California's freshwater fishes: status and management

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SUMMARY

Fishes in Mediterranean climates are adapted to thrive in streams with dynamic environmental conditions such as strong seasonality in flows. However, anthropogenic threats to species viability, in combination with climate change, can alter habitats beyond native species' environmental tolerances and may result in extirpation. Although the effects of a Mediterranean climate on aquatic habitats in California have resulted in a diverse fish fauna, freshwater fishes are significantly threatened by alien species invasions, the presence of dams, and water withdrawals associated with agricultural and urban use. A long history of habitat degradation and dependence of salmonid taxa on hatchery supplementation are also contributing to the decline of fishes in the state. These threats are exacerbated by climate change, which is also reducing suitable habitats through increases in temperatures and changes to flow regimes. Approximately 80% of freshwater fishes are now facing extinction in the next 100 years, unless current trends are reversed by active conservation. Here, we review threats to California freshwater fishes and update a five-tiered approach to preserve aquatic biodiversity in California, with emphasis on fish species diversity. Central to the approach are management actions that address conservation at different scales, from single taxon and species assemblages to Aquatic Diversity Management Areas, watersheds, and bioregions.

Keywords: alien fishes, climate change, conservation strategy, dams

ECOSYSTEM AND FISH FAUNAL CHARACTERIZATION

Mediterranean climates are characterized by seasonal cycles of cool, wet winters and warm, dry summers with most rainfall falling in winter (Gasith and Resh 1999). This seasonality in rainfall results in flow regimes with high flows in winter and spring, and low flows in summer and fall. Although the annual occurrence of high and low flow events is predictable, their intensity and frequency can vary greatly between years and locations (Gasith and Resh 1999, Grantham *et al*. 2010). Streams with high-elevation headwaters have attenuating spring-summer flows, reflecting a snow-melt flow regime (Yarnell *et al*. 2010). Streams with rainfall-driven flows respond rapidly to winter storms, and high flows can be extremely flashy. Regardless of whether flows are driven by snow-melt or rain, late summers are likely to be most stressful for fish, because sections of streams can dry for extended periods during some years (Gasith and Resh 1999). In Californian summers, streams may experience high water temperatures, high alkalinity, and low dissolved oxygen concentrations (Moyle 2002). These conditions, as well as changes in stream flow, influence the abundance and distribution of fishes, by determining the physical and biological characteristics of streams (Poff and Ward 1989). Fishes living in California's Mediterranean-climate streams are therefore adapted to varying, and often extreme, environmental conditions (Moyle *et al*. 2011).

There are 129 native and 43 alien (non-native) freshwater fish species or similar taxa (i.e. Evolutionarily Significant Units, Distinct Population Segments) recognized in California (Moyle *et al*. 2011, Appendix A); of the native fishes, 63% are endemic and another 19% are shared with adjacent states, so 82% of California fishes are regionally endemic (Moyle *et al*. 2011). Most taxa are found in areas with high water availability (Central Valley and North Coast) and highest aquatic habitat diversity. Fishes are also found in extreme habitats such as intermittent streams (e.g., California roach, *Lavinia* spp*.)*, desert springs (e.g., pupfishes *Cyprinodon* spp.) and alkaline lakes (e.g., Eagle Lake trout *Oncorhynchus mykiss aquilarum*). Most native fishes in California spawn in spring, March through May (Moyle 2002), synchronizing their life histories to flow regimes in their natal streams (Kiernan and Moyle 2012) in order to exploit favorable stream conditions for spawning and early life history stages. Other characteristics that facilitate life in highly variable conditions include high fecundity, good dispersal mechanisms, and behavioral and physiological mechanisms to survive or avoid extreme conditions (Moyle 2002; Table 1).

Most (but not all) established alien species in California have a number of traits in common; they have a mutualistic relationship with people, are tolerant of a broad suite of environmental conditions, have ecological requirements similar to the environments into which they are introduced, and have large native ranges (Marchetti *et al*. 2004a, Moyle and Marchetti 2006). Prior invasion success also increases the chance of successful establishment, as does large propagule size. However, the ability of a species to spread or integrate into the existing fauna is dependent on a combination of other characteristics that promote survival through different life history stages, which differ among species. Longevity, regional origin, and trophic status (other than herbivory) appear to facilitate spread while size, regional origin, and trophic status (other than invertivory) aid integration success (Moyle and Marchetti 2006). At the landscape level, distribution patterns of alien species are most enhanced by the magnitude of human alterations to aquatic habitats. Urbanization, water diversion, and agriculture, in particular, enable successful alien species invasion (Marchetti *et al*. 2004b, c).

TABLE 1. General characteristics of most native fishes and native fish assemblages in California (modified from Moyle 2002). Many exceptions exist to each characteristic

1	Have life history strategies that favor large size and high fecundity
2	Are morphologically distinct between regions
3	Comprise a fish fauna with low local species richness (1-7 species)
4	Anadromous species are important components of fish assemblages in streams connected to the ocean
5	Spawn from March to May
6	Provide little parental care
7	Inhabit different ecological niches during different life stages
8	Have mechanisms (behavioral, physiological) to survive or avoid extreme conditions
9	Are good dispersers
10	Are depleted by alien species in highly altered systems

CURRENT KNOWLEDGE AND STATUS

California's freshwater fish fauna as a whole has been studied extensively (Moyle 2002). However, there is a paucity of information for some taxa. Moyle *et al.* (2011, 2013) quantified available information for each taxon during their status assessments. Moyle *et al.* (2011), determined status by scoring seven metrics to evaluate the suite of threats faced by each taxon. Quality of knowledge used to determine individual metrics for each taxon was scored through certainty indices. A low certainty index score was given to taxa with little or no data, indicating that the score was largely based on expert opinion. A high score was given to taxa for which multiple sources of information were available, including peer-reviewed literature. The same approach was used to score the certainty of each taxon's climate change vulnerability in Moyle *et al.* (2013). Based on these evaluations, there is at least moderate knowledge for about 93% of the taxa in California. The 7% (9 species) of the taxa that we know little about are largely represented by lamprey and cyprinid species (Table 2).
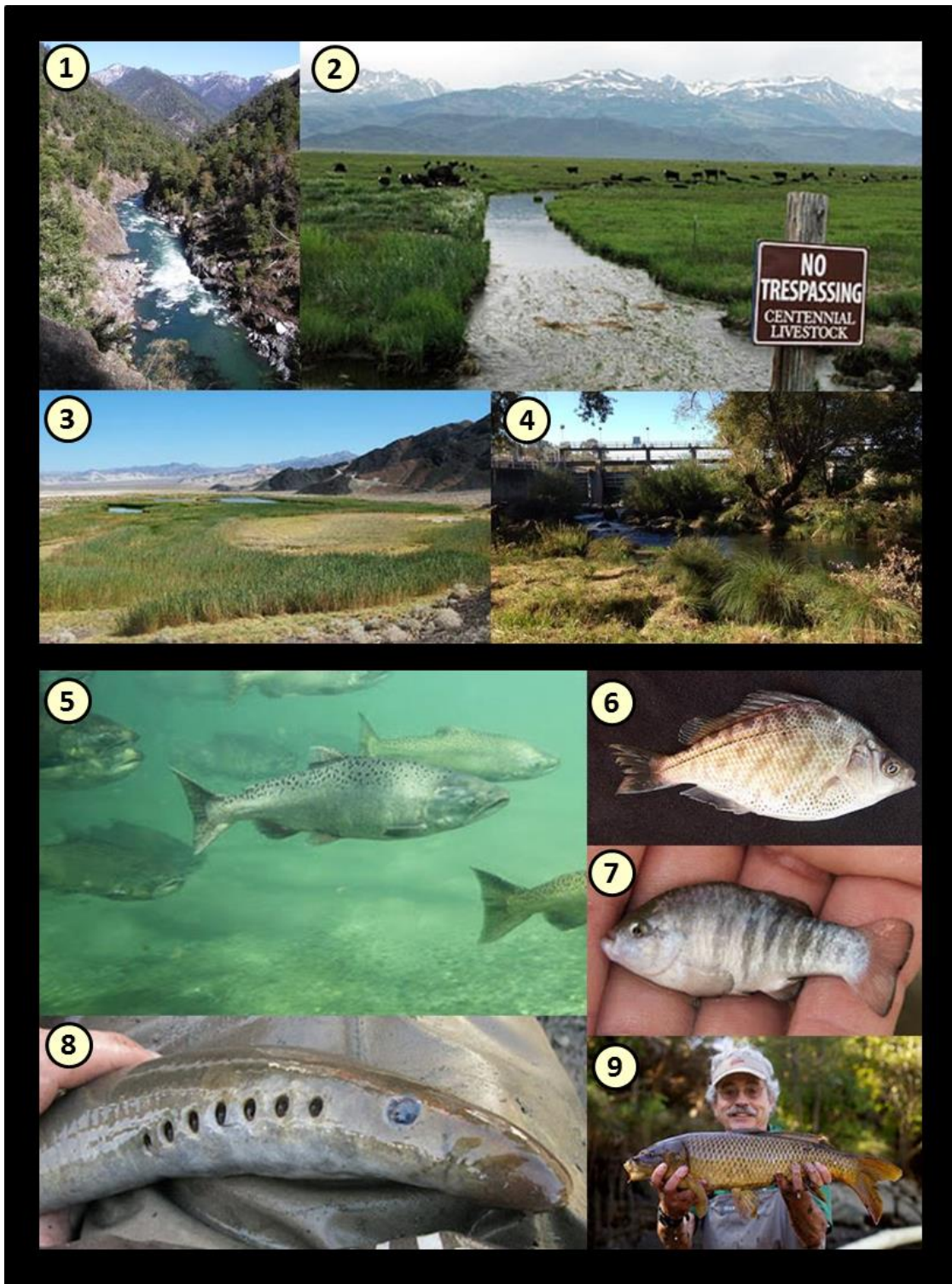
PLATE 1. Californian fish habitats and fish species. 1) Klamath River; 2) Walker River Valley; 3) Saratoga Springs; 4) Putah Creek; 5) Chinook salmon; 6) Tule perch; 7) Saratoga Springs pupfish; 8) Pacific lamprey; 9) Common carp. Photographs: J. Katz and R. Quiñones

TABLE 2. Native fish taxa of which we have least knowledge in California (low certainty scores; see Moyle et al. 2013 for details). Basic information on habitat requirements, distribution or abundance of these species in California is not currently available.

1	Klamath River lamprey, *Entosphenus similis*
2	River lamprey, *Lampetra ayersi*
3	Western brook lamprey, *Lampetra richardsoni*
4	Pit-Klamath brook lamprey, *Lampetra lethophaga*
5	Pit River tui chub, *Siphatales thalassinus* subsp.
6	Sacramento hitch, *Lavinia exilicauda exilicauda*
7	Northern Roach, *Lavinia mitrulus*
8	Klamath largescale sucker, *Catostomus snyderi*
9	Chum salmon, *Oncorhynchus keta*

These studies (Moyle *et al.* 2011, 2013) showed that the status of native fishes in California has been declining at least since the onset of large-scale damming and diversions in the mid-19th century. Status assessments of the entire fish fauna were completed in 1975 (Moyle 1976), 1989 (Moyle and Williams 1990), 1995 (Moyle *et al.* 1995), and 2010 (Moyle *et al.* 2011). Although status labels differed between reports, individual taxon were determined to be, in order of decreasing concern, extinct/extirpated, endangered (i.e. listed or eligible for listing under state and federal endangered species acts), vulnerable, or apparently secure in all assessments. Vulnerable taxa were those with populations in decline and needing active monitoring or management to avoid further endangerment.

Present trends will likely result in extinction of ~80% of California's native fishes in the next 100 years (Moyle *et al.* 2011, 2013; Katz *et al.* 2012). Seven taxa are already extinct (see Appendix A). Since the first status assessment in 1975, taxa threatened with extinction (vulnerable or endangered) increased from 41% in 1975 to 57% in 1989, to 62% in 1995, and to 77% in 2010 (Figure 1). In 1995, 16 taxa were designated as most in peril of extinction in the near future (Figure 1). Of these, 9 (53%) were salmonids, and 7 were cyprinids (44%). In 2010, the most imperiled groups were represented by twice as many taxa (33, Figure 1) in eight families (Moyle *et al.* 2011; Table 3). Of the 129 taxa assessed in 2010, only 22 (18%) were thought to be relatively secure (Figures 1); these are generally taxa that are widely distributed, able to cope with a broad range of environmental conditions, and can live with alien species (Moyle *et al.* 2011).
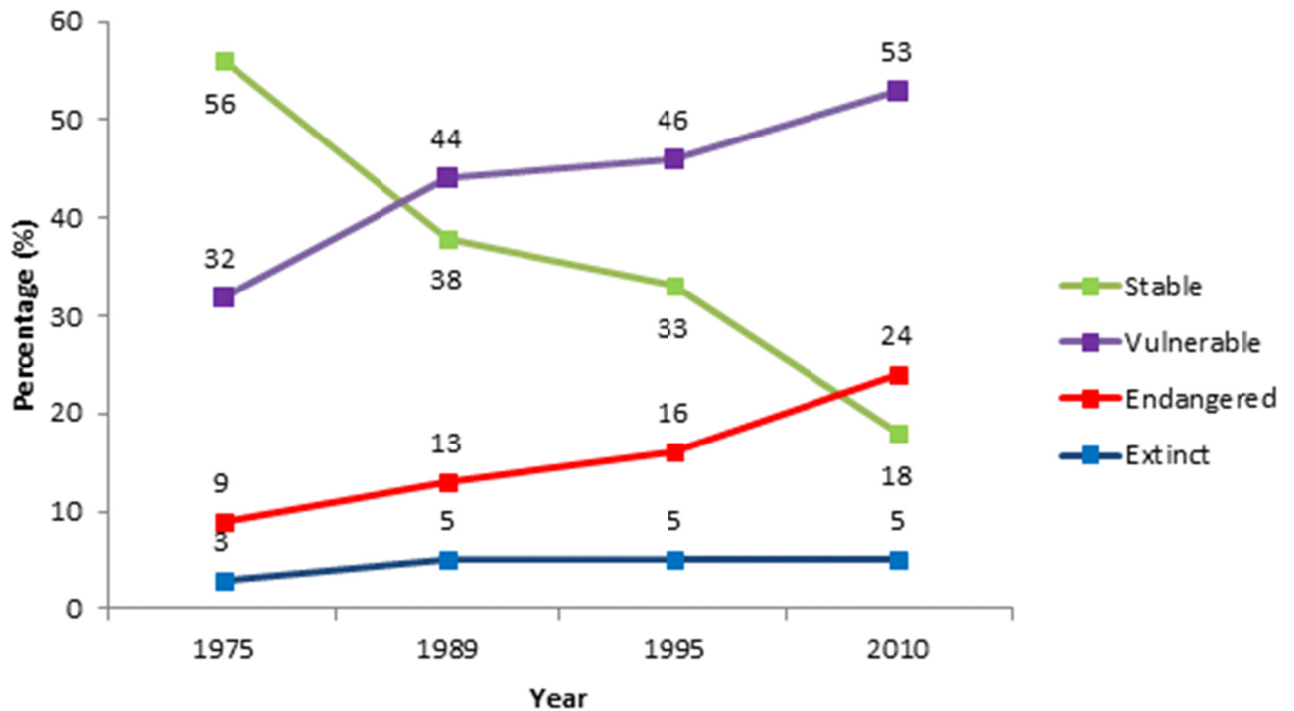
FIGURE 1. Status of California fishes 1975-2010. Proportion (%) of California native fish species in stable, vulnerable, endangered, and extinct status categories, 1975-2010 (modified from Moyle et al. 2011)

MAIN THREATS AND MANAGEMENT ISSUES

Based on multiple assessments, the major anthropogenic threats faced by California fishes have remained relatively the same since 1990, with an additional threat (climate change) identified in 2010. The relative impact of each threat, however, has changed through time. In the 1770s, the first California streams were diverted for agricultural irrigation (Hundley 1992), a process that would continue to hit its heyday in the mid-20th century (Moyle 2002). During this time cattle grazing also began to reshape the landscape, including riparian areas, as the European population grew (Moyle 2002). The magnitude of the detrimental impacts to water bodies exponentially increased with the onset of the Gold Rush in the 1850s, when hydraulic mining destroyed stream banks and hillslopes, increasing sediment delivery to streams that raised streambeds by as much as 7 m (Moyle 2002). In the late 1800s, most of the wetlands, including floodplains, in the Central valley were drained, diked, and reclaimed for agriculture. These dramatic changes caused extinction of some common species such as thicktail chub (*Gila crassicauda;* Moyle 2002). At the same time, alien species were introduced and commercial fisheries went unregulated (Moyle 2002).

TABLE 3. Fish taxa considered critically endangered in California. Taxa are listed in order of highest to lowest threat of extinction based on scores from Moyle et al. 2011. * = formally listed under at least one Endangered Species Act.

#	Taxon	#	Taxon
1	Long Valley speckled dace *Rhinichthys osculus* ssp.	18	Southern Oregon Northern California coast coho salmon *Oncorhynchus kisutch*
2	Central coast coho salmon* *Oncorhynchus kisutch*	19	Chum salmon *Oncorhynchus keta*
3	Shoshone pupfish *Cyprinodon nevadensis shoshone*	20	Sacramento perch *Archoplites interruptus*
4	Razorback sucker* *Xyrauchen texanus*	21	Lost River sucker* *Catostomus luxatus*
5	Pink salmon *Oncorhynchus gorbuscha*	22	Santa Ana sucker* *Catostomus santaanae*
6	Shay Creek stickleback *Gasterosteus aculeatus* ssp	23	Central Valley late fall Chinook *Oncorhynchus tshawytscha*
7	Owens tui chub* *Siphatales bicolor snyderi*	24	Klamath Mountains Province summer steelhead *Oncorhynchus mykiss*
8	Mojave tui chub* *Siphatales mohavensis*	25	Southern California steelhead* *Oncorhynchus mykiss*
9	Delta smelt* *Hypomesus pacificus*	26	Paiute cutthroat trout* *Oncorhynchus clarki seleneris*
10	Owens pupfish* *Cyprinodon radiosus*	27	Clear Lake hitch* *Lavinia exilicauda chi*
11	Southern green sturgeon* *Acipenser medirostris*	28	Owens speckled dace Rhinichthys osculus ssp.
12	Amargosa Canyon speckled dace *Rhinichthys osculus nevadensis*	29	Northern California coast summer steelehead* *Oncorhynchus mykiss*
13	Santa Ana speckled dace *Rhinichthys osculus ssp.*	30	McCloud River redband trout *Oncorhynchus mykiss stonei*
14	Modoc sucker* *Catostomus microps*	31	Kern River rainbow trout *Oncorhynchus mykiss gilberti*
15	Flannelmouth sucker *Catostomus latipinnis*	32	Desert pupfish* *Cyprinodon macularius*
16	Eulachon* *Thaleichthys pacificus*	33	Unarmored threespine stickleback* *Gasterosteus aculeatus williamsoni*
17	Upper Klamath-Trinity Rivers spring Chinook *Oncorhynchus tshawytscha*		

For decades, effects of environmental change on fishes went largely unquantified. The first attempts to systematically assess the conservation status of fishes in California were performed by Moyle *et al.* (1989) and Moyle and Williams (1990). They identified anthropogenic threats as, in order of decreasing impact, water diversion (impacting 31% of native taxa), alien species (24%), habitat modification (22%), overexploitation (2%), and pollution (1%). In 2010, alien species (34%) were considered the most detrimental threat, followed by major dams and associated water diversions (24%), agriculture (18%), hatcheries (14%), and estuarine alteration (12%) (Moyle *et al.* 2011). Moyle *et al.* (2013) proposed that climate change will exacerbate many of these major threats while also directly restricting suitable habitats and reducing native fish abundances. Major threats to California native fishes are discussed in greater detail below.

Alien species

The suite of factors that threatened the status of native fishes in California for many decades has changed over time, but alien (introduced) species have been a constant problem. Moyle and Williams (1990) found alien species and water diversions as the primary threats. Alien species have become the most abundant taxa in some waterways, aided by extensive stream channel and flow modifications (Moyle 2002). Reductions in native fish abundance due to the presence of alien species can occur through competition, predation, habitat alteration, introduction of disease and parasites, and hybridization (Moyle 2002). Competition with alien species alone can reduce abundance of native fishes when resources (e.g., food, space) are scarce, although it seldom results in their elimination (see Carmona-Catot *et al.* 2011 for an exception). Predation by alien species, particularly on early life stages, has caused local extirpation of native fishes in California (e.g., predation of green sunfish *Lepomis cyanellus* on California roach *Lavinia symmetricus*, Moyle 2002). Habitat alteration by alien species may reduce or eliminate native fish populations by degrading habitat (e.g., common carp *Cyprinus carpio* can increase turbidity and thereby inhibit foraging opportunities for visual feeders, Moyle 2002). Diseases or parasites introduced with alien species can weaken or kill native fishes that are not already resistant to them (e.g., whirling disease *Myxobolus cerebralis* in trout native to the Truckee River; Modin 1998). Hybridization with closely related species can compromise the genetic distinction of native fishes (e.g., hybridization between arroyo chub *Gila orcuttii* and Mojave tui chub *Gila bicolor mohavensis*, Moyle 2002). Sixty-nine percent of the extant native fishes in California are at least moderately adversely impacted by alien species (Moyle *et al.* 2011).

Dams and diversions

In California, dams, reservoirs and aqueducts are used to store and divert water from the northern half of the state, where water is plentiful but demand for water is moderate, to the southern Central Valley and southern California, where water is scarce but demand is high. Major cities (e.g., Los Angeles) import water from multiple watersheds more than 300 km away (Moyle 2002). Almost every large stream is now dammed by either water agencies (state, agricultural, and municipal) or power companies. The largest water-using sector in California (70-80% of stored water) is agriculture, which uses both diverted surface flows and groundwater for irrigation. Diversion, impoundment, and transfer of flows have many ecological impacts on California streams, most of which reduce habitat quality for fishes. The ecological impacts of dams are many and have been extensively reviewed (e.g., Poff *et al.* 1997, Grantham *et al.* 2013). In general, fishes are affected by dams and aqueducts when: 1. migrations are blocked, 2. streams and lakes are dewatered, 3. water is impounded, 4. temperature profiles and flow regimes are altered, and 5. habitats upstream and downstream (including estuaries) of dams are altered (Moyle 2002). Water diversion can also alter habitats in receiving water bodies (e.g. increasing flow, introducing alien species, translocating native species).

Dams effectively block up- and downstream movements of fishes, limiting access to habitats and shrinking species distributions. In the Sacramento-San Joaquin basin, the largest watershed in the state, dams block more than 80% of Chinook salmon *Oncorhynchus tshawytscha* spawning and rearing habitat (Yoshiyama *et al.* 1996). In the Klamath River basin, the second largest watershed in the state, dams block approximately 675 km of anadromous salmonid rearing and spawning habitat (Hamilton *et al.* 2011). Fishes that migrate within rivers may also be adversely affected if suitable habitats become unavailable to different life stages. Even when dams are made passable with fish ladders, reservoirs can inhibit further movement of migrating fishes. Juveniles may be unable to avoid predators or find food and adults may have trouble finding natal streams (as in Carey *et*

al. 2011). Furthermore, changes in water flow and velocity caused by a reservoir can also inhibit migration (Pavlov *et al*. 2008, Tiffan *et al*. 2009). Dams, reservoirs, and channelization can also adversely affect non-salmonid species, such as desert pupfish (*Cyprinodon macularis*) and razorback sucker (*Xyrauchen texanus*) by degrading habitat and harboring alien species that compete or prey on native species.

When water is captured by reservoirs and diverted, less water is available to fishes below dams (Moyle 2002). The most extreme example of this in California is that of Friant Dam. The dam essentially stopped all flow to downstream reaches of the San Joaquin River, either drying up large portions of the river channel or converting it into a drainage system for polluted agricultural return water (Moyle 2002). Dewatering, however, can be incremental rather than complete when only a fraction of water volume is diverted. Even relative small amounts of dewatering can adversely impact native fishes by reducing the amount of habitat available. Due to the large cost and impracticality, fish passage over large dams is uncommon in California, limiting the distribution and recruitment of native migratory fishes. As part of restoration efforts, dam removal (Hamilton *et al*. 2011, Quiñones *et al*. in progress) or dam repurposing (Grantham and Moyle 2013) are being evaluated in some situations, especially where water stored behind dams could be used to benefit native fish conservation.

Habitat degradation

Moyle and Williams (1990) used habitat degradation as a broad threat category recognizing that declines were largely due to multiple interacting factors; they included impacts of dams and diversions, which we treat separately here. Many aquatic habitats have been degraded simultaneously by stream channel modifications, draining of wetlands, livestock grazing, timber harvest, mining, and urbanization (Moyle 2002). A major result of straightening and dredging of stream channels is reduction in aquatic habitat quality. Such streams con-

tain fewer and smaller native fishes than more natural channels. Alien species, in contrast, tend to dominate in highly altered channels, especially in combination with reduced flows.

Most wetlands, including estuarine sloughs and marshes, historically found in California have been drained for agriculture, urban development, or flood control, significantly reducing the amount of habitat available to native fishes. Even small amounts of draining can be detrimental if young fish can no longer find extensive cover from predators, or nutrients from marshlands and floodplains are no longer available to aquatic food webs (Moyle 2002).

Livestock grazing in riparian areas for the last 300+ years has degraded quality of aquatic habitats by removing riparian vegetation and aquatic plants, reducing bank stability and increasing fine sediment erosion through trampling, compaction of soils in meadows, and contamination by animal waste (Moyle 2002). Streams within grazed areas in the Golden Trout Wilderness were found to be wider and have less canopy shading and depth than streams not subject to grazing (Knapp and Matthews 1996). These changes decrease abundance and size of native fishes in impacted waters by changing habitat morphology and suitability.

Timber harvest requires extensive road building to be successful. The combined effects of logging and road-building exaggerates high and low flow events, increase fine sediment erosion and delivery to streams, and decreases habitat complexity (Moyle 2002). Barriers to fish migration from excessive sediment delivery can develop in streams in watersheds where timber has been extensively harvested. Water temperatures can also increase if channels become shallower and riparian vegetation is removed. Aquatic habitat alterations due to streamside timber harvest can result in reduced growth and survival, and ultimately the loss of diversity, of sensitive taxa such as salmonids (Hicks *et al*. 1991).

Mining in California began in earnest during the Gold Rush of the late 1800s. Placer and hydraulic mining were used to uncover gold deposits, resulting is massive alteration of hundreds of kilometers of streambeds and channels (Moyle 2002). The loss or decline of large runs of salmon in some Central Sierra Nevada streams has been attributed to historic mining. Today, such mining is forbidden but instream gravel mining still occurs with significant changes to channel morphology and restrictions to fish distribution. Abandoned hard rock mines often pollute aquatic habitats by leaching heavy metals and acidic water (e.g., Sulphur Bank Mine along the shores of Clear Lake; Moyle 2002). Heavy metals such as mercury can bioaccumulate in macroinvertebrate and fish tissues directly affecting ecosystem health (reviewed in Alpers *et al.* 2005). Likewise, acid drainage from mines can alter ecosystems by changing biochemical properties that can result in fish kills (Filipek *et al.*1987).

Urbanization is one of the most obvious changes in land use in California. The increase of impervious surfaces can alter flow patterns to flood-like events during storms, and facilitates the delivery of pollutants to streams (Moyle 2002). Many streams in urban areas are also either canalized into concrete channels or unshaded ditches. Native fishes are essentially absent from these habitats, while alien species are common (Marchetti *et al.* 2006c). However, even small-scale urban development (e.g., rural residences) can also impact water quality via pollution from septic systems, and alter stream channels regardless of having been straightened for flood protection or dammed to create swimming holes (Moyle *et al.* 2011).

Hatcheries

In California, hatcheries have been used to mitigate loss of rearing and spawning habitats due to stream alterations (especially from dams), and reductions in native fish abundances due to overexploitation. Although most hatcheries in California were built to supplement anadromous salmonid populations (*Oncorhynchus* spp.), hatcheries and aquaculture facilities produce other native species, including delta smelt *Hypomesus transpacificus*, and white sturgeon *Acipenser transmontanus*; however, neither delta smelt nor white sturgeon are released into the wild. When used judiciously, hatcheries can help reestablish declining populations (Moyle 2002). However, hatcheries can also inhibit species recovery through degradation of genetic diversity and reproductive success (reviewed in Brannon *et al.* 2004) or through the replacement of wild stocks by hatchery-reared fishes (as in Sweeting *et al.* 2003, Quiñones *et al.* 2013). Other negative impacts from interactions between wild and hatchery-reared conspecifics include spawning interference, spread of disease and/or parasites, increased predation and competition, and increased harvest pressure (reviewed in Moyle 2002).

CLIMATE CHANGE

In 1995, naturally occurring drought was cited as the factor most likely to result in native fish extinction (Moyle *et al.* 1995). By 2010, climate change in concert with other anthropogenic stressors (alien species, dams, agriculture) was determined to be the most important threat for native taxa (Moyle *et al.* 2011, 2013); this was not a surprise because climate change will exacerbate stressful drought conditions throughout California (summarized in Mastrandrea and Luers 2012).

Climate change effects most likely to directly impact California freshwater fishes are increases in air temperatures, changes in snow retention and snowmelt patterns, increases in the occurrence of droughts and peak flows, and sea level rise. Average annual air temperatures are conservatively expected to increase ~1-3°C by 2050 and then another ~1-2°C by 2100, depending on future greenhouse gas emissions (Cayan *et al.* 2009). However, impacts to streams will vary according to latitude, elevation, and flow volume. In the case of California, differences generally are marked by southern (Sierra Nevada) vs. northern (Cascade

Mountains) mountain ranges. Paradoxically, climate change is expected to have greater impacts on northern rather than southern streams due to the differences in elevations of the Cascade Mountains as compared to the higher Sierra Nevada. Effects within these regions can be stratified further to those occurring inland or along the coast (within the fog-belt). Water temperatures in stream reaches near the coast are usually cooler than inland reaches due to the common presence of coastal fog that reduces the amount of solar radiation affecting these areas.

In western slopes of the Sierra Nevada, an average of 1.6°C (1.2-1.9°C) increase in water temperature is expected for every 2°C increase in air temperature across different elevations (Null *et al*. 2013). Elevations from 1500-2500 m are expected to have the greatest increase in water temperatures, due to the shift in precipitation to less snow and more rain (Null *et al*. 2013). Under the most aggressive warming scenario, an increase of 6°C in air temperatures, the shift from snow to rain will likely lead to changes in flow and thermal patterns that prolong low flows and warm (> 24°C) water temperatures to earlier in spring and later in summer/fall (Null *et al*. 2013). The magnitude of expected warming will have deleterious effects on cold-water native fishes (e.g., golden trout) because water temperatures in some habitats already exceed tolerance levels (> 24 ºC; Matthews 2010). Assuming this pattern holds true for the rest of the state, available cold-water habitats may shrink by 57-99% and shift northward (Null *et al*. 2013). The ability of fishes to move along with suitable habitats is severely hampered by existing barriers and interactions with resident native and non-native taxa.

Because the Cascades Mountains in northern California reach lower elevations than the Sierra Nevada, increasing air temperatures will likely result in larger increases in water temperature and longer duration of low summer flows, due to lower snow levels and shorter snow retention (Hayhoe *et al*. 2004, Stewart *et al*. 2005). In some Klamath basin watersheds (e.g., Scott River), decreasing summer stream flows are likely already resulting in smaller runs of some salmonids (e.g., fall Chinook; Quiñones 2011). In winter, decreasing snow to rain ratios will result in larger, earlier, flashier peak flows (Field *et al*. 1999, Stewart *et al*. 2005, Anderson *et al*. 2008). Native fishes that spawn and incubate in winter (e.g., river lamprey *Lampetra ayresi*, coho salmon *O. kisutch*) may be particularly vulnerable to increases in extreme high flows if adults are displaced from spawning bed or eggs scoured from the gravel.

Streams fed by groundwater and springs should fare better than those dependent on surface runoff because they are usually cooler in summer due to longer environmental response times (Managa 1999). Due to extended storage effect, spring-fed rivers usually exhibit perennial flows albeit at reduced levels following periods of drought (Thompson 2007, Tague *et al*. 2008). The characteristic features of spring-fed rivers will result in more stable flows even with the effects of climate change (Jefferson *et al*. 2008).

Regardless of their location, climate change is likely to change fish communities in all California freshwater habitats. Native fish distribution is predicted to become more constricted and fragmented while most alien species will fare better (Moyle *et al*. 2013). The most vulnerable taxa are those with small distributions or specialized habitat requirements, especially those needing cold water in some or all life stages, such as salmon and trout species. However, even native taxa with more general habitat requirements and broader environmental tolerances are expected to have diminished populations from climate change in California (Moyle *et al*. 2013). In California, the warmer the water, especially during spring and summer, the more likely that native taxa will be replaced by alien species. The result will be ecosystems increasingly dominated by alien species.

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PLATE 2. Prickly sculpin *Cottus aper* and its habitat in the North Fork of Cache Creek Photographs: J. Katz and R. Quiñones

FUTURE DIRECTIONS IN SCIENCE AND MANAGEMENT

Recently, Barbour and Kueppers (2012) proposed that conservation and management of ecosystems in California requires a statewide strategy that identifies critical habitat areas and incorporates assessment indicators in order to protect species in a changing environment. The groundwork for such an approach to protect native fishes in California was first proposed by Moyle and Yoshiyama (1994) and further developed in Moyle (2002) and Viers and Rheinheimer (2011). Recent assessments (Moyle *et al.* 2011, Katz *et al.* 2012, Moyle *et al.* 2013) of freshwater fishes in California underscore the urgent need to take action in order to protect native fishes. Here, we update the five-tiered approach proposed by Moyle and Yoshiyama (1994) and modified by Moyle (2002) for conservation of aquatic biodiversity in California.

Tier 1- Imperiled species

Seven native fish species are already extinct in California, so the first priority in conservation should to prevent extinction of additional taxa by focusing conservation on species in severe decline (imperiled species). While 33 imperiled fishes are officially protected under state and federal Endangered Species Acts (ESAs), an additional 33 taxa (Table 3) could merit such protection. Imperiled species include those with both historically wide-spread (e.g., southern steelhead *O. mykiss* ssp.) and restricted (e.g., Modoc sucker *Catostomus microps)* distributions, as well as species with (e.g., coho salmon) and without (e.g., desert pupfish *Cyprinodon macularius*) economic value. Many of the latter taxa on the list are poorly known. At the very least, the basic biology of these species should be studied to establish conservation strategies. For taxa that are not formally described, genetic and taxonomic analyses should be completed at the same resolution as has been done for endemic trout species (*Oncorhynchus spp.*). For example, individual stocks of steelhead trout (*Oncorhynchus mykiss*) in the western

United States have been identified as 12 separate Distinct Population Segments, including seven in California, in order to protect their unique genetic and ecological identity (http://www.nmfs.noaa.gov/pr/species/fish/steelheadtrout.htm).

Ideally, imperiled species would receive special attention until their numbers reach a point where their management can be incorporated into higher tiers. Most conservation efforts in California have yet to result in securing declining species. However, one successful example is that of Goose Lake redband trout (*O. mykiss* ssp.). Due to a the concentrated efforts of stakeholders in the watershed, the status of Goose Lake redband trout (and other Goose Lake fishes) has improved from endangered in the 1980s to vulnerable in recent years. The rebound of this taxon is largely due to the removal of migration barriers, maintenance of flows in spawning streams, and the removal of livestock from riparian areas.

Tier 2 - Species clusters and assemblages

The goal of Tier 2 is to manage resources for the benefit of small clusters of co-occurring species (not necessarily all fish) or for entire assemblages of species. This basic strategy gets away from single-species management (required by the ESAs) but still has a management strategy based on the needs of a cluster of taxa that have similar requirements. For example, re-establishment of a distinctive assemblage of ten native fishes in Putah Creek (Solano and Yolo Counties) was accomplished by generating a flow regime with water released from an upstream dam that favored native fishes but discouraged alien species (Kiernan *et al.* 2012).

This strategy becomes hard to maintain if one or two species in the cluster are listed under the ESAs because their individual management takes precedence over broader multi-species management. Thus the Delta Native Fishes Management Plan (Moyle *et al.* 1996) for the Sacramento-San Joaquin Delta (the upper part of the San

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Francisco Estuary), was based on a cluster of 8 species, but was never completely implemented because only one species was listed at the time; ironically, additional species in the plan eventually were listed under the ESAs. Today, water management in the Delta has to accommodate the sometimes conflicting needs of eight ESA listed fish species, which tend to be managed independently of one another, by three separate fish agencies (Hanak *et al*. 2011). The idea of managing clusters of listed species together is still viable, however, provided conflicts in policy and biology can be resolved.

Moyle and Williams (1990) indicated that the first step in finding clusters of species for co-management was to divide the state into five regions of endemism: the Sacramento, Klamath, South Coast, Great Basin, and Colorado regions. Moyle (2002) proposed 22 zoogeographic provinces for ecosystem conservation in the state (Figure 2). Quiñones (unpublished data) compared the 2011 status scores of fishes among provinces and determined that they could be ranked according to proportions of imperiled to secure species, with the highest number of imperiled species present in the Eagle Lake, Owens Valley, Mojave Desert, Colorado River, Kern River, and Clear Lake regions. Each province has its own distinct cluster of declining and/or endemic species with different habitat needs, so management recommendations for fish conservation need to address each area specifically. Thus, for the Clear Lake region, management could focus simultaneously on Clear Lake tule perch, Clear Lake sculpin, Clear Lake hitch, Sacramento blackfish, and Sacramento perch in the lake, and Sacramento sucker, Sacramento pikeminnow, and Clear Lake roach in the streams. All but the sucker and pikeminnow are California Species of Special Concern (Moyle *et al*. in press). The first step in managing this cluster is to find out what habitat requirements they have in common (e.g., spring flows in streams, tule beds and large wood for cover in the lake) that can become the focus of management.

Tier 3 - Aquatic Diversity Management Areas

Often intact clusters of native fishes are associated with relatively small watersheds (usually <50 km2) with habitat in fairly good condition; if managed properly these watersheds can sustain the fishes and other biodiversity components. Moyle and Yoshiyama (1994) called such watersheds Aquatic Diversity Management Areas (ADMAs). Their size often makes them easier to protect than larger watersheds (Tier 4) and they are often contained within protected natural areas. Moyle (2002) recognized two basic types of ADMAs: small headwaters (often protected as reserves) and reaches of streams below dams that "contain important native elements not protected elsewhere (p. 74)". Examples of the former include spring systems (e.g., Big Springs on the Shasta River) and small protected tributaries (e.g., Indian Creek, Tehama County), while examples of the latter include lower Putah Creek, discussed above, and Lagunitas Creek, Marin County.

The establishment of a system of ADMAs ensures that naturally functioning ecosystems are protected before they become too degraded, although most watersheds contain alien species and have suffered some degree of habitat alteration. The priority of management in these areas is to manage local biodiversity in a flexible manner by managing habitats so that both well known (e.g., fish) and obscure (e.g., aquatic insects) species are maintained. Because of the small size of ADMAs, their conservation value is seen as providing some level of protection for 50-100 years; the protection value of ADMAs is expected to diminish as suitable habitats are likely to shift outside of their boundaries into the future (>50-100 years) due to climate change. Desirable characteristics of an ADMA system include: (1) diverse areas with a variety of environmental conditions necessary to maintain regional biodiversity, ideally representing all the habitat types covered in Moyle and Ellison (1991), (2) linkages among ADMAs in order to reduce the probability of extinction due to stochastic events, (3) pairs of

ADMAs with similar species but located at distant enough locations so at least one of the pair is protected from regional disasters, such as a major wildfire, and (4) location within larger watersheds that have some degree of protection. Few potential ADMAs will have all these characteristics (e.g., Cowhead Lake slough, Modoc County). Thus, identification of ADMAs requires a systematic process as done by Moyle (1996) and Moyle and Randall (1998) for the Sierra Nevada.

Tier 4 - Watersheds

Watersheds (catchments) are natural landscape units, with large watersheds being aggregates of many smaller watersheds. At the Tier 4 level, most watersheds are too large to have protection of biodiversity as their main or primary function; they have to be managed as part of a human-dominated landscape containing farms, towns, and industry. Nevertheless, watersheds with exceptionally high value for aquatic biodiversity should be identified with the goal of directing management (and funds) towards their protection as aquatic refuges, especially in the face of climate change. Moyle (2002) provides six criteria that can be used to identify such "key" watersheds and provides extensive discussion of them, so they will not be covered here. Increasingly, selected watersheds will be severely altered by dams and diversions (e.g., Shasta River) or heavily invaded by alien species (e.g., Cosumnes River) but still have sufficient natural values to merit special management.

Example of priority watersheds include Blue Creek (Siskiyou County); Deer, Mill, and Antelope creeks (Tehama County); Eagle Lake (Lassen County); Goose Lake (Modoc County); Wooley Creek (Siskiyou County); South Fork Eel River (Mendocino County); Cosumnes River (El Dorado County); Sagehen Creek (Placer County); San Gabriel River (Los Angeles County), and Shasta River (Siskiyou County). Blue Creek, as an example, is important because it is located in the Klamath River basin, the second largest producer of salmon in California (Moyle 2002). Since the building of the first of six large dams on the mainstem Klamath River in the 1910s, habitat conditions in the mainstem have continued to deteriorate, becoming especially inhospitable to cold-water fishes (e.g., salmonids, lamprey). Blue Creek itself contains some of the highest quality habitat in the basin for more than five cold-water species (Beesley and Fiori 2008). Furthermore, the mouth of Blue Creek is the first cold-water pocket (< 18 ºC) that anadromous salmonids and lamprey encounter during summer spawning migrations, providing a much needed thermal refuge to long-migrating species.

Tier 5 – Bioregions

All four tiers already discussed should be pieces of a larger scheme to manage and protect biodiversity and natural processes throughout the state. Bioregions are one way to organize such efforts because they represent the largest areas of the landscape with similar biota. Bioregional management can provide proactive actions that can advance the state's capability to adapt to future conditions including those associated with climate change, while finding ways for humans to integrate the native flora and fauna into a highly managed landscape, as novel ecosystems (Moyle 2013). Bioregions in this case are analogous to the zoogeographic provinces designated in Moyle 2002 (Figure 2).

ZOOGEOGRAPHIC PROVINCES

1 Klamath Province
  1a - Upper Klamath Subprovince
  1b - Lower Klamath Subprovince
  1c - Rogue River Subprovince
  1d - Klamath-Pit fishless area
2 Sacramento-San Joaquin Province
  2a - Goose Lake Subprovince
  2b - Pit River Subprovince
  2c - McCloud River Subprovince
  2d - Central Valley Subprovince
  2e - Clear Lake Subprovince
  2f - Monterey Bay Subprovince
  2g - Upper Kern River Subprovince
3 North Coast Province
4 Great Basin Province
  4a - Suprise Valley Subprovince
  4b - Eagle Lake Subprovince
  4c - Lahontan Subprovince
  4d - Owens Subprovince
  4e - Amargosa Subprovince
  4f - Mojave Subprovince
  4g - Great Basin fishless area
5 South Coast Province
6 Colorado River Province
  6a - Colorado River Subprovince
  6b - Salton Sea Subprovince

FIGURE 2. Zoogeographic **provinces in California** (from Moyle 2002)

Novel ecosystems

A reality in California (and other Mediterranean climate areas) is that almost no aquatic ecosystem is pristine in the sense that it is not altered by human activity or not invaded by alien species such as invasive plants and invertebrates as well as fishes (Moyle 2013). With climate change, ecosystems are shifting to different states, which most likely will not benefit native taxa. Most of the areas we would propose for ADMAs or managed watersheds support novel ecosystems, with unprecedented combinations of habitats and species (Hobbs *et al*. 2009). At the same time, novel ecosys-

tems that have a strong presence of native species are legitimate targets of conservation. The key is to find ways to manage them so that native species continue to be favored. Thus highly altered lower Putah Creek, with about 50% of its fish fauna represented by alien species, can be managed for native fishes through a combination of appropriate flow regime and habitat modification (Kiernan *et al*. 2012). In a small Sierra Nevada stream, current management (including that of an upstream reservoir) facilitates the coexistence of five native fishes with two non-native trout species, which eliminated the native trout species, in what appears to be a stable fish assemblage

(Kiernan *et al*. 2012). These situations are increasingly typical of California waterways, which therefore require innovative management, such as use of a reconciliation ecology approach (Rosenzweig 2003). Consequently, it is unlikely that management efforts in California will result in reverting ecosystems to historical conditions. Conservation and management efforts should focus instead in preserving ecosystem functions that favor the persistence of native taxa.

CONCLUSIONS

The highly endemic freshwater fish fauna of California is in rapid decline, a decline which is being accelerated by climate change. Extirpation of many taxa, including economically valuable populations of salmon, trout, and sturgeon, is increasingly likely without considerable intervention (Moyle *et al*. 2013). That intervention includes developing new and better ways to manage the biodiversity of fishes at different levels of organization, from species to bioregions. Part of the solution is to improve management of California's highly developed water exploitation system so more water can be provided for the environment (Hanak *et al*. 2011). But, given that threats to native fishes are diverse and increasing, the most effective management is likely to be at the level of small to large watersheds (Tiers 3 and 4), managed as novel ecosystems. Management for native fish habitat, including adequate flows, has to be integrated into the working landscape, where humans will continue to dominate.

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RQ- led the writing and interpretation, and contributed to the idea; PM – conceived of the idea, and participated in the writing and interpretation.

CITED REFERENCES

Alpers CN, Hunerlach MP, May JT, Hothem RL (2005) Mercury contamination from historical gold mining in California. Technical Report. U.S. Geological Survey, Sacramento (USA)

Anderson J, Chung F, Anderson M, Brekke L, Easton D, et al. (2008) Progress on incorporating climate change into management of California's water resources. Climatic Change 87:91-108

Barbour E, Kueppers LM (2012) Conservation and management of ecological systems in a changing California. Climatic Change 111:135-163

Beesley S, Fiori R (2008) Restoration planning in lower Blue Creek, lower Klamath River: Phase 1. Technical Report. Yurok Tribal Fisheries Program, Klamath (USA)

Brannon EL, Amend DF, Cronin MA, Lannan JE, LaPatra S, et al. (2004) The controversy about salmon hatcheries. Fisheries 29:12-31

Carey MP, Sanderson BL, Friesen TA, Barnas KA, Olden JD (2011) Smallmouth bass in the Pacific Northwest: a threat to native species, a benefit to anglers. Reviews in Fisheries Science 19:305-315.

Carmona-Catot G, Benito J, Garcia-Berthou E (2011) Comparing latitudinal and upstream-downstream gradients: life history traits of invasive mosquitofish. Diversity and Distributions 17:214-224

Cayan D, Tyree M, Dettinger M, Hidalgo H, Das T, et al. (2009) Climate change scenarios and sea level rise estimates for the California 2009 - Climate Change Scenarios Assessment. Technical Report. California Climate Change Center, Sacramento (USA)

Field CB, Daily GC, Davis FW, Gaines S, Matson PA, et al. (1999) Confronting climate change in California: ecological impacts on the golden state. Technical Report. Union of Concerned Scientist, Cambridge (USA)

Filipek LH, Nordstrom DK, Ficklin WH (1987) Interaction of acid mine drainage with waters and sediments of West Squaw Creek in the west Shasta Mining District, California. Environmental Science and Technology 21:388-396

Gasith A, Resh VH (1999) Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. Annual Review of Ecology, Evolution, and Systematics 30:51-81

Grantham TE, Figueroa R, Prat N (2013) Water management in Mediterranean river basins: a comparison of management frameworks, physical impacts, and ecological responses. Hydrobiologia 719: 451-482

Grantham TE, Merenlender AM, Resh VH (2010) Climatic influences and anthropogenic stressors: an integrated framework for streamflow management in Mediterranean-climate California, USA. Freshwater Biology 55:188-204

Grantham TE, Moyle PB (2013) Assessing flows for fish below dams – a systematic approach to evaluate compliance of California's dams with Fish and Game Code Section 5937. Technical Report. University of California, Center for Watershed Sciences, Davis (USA)

Hamilton J, Rondorf D, Hampton M, Quiñones RM, Simondet J, et al. (2011) Synthesis of the effects to fish species of two management scenarios for the Secretarial determination on removal of the lower four dams on the Klamath River. Technical Report. US Fish and Wildlife Service, Yreka (USA)

Hanak, E, Lund J, Dinar A, Gray B, Howitt R, et al. (2011) Managing California's water- from conflict to reconciliation. PPIC, San Francisco (USA)

Hayhoe K, Cayan D, Field CB, Frumhoff PC, Maurer EP, et al. (2004) Emissions pathways, climate change, and impacts on California. Proceedings of the National Academy of Sciences 101:12422-12427

Hicks BJ, Hall JD, Bisson PA, Sedell JR (1991) Response of salmonids to habitat changes. Pages 483-518 in Influences of forest and rangeland management on salmonid fishes and their habitats, edited by Meehan WR (USA)

Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. Trends in Ecology and Evolution 24:599-605

Hundley, N (1992) The great thirst: Californians and water, 1770s-1990s. University of California Press, Berkeley (USA)

Jefferson A, Nolin A, Lewis S, Tague C (2008) Hydrogeologic controls on streamflow sensitivity to climate variation. Hydrological Processes 22:4371-4385

Katz JV, Moyle PB, Quiñones RM, Israel J, Purdy S (2012) Impending extinction of salmon, steelhead, and trout (Salmonidae) in California. Environmental Biology of Fishes DOI 10.1007/s10641-012-9974-8

Kiernan JD, Moyle PB (2012) Flows, droughts, and aliens: factors affecting the fish assemblage in a Sierra Nevada, California, stream. Ecological Applications 22:1146-1161

Kiernan JD, Moyle OB, Crain PK (2012) Restoring native fish assemblages to a regulated California stream using the natural flow regime concept. Ecological Applications 22:1472-1482

Knapp RA, Matthews KR (1996) Livestock grazing, golden trout, and streams in the Golden Trout Wilderness: impacts and management implications. North American Journal of Fisheries Management 16:805-820

Managa M (1999) On the timescales characterizing groundwater discharge at springs. Journal of Hydrology 219:56-69

Marchetti MP, Moyle PB, Levine R (2004a) Invasive species profiling? Exploring characteristics of non-native fishes across invasion stages in California. Freshwater Biology 49:646-661

Marchetti MP, Light T, Moyle PB, Viers, JH (2004b) Fish invasions in California watersheds: testing hypotheses using land-

scape patterns. Ecological Applications 14:1507-1525

Marchetti MP, Lockwood JL, Light T (2004c) Effects of urbanization on California's fish diversity: differentiation, homogenization and the influence of spatial scale. Biological Conservation 127:310-318

Mastrandrea MD, Luers AL (2012) Climate change in California: scenarios and approaches for adaptation. Climatic change 111:5-16

Matthews KR (2010) California golden trout and climate change: is their stream habitat vulnerable to climate warming? Pages 81-87 in Proceedings of the Wild Trout X Symposium, edited by Carline RF, LoSapio C, Bozeman (USA)

Modin, J (1998) Whirling disease in California: a review of its history, distribution, and impacts, 1965-1997. Journal of Aquatic Animal Health 10:132-142

Moyle PB (1976) Inland Fishes of California, first edition. University of California Press, Berkeley (USA)

Moyle PB (1976) Fish introductions in California: history and impact on native fishes. Biological Conservation 9:101-118

Moyle PB (1996) Potential aquatic diversity management areas. Pages 1493-1503 in Sierra Nevada Ecosystem Project: Final report to Congress, Vol. II, assessments, commissioned reports, and background information. University of California, Davis (USA)

Moyle PB (2002) Inland fishes of California, second edition. University of California Press, Berkeley (USA)

Moyle PB (2013) Novel aquatic ecosystems: the new reality for streams in California and other Mediterranean climate regions. River Research and Applications doi:10.1002/rra.2709

Moyle PB, Ellison JP (1991) A conservation-oriented classification system for the inland waters of California. California Fish and Game 77:161-180

Moyle PB, Katz JV, Quiñones RM (2011) Rapid decline of California's native inland fishes: a status assessment. Biological Conservation 144:2414-2423

Moyle PB, Kiernan JD, Crain PK, Quiñones RM (2013) Climate change vulnerability of native and alien freshwater fishes of California: a systematic assessment approach. Plos One 8: e63883

Moyle PB, Marchetti MP (2006) Predicting invasion success: freshwater fishes in California as a model. BioScience 56:515-524

Moyle PB, Pine R, Brown LR, Hanson CH, Herbold B, et al. (1996) Recovery plan for the Sacramento-San Joaquin Delta native fishes. US Fish and Wildlife Service, Portland (USA)

Moyle, PB, Quiñones RM, Katz JV, Weaver J, in press. Fish species of special concern in California, third edition. Technical Report. California Department of Fish and Wildlife, Sacramento (USA)

Moyle PB, Randall PJ (1998) Evaluating the biotic integrity of watersheds in the Sierra Nevada, California. Conservation Biology 12:1318-1326

Moyle PB, Williams JE (1990) Biodiversity loss in the temperate zone: decline of the native fish fauna of California. Conservation Biology 4:275-284

Moyle, PB, Williams JE, Wikramanayake ED (1989) Fish species of special concern of California, first edition. Technical Report. California Department of Fish and Game, Sacramento (USA)

Moyle PB, Yoshiyama RM (1994) Protection of aquatic biodiversity in California: a five-tiered approach. Fisheries 19:6-18

Moyle, PB, Yoshiyama RM, Williams JE, Wikramanayake ED (1995) Fish species of special concern in California, second edition. Technical Report. California Department of Fish and Game, Sacramento (USA)

Null SE, Viers JH, Deas ML, Tanaka SK, Mount JF (2013) Stream temperature sensitivity to climate warming in Cali-

fornia's Sierra Nevada: impacts to coldwater habitat. Climatic Change 116:149-170

Pavlov DS, Mikheev VN, Lupandin AI, Skorobogatov MA (2008) Ecological and behavioral influences on juvenile fish migrations in regulated rivers: a review of experimental and field studies. Hydrobiologia 609:125-138

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, et al. (1997) The natural flow regime. Bioscience 47:769-784

Poff NL, Ward JV (1989) Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46:1805-1818

Quiñones RM (2011) Recovery of Pacific salmonids (Oncorhynchus spp.) in the face of climate change: a case study of the Klamath River basin, California. PhD Thesis, University of California in Davis, Davis (USA)

Quiñones RM, Wintzer AP, Harvey BN, Kiernan JD, Klasson M, et al. in progress. Dam removal and anadromous salmonid conservation in California.

Quiñones RM, Johnson ML, Moyle PB (2013) Hatchery practices may result in replacement of wild salmonids: adult trends in the Klamath basin, California. Environmental Biology of Fishes DOI 10.1007/s10641-013-0146-2

Rosenzweig ML (2003) Reconciliation ecology and the future of species diversity. Oryx 37:194-205

Stewart IT, Cayan DR, Dettinger MD (2005) Changes toward earlier streamflow tim-

ing across western North America. Journal of Climate 18:1136-1155

Sweeting RM, Beamish RJ, Noakes DJ, Neville CM (2003) Replacement of wild coho salmon by hatchery-reared coho salmon in the Strait of Georgia over the past three decades. North American Journal of Fisheries Management 23:492-502

Tague C, Grant G, Farrell M, Choate J, Jefferson A (2008) Deep groundwater mediates streamflow response to climate change warming in the Oregon Cascades. Climatic Change 86:189-210

Thompson J (2007) Running dry: Where will the West get its water? Technical Report. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station Science Findings, Portland (USA)

Tiffan KF, Kock TJ, Haskell TA, Connor WP, Steinhorst RK (2009) Water velocity, turbulence, and migration rate of subyearling fall Chinook salmon in free-flowing and impounded Snake River. Transactions of the American Fisheries Society 138:373-384

Viers JH, Rheinheimer DE (2011) Freshwater conservation options for a changing climate in California's Sierra Nevada. Marine and Freshwater Research 62:266-2781

Yarnell SM, Viers JH, Mount JF (2010) Ecology and management of the spring snowmelt recession. BioScience 60:114-127

Yoshiyama RM, Gerstung ER, Fisher FW, Moyle PB (1996) Historical and present distribution of Chinook salmon in the Central Valley drainage of California. Technical Report. California Department of Fish and Game, Sacramento (USA)