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Rapid decline of California's native inland fishes: A status assessment

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ABSTRACT

A quantitative protocol was developed to determine conservation status of all 129 freshwater fishes native to California. Seven (5%) were extinct; 33 (26%) were found to be in danger of extinction in the near future (endangered); 33 (26%) were rated as sufficiently threatened to be on a trajectory towards extinction if present trends continue (vulnerable); 34 (26%) were rated as declining species but not in immediate danger of extinction. Only 22 (17%) species were found to be of least concern. Of 31 species officially listed under federal and state endangered species acts (ESAs), 17 (55%) were rated as endangered by our criteria, while 12 (39%) were rated vulnerable. Conversely, of the 33 species that received our endangered rating, only 17 (51%) were officially listed under the ESAs. Among the seven metrics used to assess extinction threat, climate change, area occupied and anthropogenic threats had the largest negative impacts on status. Of 15 categories of causes of decline, those most likely to diminish status were alien species, agriculture, and dams. Overall, 83% of California's freshwater fishes are extinct or at risk of becoming so, a 16% increase since 1995 and a 21% increase since 1989. The rapid decline of California's inland fishes is probably typical of declines in other regions that are less well documented, indicating a strong need for improved conservation of freshwater ecosystems.

1. Introduction

Extinction in freshwater environments is a world-wide crisis (Moyle and Williams, 1990; Saunders et al., 2002; Dudgeon et al., 2006) which is poorly documented (Strayer and Dudgeon, 2010; Vörösmarty et al., 2010). Loss of biodiversity seems to be occurring more rapidly from fresh water than from any other broad habitat type (Jenkins, 2003; Dudgeon et al., 2006). Driven by recent global assessments of mollusks (Bogan, 2008), crabs (Cumberlidge et al., 2009), amphibians (Stuart et al., 2004), and dragonflies (Clausnitzer et al., 2009), the number of freshwater species listed on International Union for the Conservation of Nature (IUCN) Red Lists has more than tripled since 2003 (Darwall et al., 2008). Nevertheless, the best-studied indicators of the problem remain freshwater fishes (Magurran, 2009) which account for about one-third of all described vertebrates, with roughly 13,000 species (Helfman, 2007; Lèvêque et al., 2008). In 1992, 20% of the world's freshwater fish fauna was estimated to be extinct or in serious decline (Moyle and Leidy, 1992). Less than 20 years later, 37% of the 3481 freshwater fish species evaluated globally by IUCN were regarded as extinct or imperiled (declining towards, or threatened, with extinction, Vié et al., 2009), although the IUCN database is likely biased towards including declining species. At the continental scale, 46% of 1187 described freshwater and diadromous fish species native to North America are extinct, imperiled, or have one subspecies or distinct population that is imperiled (Jelks et al., 2008) with the rate of extinction steadily increasing (Ricciardi and Rasmussen, 1999). Not surprisingly, the number of imperiled fish species is highly correlated with human population and economic growth (Limburg et al., 2011).

While large-scale assessments spotlight the global extent of the crisis, severity and causes are best understood through intensive studies of regional fish faunas because status can be repeatedly, systematically, and quantitatively documented over relatively short time periods. In this paper, we analyze the status of California's 129 native freshwater fishes. This regional fauna is reasonably well documented, occupies a wide variety of habitats, and exhibits a wide range of life history patterns including anadromy (Moyle, 2002; Moyle et al., 2008, 2010). Their status was previously analyzed in 1989 (Moyle and Williams, 1990) and 1995 (Moyle et al., 1995). Here, we use a new quantitative protocol to determine conservation status of each species. This protocol allows us to make status determinations independent of official agency designations and to find species needing protection that have been overlooked so far by state and federal agencies. Comparisons with official status designations also serve as a check on the usefulness of our protocol. In this paper, we answer the following questions:

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1. What is the status of California's inland fish fauna?
2. Are the fishes continuing to decline?
3. What factors are most strongly associated with declining status?
4. How do our results fit with official status designations?

1.1. The inland fishes of California

California's large size (411,000 km^2), length (1400 km and 10° latitude) and complex topography result in diverse habitats, including 50 isolated watersheds in which fish have evolved independently (Moyle, 2002, Moyle and Marchetti, 2006). For most of the state, the climate is Mediterranean; most precipitation falls in winter and spring, followed by long dry summers. This results in rivers that have high annual and seasonal variability in flows (Mount, 1995) and native fishes adapted to hydrologic extremes. There are 129 native inland fishes (defined as those breeding in fresh water) currently recognized (Appendix 1, which includes scientific names of fishes mentioned). Of these, 63% are endemic to the state and an additional 19% are also found in one adjacent state. Thus California's fishes fall within political and zoogeographic boundaries that largely coincide, important for a bioregional assessment (Moyle, 2002).

Conditions in California have produced an unusual number of anadromous fishes (24%) as well as fishes that thrive in isolated environments such as desert springs, intermittent streams, and alkaline lakes. Most fishes live in rivers of the Central Valley and North Coast, areas having the most water and most diverse aquatic habitats. Recent genetic and taxonomic studies have underscored the distinctiveness of California fishes and increased the number of taxa from 113 in 1989 (Moyle and Williams, 1990) to 129 in the present study.

Most California rivers have been dammed and diverted to move water from places of abundance to places of scarcity, where most Californians live (Hundley, 2001). Not surprisingly, native fishes have been in steady decline since the mid-19th century, although the first formal evaluation of their status was not conducted until 1989. At that time, 7 species (5%) were extinct, 15 (13%) were formally listed as Threatened or Endangered under the state or federal ESAs, and 51 (43%) were designated as Species of Special Concern by the State of California, indicating they were in decline or had small, vulnerable populations but were not yet threatened with immediate extinction (Moyle and Williams, 1990). The number of declining species has steadily increased so that in 1995, there were 18 (16%) listed and 51 (44%) in decline (Moyle et al., 1995). Today, the numbers are 30 (23%) listed and 70 (54%) in decline, meaning that 83% of California's native fishes have the potential to go extinct in coming decades or are already extinct (Appendix 1) (Fig. 1).

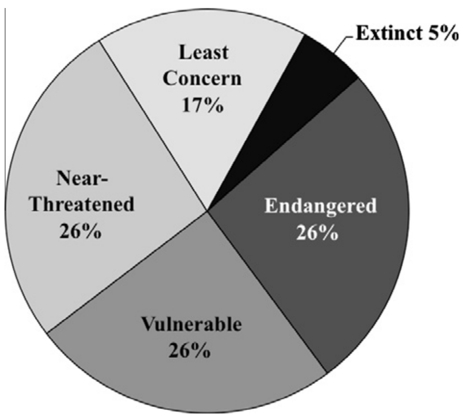

Fig. 1. Status of fishes (N = 129) native to inland waters of California in 2010. All threat categories are approximately equivalent to IUCN threat levels of the same name. Extinct = globally extinct or extirpated in the inland waters of California. Endangered = highly vulnerable to extinction in its native range, approximately equivalent to IUCN threat level of *endangered* or *critically endangered*. Vulnerable = could easily become threatened or endangered if current trends continue. Near threatened = populations in decline or highly fragmented. Least concern = no extinction threat for California populations.

2. Methods

2.1. Sources of information

Taxa used were those that qualified as species under the federal Endangered Species Act of 1973, so include species, subspecies, Evolutionarily Significant Units, and Distinct Population Segments recognized by one or more agencies. The biology and status of each species was determined from information in Moyle (2002), Moyle et al. (1995, 2008, 2010), additional reports and papers from intensive literature searches, and by personal communications with biologists working with each taxon. The information was summarized in standardized species accounts which included evaluation of status. All accounts were reviewed by experts on each species. In a few cases, information was updated by field investigations by the authors. The status of each species is as of December 31, 2010.

2.2. Quantitative evaluation of status

Species status was determined using seven metrics scored on a 1–5 scale (Table 1) where 1 was a low score indicating major negative impact on status and 5 was a high score, indicating either no or a positive impact on status. Scores were assigned according to a rubric which was standardized to each threat category (Table 2). Metrics were designed to capture all significant risk factors faced by freshwater fishes while keeping redundancy among metrics to a minimum. Principal component analysis revealed relatively equal weighting of all seven metrics on the final status scores (eigenvectors for principal component one: area occupied, 0.322; adult population, 0.398; intervention dependence, 0.405: tolerance 0.341: genetic risk 0.406; climate change 0.381: anthropogenic threats 0.382). For each species, the seven criteria were averaged to produce a single score for which the threat of near-term extinc-

Table 1
Metrics for determining the status of California fishes, with Sacramento splittail as example. Each metric is scored on a 1–5 scale where 1 is a major negative factor contributing to status, 5 is a factor with no or positive effects on status, and 2–4 are intermediate values. Scoring is described in Table 2.

Metric	Score	Justification
Area occupied	2	Two distinct populations in San Francisco Estuary, using different rivers for spawning
Estimated adult abundance	4	Large in upper estuary, likely small in lower
Intervention dependence	3	Floodplain areas need special management for spawning during droughts
Tolerance	5	One of the most physiologically tolerant native fishes
Genetic risk	3	Two populations; genetically fairly diverse
Climate change	1	Extremely vulnerable to droughts and sea level rise reducing habitat
Anthropogenic causes of decline	2	Multiple, see Table 3
Average	2.9	20/7
Certainty (1–4)	3	Well studied

tion increased as the score decreased. The scores were placed in categories following the IUCN categories for imperiled species (Vié et al., 2009). Fishes with scores between 1.0 and 1.9 were rated *endangered* and regarded as being in serious danger of extinction, while those scoring 4.0–5.0 were regarded as *least concern*. Species with scores of 2.0–2.9 were rated *vulnerable* and regarded as likely to become threatened or endangered in the near future, while those scoring between 3.0 and 3.9 were in decline but not yet in immediate danger of extinction and so were rated *near-threatened*. In order to simplify discussion, all species scoring between 1.0 and 3.9, were collectively referred to as ‘‘imperiled'' because they either had declining populations or had small, isolated populations that increased their risk of extinction. The scores only apply within California, so rare species with wide distributions and high abundance outside the state (e.g., chum and pink salmon) might receive low scores within the state even if there is no danger of extinction as species.

2.3. Metrics used to score taxon status

2.3.1. Area occupied

We assumed that extinction threat was lower for species spread over many watersheds than for those with limited distributions. Inland fishes were scored by number and interconnectedness of large watersheds occupied. Anadromous fishes were scored on number of watersheds occupied (i.e., Functionally Independent Populations, Lindley et al., 2004, 2006).

2.3.2. Estimated adult abundance

In general, the more adult individuals in a population, the more likely it is to persist through time. However, quantitative population estimates are rare, especially for non-game fishes (Jelks et al., 2008). We therefore used order-of-magnitude estimates of average annual numbers of mature individuals at the time of the study as a proxy for population size (Table 2). While we recognized

Table 2
Scoring rubric for seven metrics used to evaluate status of native freshwater fishes of California. Final status score is the average score of all seven metrics.

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

1B. Area occupied: anadromous fish
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 adult abundance
1. $\leqslant$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 extreme 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 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

5. Genetic risks/problems
1. Genetic viability reduced by fragmentation, genetic drift, and isolation by distance, owing to very low levels of migration, and/or frequent hybridization with related fish
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 causes of decline
1. 1 or more causes 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 10–25 years)
2. 1 or 2 causes rated high; species could be pushed to extinction in the foreseeable future (within 50 years)
3. No causes rated high 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. 1–4 causes rated medium; no immediate extinction risk but taken in aggregate causes reduce population viability
5. 1 medium, all others low; known causes do not imperil the species

that the effect of adult population size upon persistence differs for large, long-lived species in contrast to small, short lived species (Flather et al., 2011), we rarely found this to be an issue for California fishes.

2.3.3. Dependence on human intervention for persistence

This metric scored how dependent a species was on direct human intervention for its continued survival. Thus, Eagle Lake rainbow trout received a score of '1' because it is completely dependent on artificial propagation for its persistence, while rough sculpin (a state listed species) scored a '4', because it needs only continued protection of its spring-fed streams (managed for trout fisheries) to maintain abundance.

2.3.4. Environmental tolerance under natural conditions

This metric measures overall physiological tolerance in relation to existing conditions in a species' range. Where possible this was based on results of laboratory or field studies of responses to ranges of temperature, salinity, dissolved oxygen and similar variables. However, if a species had fairly broad physiological tolerances in the laboratory but lived in waters (e.g., streams in southern California) where habitat conditions naturally approached the species limits of tolerance to temperature and other factors, its environmental tolerance was scored lower than that of a species likely to rarely encounter such conditions.

2.3.5. Genetic risks

This metric incorporates two concepts, hybridization and genetic bottlenecks. Hybridization with a related species, especially an introduced species, can result in sterility, reduced fitness and swamping of native genomes (Perry et al., 2002). Similarly, interbreeding between artificially propagated (hatchery) and wild individuals can reduce fitness of offspring (Araki et al., 2009).

In order to avoid over-weighting the impact of small population size on status, genetic impacts of small population size were not considered here. However, low genetic variation from hatchery management and/or other past reductions of effective population size may increase extinction threat (e.g., reduce the ability of species to adapt to environmental change) irrespective of current population size and so was included under this metric.

2.3.6. Vulnerability to climate change

Climate change is already having effects, as reflected in rising water temperatures and more variable stream flow; such effects are only likely to increase (Hayhoe et al., 2004; Anderson et al., 2008; Cayan et al., 2009). Vulnerability to future climate change was determined by examining geographic range of each species, its isolation (potential for finding refuges), and the types of habitat it inhabits. Species considered to have low vulnerability included those with broad thermal tolerances and those living in aquatic environments shielded (at least for now) from climate-driven change, such as spring-fed systems with constant sources of water (e.g., bigeye marbled sculpin and Saratoga Springs pupfish).

2.3.7. Anthropogenic causes of decline

We rated fifteen major categories of landscape-level factors likely to increase extinction risk as having no, low, medium, high or critical effect on species status, based on available information for each species summarized in Moyle (2002), and Moyle et al. (2008) (Table 3). A cause rated "critical" could push the species to extinction in three generations or 10 years which ever is less. A cause rated "high" could push the species to extinction in 10 generations or 11–50 years which ever is less. A cause rated "medium" was unlikely to drive a species to extinction by itself but contributed to increased extinction risk over the next century. A cause rated "low" could reduce populations but extinction was considered unlikely as a result. A cause rated "no" (no effect) has no known negative impact to the taxon under consideration.

For some species, a single threat was considered grave enough to cause extinction (e.g., hybridization for California golden trout), but for most species, number as well as severity of potential causes contributed to our final score (Table 2). We judged any species with even one critical rating as being in danger of extinction in the near future. The 15 causes of decline are summarized below.

2.4. Anthropogenic causes of decline

2.4.1. Large dams

Dams and their reservoirs had high impacts on status if they blocked access to much of the species range, caused major changes to physical habitat, or changed water quality and quantity. We regarded dams as having a low impact if they were present within the range of the species but their effects were small or beneficial.

2.4.2. Agriculture

Effects of agriculture were rated high if agricultural effluent polluted waterways of major importance to the species, if diversions severely reduced flow, if large amounts of silt flowed into streams from farmland, if pesticides had significant effects, and if other agricultural factors directly affected waters in which a species lives. We regarded agriculture as having a low impact if it was not pervasive in the species' range or was not known to be causing significant changes to a species' habitats.

Table 3
Ratings of major anthropogenic factors causing declines of freshwater fishes of California, using Sacramento splittail as an example. See text for definitions of ratings of causes.

Status metric	Rating	Explanation
Major dams	High	All waters have flows regulated by dams and diversions; frequency of flooding of spawning areas reduced
Agriculture	Medium	Pollution, channel modification, entrainment in major diversions
Grazing	Low	Little known impact but occurs in spawning areas
Rural residential	Low	Residences on the edges of rearing marshes
Urbanization	Medium	Most habitat is on urban fringes; sewage; water diversion and entrainment
Instream mining	Low	Some gravel mining in floodplain areas
Mining	Low	Legacy effects of gold mining, e.g. mercury
Transportation	Medium	Migratory corridors lined with roads and railroads,
Logging	No	No known impact
Fire	Low	Indirect impacts from marsh/floodplain fires possible
Estuarine alteration	High	Major habitat areas highly altered
Recreation	Low	Recreational boating etc. may affect habitat
Harvest	Medium	Some harvest for bait and of migrating adults for food
Hatcheries	No	No known impact
Alien species	Medium	Effects of new invaders unpredictable; predation and competition possible

2.4.3. Grazing

We separated livestock grazing from other agriculture because its effects are widespread on range and forest lands throughout California. Impacts were rated high where stream banks were trampled and riparian vegetation was removed, resulting in incised streams, drying of adjacent wetlands, and lowering of water tables. Removal of vegetation can also result in increased siltation, higher water temperatures, and decreased summer flows. Impacts were rated low where grazing was present but had minimal negative effects.

2.4.4. Rural residential

As California's human population grows, people spread across the landscape, often settling in diffuse patterns along or near streams. Rural development results in water removal, streambed alteration (to protect houses, create swimming holes, construct road crossings, etc.), and pollution (especially from septic systems). We rated such housing as having high effect on fishes where it was abundant and unregulated and caused major changes to streams. Where such housing was present but scattered, the effects were usually rated as low.

2.4.5. Urbanization

Streams that flow mostly through cities are generally highly altered to reduce flooding and remove water, while pollution is pervasive, from sewage, runoff, and storm drain discharges. Generally, the more the important waters for a species were encompassed by urban development, the higher we rated the effects of urbanization on the species.

2.4.6. Instream mining

The most severe instream mining in California took place during the 19th and early 20th centuries when miners buried (through hydraulic mining), excavated, and dredged riverbeds for gold. We often gave the legacy effects on fishes of mining medium or high ratings. Similar scores were given to species affected by legacy effects of instream gravel mining, which creates large pits in streambeds and alters stream banks. Such mining is largely banned (in favor of mining off-channel areas) today. Impacts of contemporary recreational and professional suction dredge mining resulted in some intermediate ratings.

2.4.7. Mining

The effects of hard-rock mining (mostly for gold and mercury) were rated according to how much of a species' habitat was affected by tailings and acidic mine drainage. We gave high ratings where major mines, even if abandoned, had toxic tailings poised on edges of waterways (e.g., Iron Mountain Mine near Redding, on the Sacramento River). Our low threat scores usually came from situations where old mines were present but effects on biota of nearby streams were not evident.

2.4.8. Transportation

Many rivers and creeks have roads and railroads running along one or both sides, confining stream channels and causing pollution from siltation, vehicle emissions, waste disposal, and accidents. In addition, culverts and other hydrologic modifications associated with transportation often restrict fish movements. Our ratings here were based on how much a species depended on streams altered by roads and railways and how severe the alterations were.

2.4.9. Logging

Timber harvest is a major use of forested California watersheds which support many native fishes, including anadromous salmonids. Logging was relatively unregulated until mid-20th century, resulting in major alteration and degradation of stream habitats. Although better regulated today, logging is still a pervasive activity resulting in siltation of streams and reduced habitat complexity. We gave high threat ratings to species dependent on streams degraded by either legacy or contemporary effects of logging. Low threat ratings were given where such effects are of small significance.

2.4.10. Fire

Wildfires are part of California's natural landscape but human activities have increased their intensity and frequency. High ratings were given where fish habitat was, or has the potential to be, seriously degraded by catastrophic wildfire, via post-fire erosion, loss of riparian canopy, increased temperature and spilled fire-fighting chemicals. We assigned low ratings to fishes that live in areas where wildfires occur but for various reasons, such as low fuel load, have minimal impact on streams.

2.4.11. Estuary alteration

Many California fishes depend on estuaries for at least part of their life cycle. All California estuaries are highly altered by human activity, including siltation, pollution, diking and draining, bridge construction, and removal of sandbars between the estuary and ocean. Thus, the more estuarine-dependent a fish species is, the more likely we were to assign a high rating to estuary alteration as a cause of decline.

2.4.12. Recreation

Recreational use of streams has greatly increased with the human population. We found recreational effects usually to be low, although they were often concentrated when stream flows were low. We rated recreation effects as high when a taxon depended on streams that are heavily disturbed (e.g., by off-road vehicles) or contains enough boaters and swimmers to disturb spawning or holding (e.g., salmon and steelhead).

2.4.13. Harvest

We rated harvest effects as high for fishes known to be subject to overharvest, especially large species (e.g., sturgeons) or species that become isolated and are therefore vulnerable to poaching (e.g., summer steelhead). We rated both legal and illegal harvest, although for most native resident fishes, legal fishing was rarely an issue.

2.4.14. Hatcheries

Most fishes are not supported by fish hatcheries but for those that are, hatchery fish often have negative effects on wild populations through competition for habitat and food, direct predation, and interbreeding which results in loss of genetic diversity (Moyle, 2002). We rated severity of these effects based in part on hatchery dependence and/or known interbreeding between wild and hatchery populations. We regarded conservation hatcheries that focus on rare species as having relatively low impacts because of their efforts to reduce negative hatchery effects as much as possible.

2.4.15. 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). We rated this category as high for a species if there were major direct or indirect impacts of alien invaders. We rated it as low if contact with alien species was infrequent or not known to be negative.

2.5. Certainty index

Because quality, amount and reliability of information varied among species, we developed a certainty index for our scores, on a 1–4 scale, where we scored status evaluations as follows:

1. Based on expert opinion (including our own) with little hard data.
2. Based on expert opinion supplemented with limited data and reports.
3. Based on extensive information found mainly in agency reports.
4. Based on reports from multiple sources including peer-reviewed literature.

This index lets managers know the risks involved in basing management decisions on our results.

3. Results

Of 129 freshwater fishes native to California, four are globally extinct (3%) and three (2%) are extirpated from the state (scores of 0). Another 33 (26%) are in danger of extinction in the near future if present trends continue (endangered, scores of 1.0–1.9) while 33 (26%) are sufficiently threatened to be on a trajectory towards extinction if present trends continue (vulnerable, scores of 2.0–2.9). Thirty-four (26%) are in long-term decline or have small isolated populations but do not face extinction in the foreseeable future, unless conditions change (near-threatened, scores of 3.0–3.9). The remaining 22 species (17%) are of least concern (4.0–5.0) (Fig. 1). The average status score of all extant taxa was 2.7. The certainty ratings of our status evaluations averaged 2.7 out of 4.0 (SD 1.2), with 66% of accounts based on extensive literature (4.0) and only 5% based mainly on our professional judgment (1.0).

Of the 31 species currently listed as Endangered or Threatened under federal and/or state endangered species acts, 17 had status scores of 1.0–1.9 and 12 had scores of 2.0–2.9 by our rating system (Appendix Table 1). Listed species made up half of the 33 species to which we gave status scores of 1.0–1.9 and 44% of extant species with scores <2.9. The number of listed species increased from 14 in 1989 to 18 in 1990 to 31 in 2010, a listing rate of about 0.8 species per year (Fig. 2). The total number of imperiled species increased from 55 to 100 in this same period (2.1 species per year) (Fig. 2). While the increase was partly the result of 14 taxa being added to the fauna, most of the increase reflects real declines in species status. Previous status determinations (Moyle and Williams, 1990; Moyle et al., 1995) were made without benefit of our systematic approach and were constrained by prior agency designations. However, because the senior author was in charge of all three assessments, the evaluations are fairly consistent.

In this status review, the metrics contributing most often to overall status scores of 1.0–2.9 were climate change (62% of species with such scores), anthropogenic threats (56%) and area occupied (55%). In contrast, fishes with scores of 4.0 and above had large populations, wide distributions, and high tolerance of environmental change. The anthropogenic threats that led to the most species with "critical" or "high" ratings were alien species (34%), dams (24%) and agriculture (18%) (Table 4). Twenty-five species (19%) had at least one "critical" rating, indicating high likelihood of extinction in the near future, while 63 species (49%) 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 4
Percentages of 122 extant California freshwater fishes assigned ratings of severity for 15 causes of fish declines. A cause rated 'critical' had the most severely negative effect on a species. See text for descriptions of causes and for definitions of critical, high, medium, and low rating levels.

Cause	Critical	High	Medium	Low	No effect
Percent of fish taxa with rating					
Major dams	3	21	32	27	17
Agriculture	1	17	50	25	7
Grazing	0	9	48	41	2
Rural residential	2	1	28	65	5
Urbanization	0	9	30	39	22
Instream mining	0	3	28	44	5
Mining	0	3	8	84	6
Transportation	0	4	46	48	3
Logging	2	4	27	55	12
Fire	0	4	42	50	4
Estuary alteration	2	10	22	7	61
Recreation	0	2	16	77	6
Harvest	1	8	13	29	49
Hatcheries	3	11	7	14	66
Alien species	11	23	35	30	1

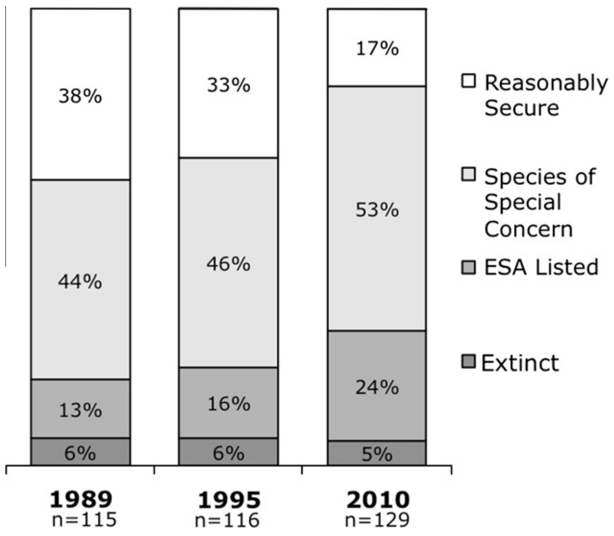

Fig. 2. Status of the native fishes of California from three surveys over 21 years, as shown by percentages of known species in conservation categories used by the state of California. Listed species are those listed under the state and federal endangered species acts as either Threatened or Endangered. Special Concern species are those in decline or in small isolated populations that are likely to be eligible for listing in the near future. For 2010, some Special Concern status determinations have not yet been officially recognized.

4. Discussion

4.1. What is the status of California's freshwater fish fauna?

In 1989, only 14 species were formally ESA listed as Threatened or Endangered (Moyle and Williams, 1990). Today, 31 species are formally listed and about one additional species is being listed every two years, despite a general slow-down in the listing process (Greenwald et al., 2006). In addition, seven species have gone extinct in the past 50 years. Clearly, the native fish fauna of California is in serious decline by official standards. However, our analysis indicates that the decline is more severe than recognized, with 107 (83%) of the native fishes prone to extinction. The major cause of decline is a growing human population that enjoys living in a mild Mediterranean climate where water is in short supply, especially in the dry summer season or during periods of drought. This shortage results in most waterways being dammed, diverted, polluted, or otherwise altered, with the additional threat of frequent invasions of alien fishes (Moyle, 2002; Moyle and Marchetti, 2006). The highly endemic fishes of the region are vulnerable to change because many are confined to limited geographic areas or to habitats where conditions are naturally stressful. However, even many wide-ranging species (e.g., all salmon species and steelhead rainbow trout) are imperiled (Moyle, 2002; Moyle et al., 2008). Native species that have managed to thrive under altered conditions are those that have naturally large ranges, broad habitat requirements, high tolerance of adverse conditions, and an ability to become part of new fish assemblages that include alien species (e.g., Tahoe sucker, Sacramento pikeminnow).

4.2. Are the fishes continuing to decline?

Today, 83% of California's freshwater fishes are imperiled or extinct, a 16% increase since the last assessment in 1995 and a 21% increase since 1989. The increase is partly the result of improved information, but declines of most species are also real, as illustrated below by coho salmon, Central Valley fall Chinook salmon, delta smelt, Clear Lake hitch, and Sacramento perch.

Coho salmon (Salmonidae) are native to hundreds of coastal streams from Monterey Bay north to the Oregon border and once supported sport and commercial fisheries (Moyle, 2002). In the 1940s, estimated numbers of adults spawning in California streams were 200,000–400,000 (Moyle et al., 2008). They were regarded by Moyle and Williams (1990) as being in sharp decline but still common. Subsequent studies documented their rapid disappearance from their native streams throughout the state and by 1996 the two Evolutionary Significant Units (ESUs) of coho salmon present in California had been listed as federal Threatened or Endangered species. Our analysis scored status of the Central Coast ESU as 1.1 and the Southern Oregon Northern California Coast ESU as 1.7. The 2010 federal ESA recovery plan for California coho salmon is consequently regarded as more an extinction prevention plan than a real plan for recovery (NMFS, 2010).

Central Valley fall Chinook salmon ESU once historically made up the largest run of salmon in the Sacramento and San Joaquin River basins, with runs once estimated to be around a million fish annually; adult populations through most of the 20th century were 200,000–400,000 fish. Moyle and Williams (1990) considered it to be abundant and perhaps even increasing in abundance. However, its status score here is 2.0, because of a recent precipitous population crash (Moyle et al., 2008) which is apparently the indirect result of the population being almost entirely composed of fish of hatchery origin (Barnett-Johnson et al., 2007).

Delta smelt (Osmeridae) are endemic to the San Francisco Estuary and require fresh water for spawning (Moyle, 2002). In the 1970s, they were still one of the most abundant fish in the upper estuary but declined rapidly so that Moyle and Williams (1990) indicated they merited listing as a threatened species. They were listed as Threatened by both state and federal governments in 1993. Nevertheless, their decline has continued as the result of major environmental changes to the upper estuary related to increasing water exports and other factors (Bennett, 2005), despite major efforts to curtail mortalities in recent years. With a 1-year life cycle, they may be on verge of extinction and accordingly were given a score of 1.4.

Clear Lake hitch (Cyprinidae) is endemic to Clear Lake, a large natural lake in the Coast Range of California (Moyle, 2002). Although the lake has been highly altered for human use and has been heavily invaded by alien species, hitch are one of the few native species that have persisted; Moyle and Williams (1990) found them to be abundant but possibly declining. However, dramatic reduction in numbers of individuals in spawning streams, presumably related to the expanding population of piscivorous Florida largemouth bass (*Micropterus floridae*) in the lake as well as continued environmental degradation, resulted in a status score of 1.9.

Sacramento perch (Centrarchidae) were once one of the most abundant fish in the Central Valley and subject to commercial fisheries in the 19th century (Moyle, 2002). Today they are extirpated from their native range largely from competition and predation by introduced centrarchids (Crain and Moyle, 2011). They have persisted only because they have been introduced into scattered reservoirs and lakes in other parts of California and the western USA. However, many introduced populations are now gone and most others are located in waters that are not secure (Crain and Moyle, 2011). Moyle and Williams (1990) indicated concern about its decline but thought it did not merit listing as a threatened species. Because so many populations have disappeared or declined since then, it scored 1.6 in our evaluation.

4.3. What factors are most strongly associated with conservation status?

The causes of the declines have their roots in the 19th and early 20th centuries when unrestricted mining, logging, and wetland conversion, combined with wide-scale dam building, severely altered most rivers, lakes, and estuaries. In addition, approximately 50 species of alien fishes were successfully introduced, many of them better suited to altered environments than native species (Moyle and Marchetti, 2006). Nevertheless, each native species has its own idiosyncratic response to this changing environment, as a result of its natural characteristics interacting with changes occurring in its particular habitats. Our analyses showed that each imperiled species has its own combination of causes of decline but most common were factors reflecting large-scale landscape changes (dams, agriculture, logging, urbanization, Table 4). An issue common to all species is climate change, which was often an important factor affecting our final status score for each species. Increases in water temperatures and variability in stream flows are becoming an increasingly important limiting factor for most species, but especially those relying on streams with perennial flows of cool (<20–22 °C) water. Thus a systematic conservation approach has to deal both with broad issues and those particular to each species.

4.4. How do our results fit with official status designations?

Of the 31 California fish species listed under the ESA, 94% fell into our two most at-risk status categories, indicating that our scoring system approximates the criteria used in official ESA listing determinations. However, only 51% of 33 species that we rated as endangered (scores <2.0) were officially listed under the ESA, indicating that official protection is not keeping pace with the rapid decline of California's inland fishes. That ESA designations are not concordant with current status is also born out by the fact that 12 (36%) of the 33 species we rated as vulnerable (scores of 2.0–2.9) and two (6%) of the species we rated as near-threatened (scores of 3.0–3.9) were listed as threatened or endangered under the ESA. The reasons for the discrepancies between our ratings and official status are complex but largely stem from better information being available now than at the time of listing. For example, the rough sculpin (score of 3.4) was one of the first fishes listed under state law, when little was known about its distribution and biology. Subsequent studies have indicated it is fairly widespread in spring streams of the Pit River watershed and is even expanding its range in reservoirs (Moyle, 2002). However, recent genetic studies suggest rough sculpin is actually two disjunct populations (A. Kinziger, pers. comm. 2010), perhaps species, which might qualify for listing if treated independently.

Rating the quality (certainty) of the information on which each species status score was based enables managers to determine which species need more study. Most of our species status determinations are based on strong published evidence. However, species with low certainty scores should be re-evaluated for status frequently.

5. Conclusions

The native inland fish fauna of California is in rapid decline and many species are likely to disappear from the state within the next century if present trends continue. Unfortunately, global climate change and human population growth are likely to increase fish extinction rates as competition with humans for increasingly scarce water intensifies, stream flows become more variable, and water quality, especially temperature, changes. For coldwater fishes, thermal refuges may disappear from streams in many areas, leaving no place to escape unfavorable conditions. The patterns of decline we see in California have been documented in freshwater fishes in other arid climates (Moyle and Leidy, 1992; Aparicio et al., 2000; Maceda-Veiga et al., 2010). However, the decline of California's inland fishes is likely characteristic of freshwater fishes and their ecosystems worldwide. As better information and similar systematic approaches are employed in other regions, we predict more imminent extinctions will be detected than are presently appreciated. Given trends of rapid decline that we have documented it is likely that many species will be lost before effective conservation plans can be implemented. There is, therefore, no time to be lost in designing and implementing conservation efforts for freshwater species in California and worldwide.

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Appendix

Table 1. List of all native fishes known to breed in the inland waters of California, ranked by level of extinction threat. Asterisks denotes taxon listed by federal or state Endangered Species Acts. Extinct= globally extinct or extirpated from the inland waters of California. Status scores of 1.0-1.9 are roughly equivalent to IUCN threat level of *endangered* or *critically endangered*; 2.0-2.9, IUCN threat level of *vulnerable*; 3.0-3.9, IUCN threat level of *Near Threatened;* 4.0-5.0, IUCN threat level of *Least Concern*.

Species	Status Score
Thicktail chub, Siphatales crassicauda	Extinct
High Rock Springs tui chub, *S. b. subsp.*	Extinct
Bonytail, *Gila elegans*	Extinct
Clear Lake splittail, *P. ciscoides*	Extinct
Colorado pikeminnow, *P. lucius*	Extinct
Bull trout, *Salvelinus confluentus*	Extinct
Tecopa pupfish, *C. n. calidae*	Extinct
Long Valley speckled dace, *R. o. subsp.*	1.0
Central coast coho salmon, *O. kisutch*	1.1*
Shoshone pupfish, *C. n. shoshone*	1.1
Razorback sucker, *Xyrauchen texanus*	1.3*
Pink salmon, *O. gorbuscha*	1.3
Shay Creek stickleback, *G. a. subsp.*	1.3
Owens tui chub, *S. b. snyderi*	1.4*
Mojave tui chub, *S. mohavensis*	1.4*
Delta smelt, *Hypomesus pacificus*	1.4*
Owens pupfish, *C. radiosus*	1.4*
Southern green sturgeon, *A. medirostris*	1.6*
Amargosa Canyon speckled dace, *R. o. nevadensis*	1.6
Santa Ana speckled dace, *R. o. subsp.*	1.6
Modoc sucker, *Catostomus microps*	1.6*
Flannelmouth sucker, *C. latipinnis*	1.6
Eulachon, *Thaleichthys pacificus*	1.6*
Upper Klamath-Trinity spring Chinook salmon, *O. tshawytscha*	1.6
Southern Oregon Northern California coast coho salmon, *O. kisutch*	1.6*
Chum salmon, *O. keta*	1.6
Sacramento perch, *Archoplites interruptus*	1.6
Lost River sucker, *C. luxatus*	1.7*
Santa Ana sucker, *C. santaanae*	1.7*
Central Valley late fall Chinook salmon, *O. tshawytscha*	1.7
Klamath Mountains Province summer steelhead, *O. mykiss*	1.7
Southern California steelhead, *O. mykiss*	1.7*
Paiute cutthroat trout, *O. c. seleneris*	1.7*
Clear Lake hitch, *L. e. chi*	1.9
Owens speckled dace, *R. o. subsp.*	1.9
Northern California coast summer steelhead, *O. mykiss*	1.9*
McCloud River redband trout, *O. m. stonei*	1.9
Kern River rainbow trout, *O. m. gilberti*	1.9
Desert pupfish, *Cyprinodon macularius*	1.9*
Unarmored threespine stickleback, *G. a. williamsoni*	1.9*
Kern brook lamprey, *L. hubbsi*	2.0
White sturgeon, *A. transmontanus*	2.0
Red Hills roach, *L. s. subsp.*	2.0
Klamath largescale sucker, *C. snyderi*	2.0
Shortnose sucker, *Chasmistes brevirostris*	2.0*
Longfin smelt, *Spirinchus thaleichthys*	2.0*
Central Valley winter Chinook salmon, *O. tshawytscha*	2.0*
Central Valley spring Chinook salmon, *O. tshawytscha*	2.0*
Central Valley fall Chinook salmon, *O. tshawytscha*	2.0
California golden trout, *O. m. aguabonita*	2.0
Little Kern golden trout, *O. m. whitei*	2.0*
Eagle Lake rainbow trout, *O. m. aquilarum*	2.1
Lahontan cutthroat trout, *O. c. henshawi*	2.1*
Cow Head tui chub, *S. t. vaccaceps*	2.1
Goose Lake sucker, *C. o. lacusanserinus*	2.1
Saratoga Springs pupfish, *C. n. nevadensis*	2.1
Arroyo chub, *Gila orcutti*	2.3
Amargosa River pupfish, *C. n. amargosae*	2.3
Lahontan Lake tui chub, *S. b. pectinifer*	2.4

(*continued on next page*)

Appendix (*continued*)

Species	Status Score
Cottonball Marsh pupfish, *C. s. milleri*	2.4*
Northern green sturgeon, *Acipenser medirostris*	2.4
Upper Klamath-Trinity fall Chinook salmon, *O. tshawytscha*	2.4
California Coast fall Chinook salmon, *O. tshawytscha*	2.4*
Central Valley steelhead, *O. mykiss*	2.4*
South Central California coast steelhead, *O. mykiss*	2.4*
Salt Creek pupfish, *C. s. salinus*	2.6
Goose Lake lamprey, *Entosphenus sp.*	2.6
Monterey hitch, *L. e. harengeus*	2.7
Central California coast winter steelhead, *O. mykiss*	2.7*
Bigeye marbled sculpin, *C. klamathensis macrops*	2.7
Sacramento splittail, *Pogonichthys macrolepidotus*	2.9
Tidewater goby, *Eucyclogobius newberryi*	2.9*
Northern Roach, *L. mitrulus*	2.9
Russian River roach, *L. s. subsp*	3.0
Navarro Roach, *L. s. navarroensis*	3.0
Gualala roach, *L. parvipinnus*	3.0
Tomales Roach, *L. s. subspecies*	3.0
Upper Klamath marbled sculpin, *C. k. klamathensis*	3.0
Clear Lake tule perch, *H. t. lagunae*	3.0
Western brook lamprey, *L. richardsoni*	3.1
Clear Lake roach, *L s. subsp.*	3.1
Clear Lake prickly sculpin, *C. a. subsp.*	3.1
Russian River tule perch, *H. t. pomo*	3.1
Eagle Lake tui chub, *S. b. subsp.*	3.3
Sacramento hitch, *Lavinia e. exilicauda*	3.3
Monterey roach, *L. s. subditus*	3.3
Mountain sucker, *C. platyrhynchus*	3.3
Northern California coast winter steelhead, *O. mykiss*	3.3
Goose Lake redband trout, *O. m. subsp.*	3.3
Lower Klamath marbled sculpin, *C.k. polyporus*	3.3
Blue chub, Gila coerulea	3.4
Central California roach, *L. s. symmetricus*	3.4
Pacific lamprey, *Entosphenus tridentata*	3.4
Goose Lake tui chub, *S. t. thalassinus*	3.4
Hardhead, *Mylopharodon conocephalus*	3.4
Coastal cutthroat trout, *O. clarki clarki*	3.4
Rough sculpin, *Cottus asperrimus*	3.4*
Riffle sculpin, *C. gulosus*	3.4
Sacramento tule perch, *Hysterocarpus t. traski*	3.4
River lamprey, *Lampetra ayersi*	3.6
Pit-Klamath brook lamprey, *L. lethophaga*	3.6
Southern Oregon Northern California coast fall Chinook salmon, *O. tshawytscha*	3.7
Klamath River lamprey, *E. similis*	3.9
Reticulate sculpin, *C. perplexus*	3.9
Owens sucker, *C. fumeiventris*	3.9
Mountain whitefish, *Prosopium williamsoni*	3.9
Klamath Mountains Province winter steelhead, *O. mykiss*	3.9
Pit River tui chub, *S. thalassinus subsp.*	4.0
Klamath tui chub, *S. b. bicolor*	4.1
Sacramento speckled dace, *Rhinichthys osculus subp.*	4.1
Monterey sucker, *C. o. mnioltiltus*	4.1
Klamath smallscale sucker, *C. rimiculus*	4.1
California killifish, *Fundulus parvipinnis*	4.1

Appendix (*continued*)

Species	Status Score
Inland threespine stickleback, *G. a. microcephalus*	4.1
Humboldt sucker, *C. o. humboldtianus*	4.3
Pit sculpin, *C. pitensis*	4.3
Coastrange sculpin, *C. aleuticus*	4.4
Sacramento blackfish, *Orthodon microlepidotus*	4.4
Paiute sculpin, *C. beldingi*	4.4
Coastal threespine stickleback, *Gasterosteus a. aculeatus*	4.6
Lahontan stream tui chub, *S. b. obesus*	4.7
Sacramento pikeminow, *Ptychocheilus grandis*	4.7
Coastal rainbow trout, *O. m. irideus*	4.7
Coastal Prickly sculpin, *C. asper subsp.*	4.7
Lahontan redside, *Richardsonius egregius*	4.8
Lahontan speckled dace, *R. o. robustus*	4.8
Klamath speckled dace, *R. o. klamathensis*	4.8
Tahoe sucker, *Catostomus tahoensis*	5.0
Sacramento sucker, *C. o. occidentalis*	5.0

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