harvest has always been one of the major uses of forested watersheds in California. These same watersheds support the most species and highest abundances of fish, including anadromous salmon and steelhead. Logging was relatively unregulated until the mid-20th century, resulting in major degradation of streams through removal of trees as cover and landscape stabilizers. Legacy effects include incised streams with little large wood providing structure and many silt-bottomed reaches. Logging is still a pervasive activity in forested watersheds and is better regulated today than previously, but its effects can still result in siltation of streams, reduced complexity of habitat, and other alterations. High ratings were given when a species occupied streams degraded by either the legacy or contemporary effects of logging. Low ratings were awarded to species that used forested watersheds but where the effects of logging were either mitigated or of small significance.

Fire Forest, range, and scrub fires are part of California's natural landscape but human activities have made them more severe (Gresswell 1999; Noss et al. 2006; Sugihara et al. 2006). Transition from relatively frequent understory fires to less frequent but catastrophic crown fires has been shown to be a major driver in the extinction risk of Gila trout (*Oncorhynchus gilae*) in New Mexico (Brown et al. 2001). There is little reason to think that similar factors are not pervasive in California. A fish species rated high for fire is one in which most of its streams are affected by fire, through increased erosion, increases in temperature, spills of fire-fighting chemicals, and effects of ash and other materials. Low ratings generally applied to fish that lived in areas where fires occur but for various reasons have minimal impact on streams.

Estuary alteration Many California fishes depend on estuaries for at least part of their life cycle. All estuaries in the state are highly altered by human activity, from siltation to pollution, to diking and draining, to removal of sandbars between the estuary and ocean. Thus the more estuarine dependant a fish species is, the more likely it was to get a high rating for this factor.

Recreation Human use of streams as playgrounds has greatly increased along with the human population but the effects are usually minor, although concentrated at periods of time when stream flows are low. Recreation is likely to be rated high as a factor when there is, for example, heavy off-road vehicle use in limited habitat, ski resorts that increase sedimentation (from cleared areas for ski runs), or rafters and swimmers disturbing spawning or holding fish (salmon and steelhead).

Harvest Harvest of fishes is both legal and illegal. Both can have severe impacts on fish populations, especially of large fishes or ones that are isolated and therefore easy to catch (e.g. summer steelhead).

Hatcheries Most fishes do not have populations supported in part by fish hatcheries but for those that do, hatcheries often have negative effects on wild populations through competition for space and food, direct predation, and loss of fitness and genetic diversity (Kostow 2009; Chilcote et al. 2011). The severity of these effects was rated based in part on hatchery dependence and/or the threat of interbreeding between wild and hatchery populations.

Alien species Non-native species are present in every California watershed and their impacts on native species through hybridization, predation, competition, and disease are often severe (Moyle and Marchetti 2006). Fish species were rated high in this category if there were studies demonstrating major direct or indirect impacts of alien invaders. They were rated low if contact with aliens was frequent but not negative.

Appendix B

Table 7 Principal component analysis (JMP 9) revealed relatively equal weighting of all seven metrics on the final status scores of 31 extant taxa. Standard deviation for eigenvectors for principal component one was .051

	Prin1	Prin2	Prin3
Area occupied	0.39254	0.26367	−0.3819
Adult population	0.39413	0.17271	0.34441
Intervention dependence	0.3584	0.40222	0.25614
Tolerance	0.304	0.60252	0.59553
Genetic risk	0.43836	0.01002	0.27654
Climate change	0.3152	0.56583	0.43763
Anthro threats	0.42213	0.23574	0.21744

Appendix C

Table 8 Example of Anthropogenic Threats Analysis to determine viability of California golden trout

Threat	Rating	Explanation
Major dams	Low	Isabella Reservoir effects water quality in the South Fork Kern River
Agriculture	No	No known impact
Grazing	High	Pervasive in the area, although less severe than in the past
Rural residential	No	No known impact
Urbanization	No	No known impact
Instream mining	No	No known impact
Mining	Low	Relatively few effects of mining
Transportation	Low	Trails and off-road vehicle routes can be a source of sediment for streams
Logging	Low	This is an important land use in the region but probably has little direct effect on golden trout streams
Fire	Low	Because of fire suppression, headwater areas contain greater fuel loads than historically, although hot fires are unlikely given the sparse plant communities
Estuary alteration	No	No estuaries in range
Recreation	Medium	Human use of meadows is a constant threat, but more in past than present
Harvest	Low	Potentially a problem; most fishing is catch and release
Hatcheries	Low	Constant genetic and demographic threats from hatchery fish to support fishery
Alien species	Critical	Hybridization with rainbow trout is primary extinction threat and a major cause of limited distribution

Table 9 Example of a conservation status assessment summary table for California golden trout

Metric	Score	Justification
Area occupied	1	Unhybridized trout are confined to a few small tributaries in one watershed
Estimated adult abundance	3	Tributary populations show signs of genetic bottlenecking but probably still contain 100–1000 adults
Intervention dependence	3	Persistence requires maintenance of upstream migration barriers and continued monitoring and nonnative removal
Tolerance	2	Require conditions present in relatively undisturbed small alpine meadow streams
Genetic risk	1	Hybridization with rainbow trout is a constant high risk
Climate change	3	High southern Sierra Nevada will likely retain significant snowpack, effects of climate change may be partially mitigated by improved management
Anthropogenic threats	1	See Table 4
Average	2.0	14/7
Status Category		Vulnerable
Certainty (1–4)	4	Well documented in scientific and agency literature

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