Native Fishes of the Sacramento–San Joaquin Drainage, California: A History of Decline

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Abstract.—In this paper, we review information regarding the status of the native fishes of the combined Sacramento River and San Joaquin River drainages (hereinafter the "Sacramento–San Joaquin drainage") and the factors associated with their declines. The Sacramento–San Joaquin drainage is the center of fish evolution in California, giving rise to 17 endemic species of a total native fish fauna of 28 species. Rapid changes in land use and water use beginning with the Gold Rush in the 1850s and continuing to the present have resulted in the extinction, extirpation, and reduction in range and abundance of the native fishes. Multiple factors are associated with the declines of native fishes, including habitat alteration and loss, water storage and diversion, flow alteration, water quality, and invasions of alien species. Although native fishes can be quite tolerant of stressful physical conditions, in some rivers of the drainage the physical habitat has been altered to the extent that it is now more suited for alien species. This interaction of environmental changes and invasions of alien species makes it difficult to predict the benefits of restoration efforts to native fishes. Possible effects of climate change on California's aquatic habitats add additional complexity to restoration of native fishes. Unless protection and restoration of native fishes is explicitly considered in future water management decisions, declines are likely to continue.

Introduction

Loss of aquatic biodiversity is a worldwide problem. Aquatic conservation in regions with Mediterranean climates is particularly challenging. Such regions are generally arid with highly seasonal precipitation and surface water runoff, while human water demand is relatively constant throughout the year (Moyle and Leidy 1992; Moyle 1995). Mismatches between water supply and demand generally result in development of major water storage and diversion systems. In the arid western United States, these engineering solutions have led to some of the most extensive storage and diversion systems in the world (Reisner 1986). In California, the combination of Mediterranean climate, agricultural development, and growing urban demand in out-of-basin areas has resulted in one of the most complex water systems in the world (Mount 1995). The fish fauna of the western United States has also been "engineered" to a significant degree. Eastern settlers unfamiliar with the native fishes introduced familiar sport and food species (Dill and Cordone 1997). The introduction of alien species is often cited as an important factor in the decline of native species (Williams et al. 1989a; Moyle 2002). This combination of water development and ecological engineering has

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had profound effects on the fish fauna of California (Moyle and Williams 1989; Moyle 2002).

The combined Sacramento River and San Joaquin River drainages (hereinafter the "Sacramento–San Joaquin drainage") (Figure 1) is the center of fish evolution in California (Moyle 2002). The complex hydrology and geology of the drainage combined with its isolation from other major river systems for the last 10–17 million years (Minckley et al. 1986) has produced 17 species endemic to the drainage (Moyle 2002). The number of endemic forms increases to between 40 and 50 when subspecies and distinct runs of salmon are considered (Moyle 2002). In addition to its importance as a center of endemism, in pre-European times the aquatic resources of the drainage were highly productive. Resident and anadromous fishes, shellfish, reptiles, amphibians, and waterfowl supported what is believed
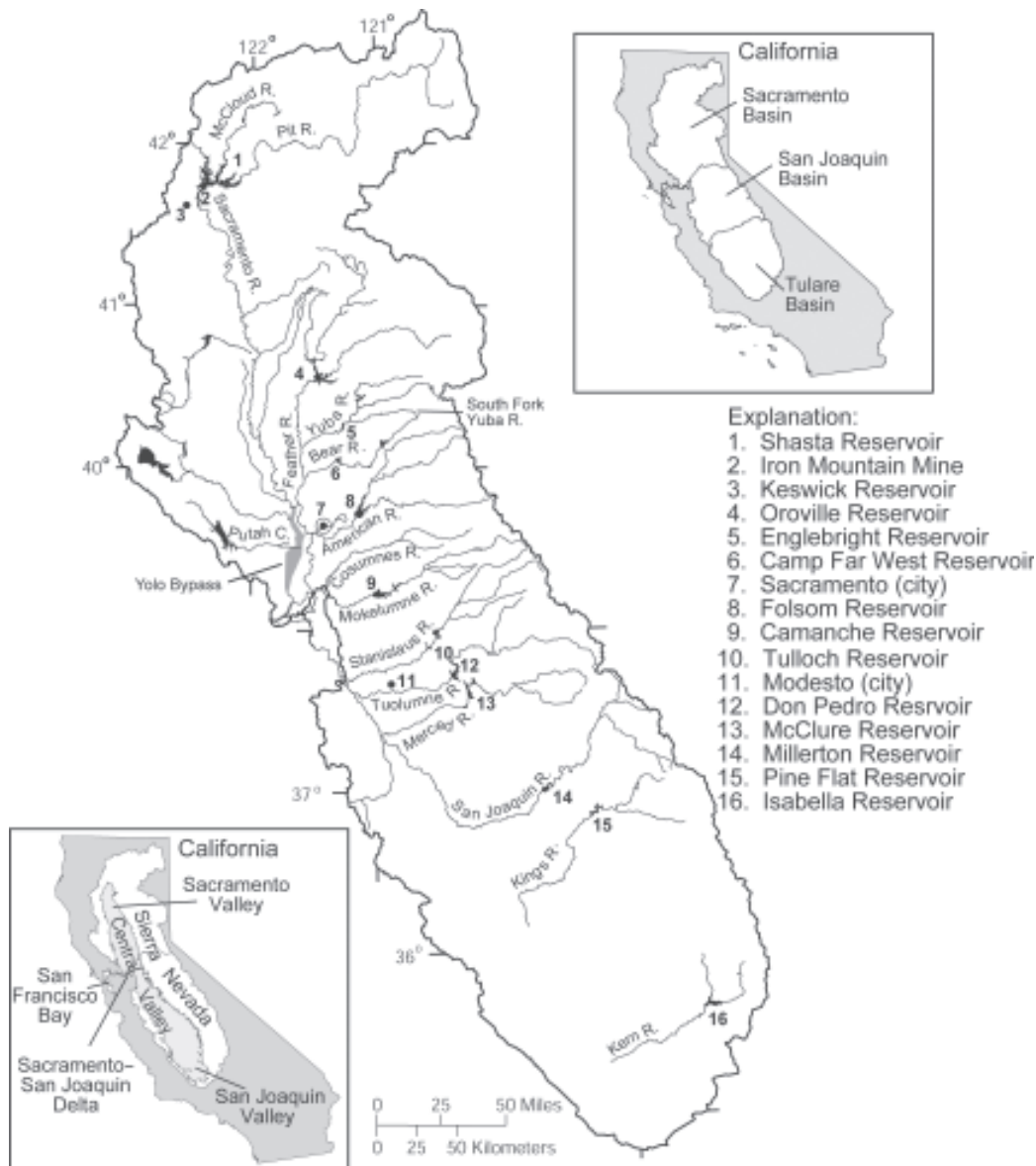

Figure 1.—Location map for the Sacramento–San Joaquin River drainage, including reservoirs [R., river].

to be some of the highest population densities of non-agricultural Native Americans known in North America (Kroeber 1939, 1963; Baumhoff 1963).

Beginning with the Gold Rush in the mid-1800s, land use in the Sacramento–San Joaquin drainage changed rapidly. Mining activities had direct and indirect effects on river systems. Perhaps more important, the rapid influx of people resulted in increased agriculture and urban land uses. All of these activities require water. The population of California continues to grow and is expected to reach 42.4 million people by 2010 (California Institute 1999), resulting in further demands on the water resources of California, including the Sacramento–San Joaquin drainage.

The objective of this article is to review and synthesize existing information on the present status of the fish fauna of the Sacramento–San Joaquin drainage and the human activities associated with changes in the fish fauna since the mid-1800s. Moyle (2002) divided California into six ichthyological provinces, including the Sacramento–San Joaquin Province. Of the seven subprovinces within the Sacramento–San Joaquin Province, this article emphasizes the Central Valley subprovince. Further, this paper emphasizes the nontidal, lower elevation reaches of the larger streams and rivers of the subprovince (Figure 1, but excluding the McCloud River, Pit River, Clear Lake, and the Kern River upstream of Isabella Reservoir). Interested readers are referred to Moyle (2002) and Moyle et al. (1982) for more information on subprovinces and habitats not covered in this paper. Readers interested in more detail on Sacramento–San Joaquin Delta (hereinafter the "Delta") fish issues should consult Bennett and Moyle (1996), Moyle (2002), and Brown (2003a).

Study Area

The Sacramento–San Joaquin drainage is the largest drainage wholly contained in the state of California, with an area of 151,000 km². The Sacramento River drainage with 70,000 km² is slightly smaller than the San Joaquin River drainage (combined San Joaquin and Tulare basins, Figure 1) with 81,000 km². Vertical relief is from sea level in the Sacramento–San Joaquin Delta to over 4,200 m at the top of Mount Whitney, the tallest mountain in the contiguous United States. The mean annual runoff in the Sacramento River drainage is about 27.6 billion m³ × year⁻¹ and in the San Joaquin River drainage is about 11 billion m³ × year⁻¹ (California Department of Water Resources 1993). Precipitation is greatest in the mountains on the eastern border of the drainage, where precipitation falls largely as snow and can exceed 200 cm per year. In the Central Valley (Figure 1), rain is the primary form of precipitation and ranges from about 60 cm per year in the northernmost part of the valley to about 12 cm per year in the southernmost part of the valley. The Sacramento and San Joaquin rivers and their tributaries are generally high gradient with cold water and coarse substrates in the mountains. Runoff is captured by storage reservoirs on all of the larger rivers at the foothill transition between the Sierra Nevada and the Central Valley (Figure 1). Within the Central Valley, rivers become more meandering and progressively warmer with finer substrates until the Sacramento and San Joaquin rivers meet in the tidal Delta, which is largely a freshwater system.

Historically, terrestrial and riparian habitats in the mountains primarily consisted of mixed conifer forest, red fir forest, and lodgepole pine/subalpine forest, and mixed coniferous deciduous forests (Omernik 1987). The foothills and Coast Ranges were dominated by oak woodlands, chaparral, and California steppe (Omernik 1987). The Central Valley consisted of a mosaic of habitat types, including permanent and seasonal tule marsh, riparian forest, valley oak savanna, and native grasslands (San Joaquin Valley Drainage Program 1990). Tulare Lake, the largest (surface area) lake west of the Rocky Mountains, was the dominant feature of the southern San Joaquin Valley. The semiclosed Tulare basin at the southern end of the Central Valley (Figure 1) was dominated by Tulare Lake and two other smaller lakes (not shown). Tulare Lake was connected to the San Joaquin basin by surface water during high flows and probably by groundwater flow through the alluvium forming the basin divide during most other periods. Permanent and seasonal tule marshes were the dominant feature of the Delta and other floodplain wetlands.

Present conditions vary considerably from historic conditions. In general, high mountain areas

have not changed much in appearance, in part because much of the land is in national parks, wilderness areas, or national forest. However, water development, logging, mining, grazing, roads, towns, and recreational development have altered the aquatic ecosystems in major ways (Sierra Nevada Ecosystem Project 1996). Such activities continue to expand, especially in the Sierra Nevada foothills. The most obvious manifestations of these changes are large storage reservoirs that have been constructed on most of the rivers.

Land use changes in the Central Valley have been more dramatic, especially in the San Joaquin Valley. Tulare Lake and the smaller lakes have been completely drained and converted to agricultural uses. Less than 10% of the natural habitats remain in the San Joaquin Valley primarily because of conversion to agricultural land uses (San Joaquin Valley Drainage Program 1990). In the Delta, over 95% of the original wetlands have been lost (The Bay Institute 1998). These areas have been leveed and converted to other uses, primarily agriculture.

Fish Fauna and Evidence of Decline

Moyle (2002) lists 28 species as native to the Central Valley subprovince, including the Delta and the drainages around San Francisco Bay (Table 1). Historically, the fishes of the larger rivers and streams were generally organized into three distinct assemblages with somewhat overlapping ranges, depending on the characteristics of particular streams (Figure 2) (Moyle 2002). A fourth assemblage, the California roach assemblage, was characteristic of intermittent streams and is not discussed further in this paper.

Historically, the rainbow trout *Oncorhynchus mykiss* assemblage occurred in steep, cold rivers and streams at higher elevations (roughly above 450 m). The upstream limit of this assemblage was determined by barriers to dispersal. Most of the streams, rivers, and lakes above 1,500 m were fishless and dominated by native amphibians. Riffle sculpin *Cottus gulosus*, Sacramento sucker *Catostomus occidentalis*, and speckled dace *Rhinichthys osculus* are often part of this assemblage. California roach *Hesperoleucus symmetricus* are sometimes included.

The pikeminnow-hardhead-sucker assemblage occurred in the warmer, lower gradient reaches of the rivers and streams as they flow out of the Sierra Nevada, through the foothills, and onto the valley floor. This assemblage occurred from about 30–450 m in the San Joaquin River drainage, where the transition from the mountains to the valley is relatively abrupt. The elevational range was somewhat broader in the Sacramento River drainage. The assemblage was dominated by Sacramento pikeminnow *Ptychocheilus grandis* and Sacramento sucker. Hardhead *Mylopharodon conocephalus* were largely confined to cooler stream reaches with deep, rock-bottomed pools. Tule perch *Hysterocarpus traskii*, speckled dace, California roach, riffle sculpin, and rainbow trout were often found with this assemblage. Chinook salmon *Oncorhynchus tshawytscha*, steelhead (the anadromous form of *O. mykiss*), and lampreys often had major spawning grounds in the regions occupied by this assemblage.

Historically, the deep-bodied fishes assemblage occupied the low elevation rivers (<30 m), oxbows, floodplain lakes, swamps, and sloughs of the Sacramentoan–Joaquin drainage. This assemblage no longer exists for the reasons discussed in the following sections. The assemblage was dominated by Sacramento perch *Archoplites interruptus*, thicktail chub *Gila crassicauda*, tule perch, Sacramento blackfish *Orthodon microlepidotus*, hitch *Lavinia exilicauda*, and splittail *Pogonichthys macrolepidotus*. Large Sacramento pikeminnows and suckers were common and migrated upstream in the spring to spawn. Anadromous fishes also moved through the areas occupied by this assemblage on their way to upstream spawning grounds.

Of the native fishes, one, the thicktail chub, is globally extinct. The thicktail chub was once very abundant in low elevation lakes and rivers. Thicktail chub bones are among the most abundant fish remains in Native American middens (Schulz and Simons 1973; Mills and Mamika 1980).

Three species have been extirpated from the subprovince. The tidewater goby has been extirpated from the tributary streams to San Francisco Bay (Moyle 2002), but the species was probably not present in the upstream, nontidal reaches of the Sacramento and San Joaquin rivers. The bull trout

Table 1.—Native and alien fish species of the Sacramento–San Joaquin River drainage, California.

Common name	Scientific name	Native	Status[a]	Date of introduction[b]	Reason for introduction[c]
lampreys	Petromyzontidae				
Pacific lamprey	Lampetra tridentata	yes	WL	NA	NA
river lamprey	L. ayresi	yes	WL	NA	NA
western brook lamprey	L. richardsoni	yes	WL	NA	NA
Kern brook lamprey	L. hubbsi	yes	SC	NA	NA
sturgeons	Acipenseridae				
white sturgeon	Acipenser transmontanus	yes	SI	NA	NA
green sturgeon	A. medirostris	yes	SC	NA	NA
herrings	Clupeidae				
American shad	Alosa sapidissima	no	SI	1871	food
threadfin shad	Dorosoma petenense	no	SI	1954	forage
minnows	Cyprinidae				
California roach	Hesperoleucus symmetricus[d]	yes	SI[e]	NA	NA
common carp	Cyprinus carpio	no	SI	1872	food
fathead minnow	Pimephales promelas	no	SI	1953 (?)	forage/bait
golden shiner	Notemigonus crysoleucas	no	SI	1891 (?)	forage
goldfish	Carassius auratus	no	SI	1860s (?)	ornamental
hardhead	Mylopharodon conocephalus	yes	WL	NA	NA
hitch	Lavinia exilicauda	yes	WL	NA	NA
Lahontan redside	Richardsonius egregius	no[f]	SI	?	bait
Sacramento blackfish	Orthodon microlepidotus	yes	SI	NA	NA
Sacramento pikeminnow	Ptychocheilus grandis	yes	SI	NA	NA
splittail	Pogonichthys macrolepidotus	yes	SC[g]	NA	NA
speckled dace	Rhinichthys osculus	yes	SI	NA	NA
thicktail chub	Gila crassicauda	yes	extinct	NA	NA
tui chub	Gila bicolor	no[f]	SI	?	bait
red shiner	Cyprinella lutrensis	no	SI	c. 1950	bait
suckers	Catostomidae				
mountain sucker	Catostomus platyrhynchus	no[f]	SI	?	diversion
Sacramento sucker	C. occidentalis	yes	SI	NA	NA
catfishes	Ictaluridae				
black bullhead	Ameiurus melas	no	SI	1930s	sport/food
blue catfish	Ictalurus furcatus	no	SI	1969	sport
brown bullhead	A. nebulosus	no	SI	1874	food
channel catfish	Ictalurus punctatus	no	SI	1891 (?)	food/sport

Table 1.—continued

Common name	Scientific name	Native	Status[a]	Date of introduction[b]	Reason for introduction[c]
white catfish	*Ameiurus catus*	no	SI	1874	food
pikes	Esocidae				
northern pike	*Esox lucius*	no	SI	c. 1994	sport
smelts	Osmeridae				
delta smelt	*Hypomesus transpacificus*	yes	FT, ST	NA	NA
longfin smelt	*Spirinchus thaleichthys*	yes	SC	NA	NA
wakasagi	*H. nipponensis*	no	SI	1959	forage
salmon and trout	Salmonidae				
brook trout	*Salvelinus fontinalis*	no	SI	1871 or 1872	sport
brown trout	*Salmo trutta*	no	SI	1893	sport
bull trout	*Salvelinus confluentus*	yes	extirp	NA	NA
Chinook salmon	*Oncorhynchus tshawytscha*	yes			
winter run			FE, SE	NA	NA
spring run			FT, ST	NA	NA
fall/late fall run			SC	NA	NA
coho salmon	*O. kisutch*	yes	extirp	NA	NA
cutthroat trout	*O. clarkii*	no	SI	?	sport
kokanee	*O. nerka*	no	SI	1941	sport
lake trout	*Salvelinus namaycush*	no	SI	1889 (?)	sport/food
rainbow trout	*O. mykiss*	yes			
resident			SI	NA	NA
steelhead (anadromous)			FT	NA	NA
killifish	Fundulidae				
rainwater killifish	*Lucania parva*	no	SI	1950s	unintentional
livebearers	Poeciliidae				
western mosquitofish	*Gambusia affinis*	no	SI	1922	insect control
silversides	Atherinidae				
inland silverside	*Menidia beryllina*	no	SI	1967	insect control
sticklebacks	Gasterosteidae				
threespine stickleback	*Gasterosteus aculeatus*	yes	SI	NA	NA
bass and sunfish	Centrarchidae				
black crappie	*Pomoxis nigromaculatus*	no	SI	1891 or 1908	sport/food
bluegill	*Lepomis macrochirus*	no	SI	1908	sport
green sunfish	*L. cyanellus*	no	SI	1891 or 1908	unintentional
largemouth bass	*Micropterus salmoides*	no	SI	1891 or 1895	sport/food
pumpkinseed	*L. gibbosus*	no	SI		

Table 1.—continued

Common name	Scientific name	Native	Status[a]	Date of introduction[b]	Reason for introduction[c]
redear sunfish	*L.microlophus*	no	SI	c. 1950 and 1954	sport
redeye bass	*Micropterus coosae*	no	SI	1962	sport
Sacramento perch	*Archoplites interruptus*	yes	SC	NA	NA
smallmouth bass	*M. dolomieu*	no	SI	1874	sport/food
spotted bass	*M. punctulatus*	no	SI	1936	sport
warmouth	*Lepomis gulosus*	no	SI	1891(?)	sport/food
white crappie	*Pomoxis annularis*	no	SI	1891 or 1908	sport/food
temperate basses	Moronidae				
striped bass	*Morone saxatilis*	no	SI	1879	sport/food
white bass	*M. chrysops*	no	SI	1965	sport
perches	Percidae				
yellow perch	*Perca flavescens*	no	SI	1891	sport/food
bigscale logperch	*Percina macrolepida*	no	SI	1953	unintentional
surfperches	Embiotocidae				
tule perch	*Hysterocarpus traskii*	yes	SI	NA	NA
gobies	Gobiidae				
tidewater goby	*Eucyclogobius newberryi*	yes	extirp[h]	NA	NA
yellowfin goby	*Acanthogobius flavimanus*	no	SI	early 1960s	ballast water
shimofuri goby	*Tridentiger bifasciatus*	no	SI	c. 1980	ballast water
Shokihaze goby	*T. barbatus*	no	SI?	late 1990s	ballast water
sculpins	Cottidae				
Pacific staghorn sculpin	*Leptocottus armatus*	yes	SI	NA	NA
prickly sculpin	*Cottus asper*	yes	SI	NA	NA
riffle sculpin	*C. gulosus*	yes	SI	NA	NA
righteye flounders	Pleuronectidae				
starry flounder	*Platichthys stellatus*	yes	SI	NA	NA

[a] Status: Extinct, globally extinct; Extirp, extirpated from the Sacramento–San Joaquin drainage; FE, federally endangered; FT, federally threatened; ST, state threatened; SC, special concern because declining populations could lead to threatened or endangered status; WL, watch list because populations appear to be declining; SI, stable or increasing.

[b] NA, not applicable; ?, date of introduction is unknown or approximate (Dill and Cordone 1997; Moyle 2002).

[c] NA, not applicable. Data from Dill and Cordone (1997) and Moyle (2002).

[d] Moyle (2002) places this species in the genus *Lavinia*.

[e] As the species is presently defined, California roach is secure. The status of genetically and morphologically distinctive subpopulations varies from threatened to stable or increasing (Moyle 2002).

[f] These species are native to California, but not the Sacramento–San Joaquin drainage.

[g] Splittail was removed from the federal list of threatened species in 2003 (U.S. Fish and Wildlife Service 2003).

[h] Tidewater goby has been extirpated from the Sacramento–San Joaquin drainage and is listed as federally endangered in the remainder of California.

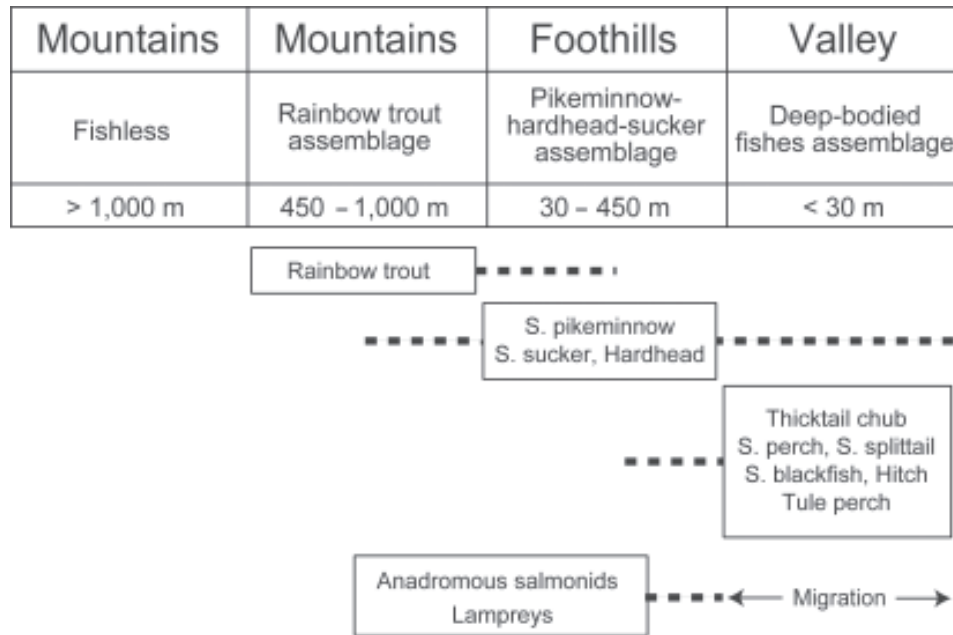| Mountains	Mountains	Foothills	Valley
Fishless	Rainbow trout assemblage	Pikeminnow-hardhead-sucker assemblage	Deep-bodied fishes assemblage
> 1,000 m	450 – 1,000 m	30 – 450 m	< 30 m

Figure 2.—Distribution of species in the San Joaquin River drainage before European settlement (Moyle 2002). The boxes indicate where the indicated groups of species are most abundant and the dashed lines indicate the approximate range of the species. Only the most common species are included [S., Sacramento].

was native to the McCloud River (a separate subprovince of the Sacramento–San Joaquin Ichthyological Province) but may have occupied similar habitats in the Pit River and upper Sacramento River (Figure 1) (Moyle 2002). Coho salmon was probably never common in the Sacramento–San Joaquin drainage, but there were populations in the tributaries to San Francisco Bay (Leidy 1984) and there were likely small populations in the McCloud River and upper Sacramento River drainages (Moyle 2002).

Another 10 species are considered to be of special concern because of declining populations or have already been listed as threatened or endangered (Table 1) (Moyle 2002). Delta smelt (listed as threatened by state and federal agencies) and longfin smelt (special concern) are primarily estuarine species and rarely enter nontidal freshwaters. The Kern brook lamprey (special concern) is a little known endemic species of nonparasitic lamprey that is mainly of concern because of its limited range (Moyle et al. 1995). Green sturgeon, an anadromous species, is typical of many of the native species because it received little attention until nongovernmental groups petitioned

to list the species under the federal Endangered Species Act, a petition that was eventually rejected (NMFS 2003). However, the fact that there were no data available to determine long term population trends and concerns over various threats to the species, especially the Sacramento River population, led the National Marine Fisheries Service (NMFS) to add the species to the list of candidate species.

Similar to thicktail chub, Sacramento perch and splittail were once common in low elevation lakes and rivers of the Central Valley, and the loss and alteration of these habitats presumably led to a reduction in numbers of both species. Sacramento perch is the only native centrarchid west of the Rocky Mountains. Although largely extirpated from its native habitats, it has been widely introduced into ponds and reservoirs in California and elsewhere, where introduced centrarchids are not successful (Moyle 2002). If it were not for these transplanted populations, the species would almost certainly be listed as an endangered species. The status of splittail has been the topic of some controversy (USFWS 2003). The presence of splittail remains in Native American middens near the former large lakes of

the Tulare basin (Hartzell 1992; Gobalet and Fenenga 1993) suggests major reductions in population concurrent with losses of habitat. The controversy regarding this species concerns abundance trends in the last several decades. The species was listed as threatened by the U.S. Fish and Wildlife Service (USFWS) in 1999, but was removed from the threatened list in 2003 because of continuing uncertainty over recent trends in abundance and ongoing and future habitat restoration that is expected to improve conditions for the species (USFWS 2003).

The best quantitative evidence of decline for the 10 species of special concern or listed species is for Chinook salmon. Chinook salmon is represented by four different runs in the Sacramento River drainage—winter run, spring run, fall run, and late-fall run. National Marine Fisheries Service includes late-fall run Chinook salmon with fall-run Chinook salmon (Moyle 2002). Only fall-run Chinook salmon occur in the San Joaquin River drainage. Spring-run Chinook salmon, once the dominant run (California Department of Fish and Game 1998; Campbell and Moyle 1991) were extirpated by 1950 (Warner 1991). Sacramento River winter-run Chinook salmon was designated an endangered species by both federal and state agencies (Moyle 2002). Sacramento spring-run Chinook salmon was designated as threatened by both federal and state agencies (Moyle 2002). The fall-run Chinook salmon is a candidate for listing by NMFS. Yoshiyama et al. (1998) compiled annual catch statistics and determined that the Sacramento–San Joaquin in-river fishery alone harvested 4–10 million pounds of Chinook salmon per year for all runs combined (earliest record 1856). On the basis of these and other commercial catch statistics, a conservative estimate for early Central Valley spawning stocks is 1–2 million spawners annually. Recent estimates (1970–2001) of Central Valley spawning escapements range from 94,000 to 566,000 spawners annually (mean = 249,000, SD = 94,000) (Pacific Fishery Management Council 2003). Based on the minimum historical estimate of 1 million spawners annually, the present population corresponds to 9–57% (mean = 25%) of the historic abundance, at best. Also, this estimate is based on natural spawn-

ing fish, which includes an unknown, but likely substantial component of hatchery-produced fall-run Chinook salmon. Central Valley steelhead, is listed as federally threatened (Moyle 2002). The principal populations of this anadromous fish are in the Sacramento River drainage, but there is recent evidence of a remnant population in the San Joaquin drainage where the species was once abundant (McEwan 2001). Estimates of historic population size are not possible because historic catch statistics are not available. The population in the 1990s was estimated to be about 10,000 fish for the entire Sacramento–San Joaquin drainage (McEwan 2001). Population estimates at a large diversion dam on the Sacramento River suggest continued declines even in recent times. Annual counts have declined from an average of 11,187 adults for the 10-year period starting in 1967 to 2,202 adults annually in the 1990s (McEwan 2001).

Although extinction, extirpation, and listing of species as threatened, endangered, or special concern are clear indications of a declining fish fauna, there are few quantitative data documenting numeric declines of native species from the mid-1800s to the present, except for the data for Chinook salmon already presented. Presumably the same losses of habitat and other factors (discussed in detail in the next section) leading to extinctions, extirpations, and listings resulted in declines of other native fishes. Further declines have been associated with invasions of alien fishes (see next section for details). Native species have been replaced by alien species in many streams and rivers, particularly in the San Joaquin River drainage (Moyle and Nichols 1973; Saiki 1984; Brown and Moyle 1993; Brown 2000; Saiki et al. 2001a; Moyle et al. 2003). Alien species are not as dominant in the Sacramento River drainage but still occur there and are abundant in some areas (Marchetti and Moyle 2000, 2001; May and Brown 2002).

Invasions of alien fishes have been a major change in California's fish fauna. Moyle (2002) lists a total of 40 alien species as present in the Central Valley subprovince, but new species continue to arrive and the current total is 42 (Table 1). The shokihaze goby, likely a ballast water introduction, has appeared in the Delta and there is a population

of northern pike, an illegal introduction, in a reservoir in the headwaters of the Feather River that will spread downstream if not eradicated (Moyle 2002). Dill and Cordone (1997) described the history and motivation for introducing alien species into California in detail. In short, early introductions were usually done for sport or food purposes, and the most recent introductions largely resulted from other human activities, such as ballast water introductions (Table 1).

Causes of Decline and Change

Habitat Alteration and Loss

Some of the first and most dramatic changes in land and water use in California are linked to gold mining. Once easily accessible surface deposits were exhausted, miners turned to large-scale hydraulic mining of ancient alluvial deposits. Hydraulic mining required large quantities of water to supply the water cannons used to expose buried gravels. This water was often supplied via temporary dams and diversions on streams, which often formed barriers to fish passage. The most devastating aspect of this mining was the tremendous quantities of sediment introduced into stream systems. Mount (1995) estimates that 63.7 million m³ of sediment were washed into the Central Valley from just five heavily mined rivers. The immediate effects of the increased sediment load were to increase fine materials, which smothered spawning gravels. Over the longer term, aggradation of river channels and subsequent incision of rivers isolated many streams from their floodplains. Flooding of surrounding towns and agricultural lands that was due to channel aggradation resulted in leveeing and dredging of many of the most affected river channels. These efforts were successful at moving sediment out of the system (Mount 1995), but further isolated the streams from their floodplains. Indirect effects may also have been important. For example, Herbold and Moyle (1989) suggest that increases in fine sediments may have facilitated invasion of the system by alien striped bass and American shad. These species produce semibouyant eggs that are more likely to survive in systems with high loads of fine sediments than the

benthic eggs produced by salmon and many other native California stream fishes (Moyle 2002).

The Gold Rush accelerated the influx of settlers into California (Thomas and Phoenix 1976), stimulating the need for agricultural products. Because of the semiarid Central Valley climate, most early agriculture (early 1800s) occurred near surface water sources (California Department of Water Resources 1982). This demand eventually resulted in construction of thousands of miles of canals used both to drain wetlands, including the large lakes of the Tulare basin, and to supply water to irrigated farmland. Flood control activities allowed agriculture to expand onto the historic floodplains of many rivers, resulting in losses of riparian habitat. Losses of wetland habitat in combination with the introduction of alien predators and competitors were probably key factors in the extinction of thicktail chub and declines of splittail, Sacramento perch, Sacramento blackfish, hitch, and tule perch (Moyle 2002). In addition to the very direct effects of land use change, agricultural activities have a variety of less direct effects on fishes and fish habitat that are covered in subsequent sections.

Flood protection for the Sacramento urban area and other smaller urban areas resulted in channelization and levee construction along many streams and rivers, causing further losses of habitat, particularly for the fishes of the deep-bodied fishes assemblage. Also, several large flood bypasses have been constructed along the Sacramento River. These engineering solutions are successful at providing flood protection but isolate the rivers from their floodplains and associated riparian habitat (Mount 1995). Agriculture and urban development often occur in the isolated floodplains resulting in permanent loss of that habitat. Loss of floodplain habitat that is due to flood control structures and activities has been extensive in the Central Valley. The largest areas of remaining floodplain habitat are largely artificial consisting of the bypasses that are farmed during the summer and may or may not flood during the winter, depending on precipitation and the design of the bypass. For example, the Yolo Bypass only floods when the Sacramento River exceeds 2,000 m³/s (Sommer et al. 2001a).

Even these artificial floodplains can have important biological functions. Research in the Yolo Bypass has shown that young Chinook salmon grow

faster in the warmer food-rich bypass compared with the nearby leveed Sacramento River (Sommer et al. 2001b). The bypass also provides important habitat for splittail in years when it remains flooded for the approximately 30 d needed for spawning and successful recruitment of young of the year (Sommer et al. 1997). The bypass may also serve other less direct functions such as a source of organic matter to the Delta (Sommer et al. 2001a). The importance of bypasses as substitute floodplains provides a strong argument for restoring natural floodplains wherever possible; presumably natural floodplains would have an even higher degree of function. However, some features of floodplain may be less beneficial than anticipated. For example, Feyrer et al. (2004) found that permanent floodplain ponds in the Yolo Bypass primarily supported alien species. Native fishes were less than 1% of fish numbers and less than 3% of fish biomass in the study.

Water Storage and Diversion

Dams constructed for water storage, water diversion, and other purposes are one of the most visible aspects of California's water management system. There are presently over 1,400 reservoirs in California capable of storing almost 60% of the average annual runoff (California Department of Water Resources 1993). This water storage infrastructure supplies water and hydroelectric power for both agricultural and urban needs, and those needs are large. The Central Valley is one of the most productive agricultural areas in the world. In 2000, the agricultural industry of California produced a gross cash income of US$27 billion and supplied more than half the nation's fruits, nuts, and vegetables (California Department of Food and Agriculture 2001). Much of this production occurred in the Central Valley. Most of the agriculture in the Central Valley and elsewhere in California is irrigated. This makes agriculture the largest user of water in the state, taking between 70% and 80% of the stored water (Mount 1995; Moyle 2002). In addition to agricultural demands, urban demands on the water of the Sacramento–San Joaquin drainage are large. Although several urban areas within the Central Valley are growing rapidly, they tend to take rela-

tively little surface water compared with agriculture, at the present time. The bulk of the urban water demand occurs in Southern California and the San Francisco Bay area. Water pumped out of the Delta supplies all or part of the drinking water supply for over 22 million Californians in these two large urban areas (CALFED 2002).

From the perspective of fishes, many of these dams present barriers to movement. Yoshiyama et al. (2001) estimated that only 48% of the over 3,500 km of stream formerly available to anadromous fishes remains accessible. When only Chinook salmon spawning habitat is considered, the loss is much larger with greater than 70% of the habitat now inaccessible. It is likely that the loss for steelhead has been even greater because the species has a greater tendency to spawn in smaller tributary systems and has the ability to ascend higher into many drainages than Chinook salmon (Yoshiyama et al. 2001). The loss for anadromous Pacific lamprey probably parallels that for steelhead. Although large reservoirs on the larger river systems (built in the 1940s or later), such as Shasta Reservoir on the Sacramento River, Oroville Reservoir on the Feather River, and Millerton Reservoir on the San Joaquin River (Figure 1), blocked large areas of habitat, additional reductions in access to the smaller tributary river systems occurred continuously from the Gold Rush era onward (Yoshiyama et al. 2001). For example, access for anadromous fishes to most of the Tuolumne River basin was cut off by the construction in 1893 of a dam just downstream of present day Don Pedro Reservoir (Figure 1) (Brown and Ford 2002).

In addition to blocking access to upstream habitat, dams act as sediment traps, preventing renewal of downstream spawning gravels (Mount 1995). Continued discharge from the dam transports smaller particles, such as gravels, downstream leaving only larger cobbles, boulders, hardpan clay or bedrock. This is mainly perceived as a problem for anadromous fishes, although many other native fishes spawn over gravel riffles (Moyle 2002). Management agencies have attempted to address this problem with gravel augmentation projects and construction of spawning riffles. Such "imported" gravels are often used by Chinook salmon, but not al-

ways (Mesick 2001). However, the long-term effectiveness of such programs is questionable. Because rivers continue to move sediment downstream, the positive effects of such projects are transitory (Mount 1995; Kondolf et al. 1996), unless there is a commitment for periodic augmentation over the life of the reservoir.

The impacts of barriers on resident native species are less well known. Sacramento sucker, Sacramento pikeminnow, and Sacramento hitch are all known to make spawning migrations (Moyle 2002); however, it is unclear how important the loss of upstream spawning habitat has been to these species. Perhaps a more important function of barriers and reservoirs has been to fragment the ranges of native stream fishes, particularly the pikeminnow-hardhead-sucker assemblage. Most California stream fishes do not persist in reservoirs for more than 5–10 years because their young do not survive predation by introduced alien fishes such as centrarchid basses and catfishes (Moyle 2002). The reservoirs also provide a source and refuge for alien species that invade upstream reaches of rivers above the reservoirs. For example, electrofishing and snorkeling surveys of the Merced River above McClure Reservoir indicated that alien smallmouth bass dominated the river except for a limited reach near their upstream limit (Brown and Short 1999) (Table 2). Similarly, Gard (1994) found smallmouth bass to be the dominant species in much of the South Fork Yuba River above Englebright Reservoir. This process of fragmentation and isolation by barriers followed by negative interactions with alien species is one of general concern in the Sacramento–San Joaquin drainage (Brown and Moyle 1993).

Entrainment of fishes into water diversion structures has been a major concern in the Sacramento–San Joaquin drainage. In areas accessible to anadromous fishes, Herren and Kawasaki (2001) documented 2,209 diversions in the Delta, 424 diversions on the Sacramento River, and 298 diversions on the San Joaquin River. The large state and federal pumping plants in the Delta are of the most concern because their location is such that they can entrain protected anadromous (Chinook salmon and steelhead) and resident fishes (delta smelt and Sacramento splittail) in large numbers (Arthur et al. 1996; Bennett and Moyle 1996; Brown et al. 1996). Consequently, fish screens and fish salvage facilities were developed at those sites to mitigate their impacts (Brown et al. 1996). Fish screens have also been installed at many of the other larger diversion points in the rivers and in the Delta; however, adequate preproject and postproject assessments are usually not available for evaluating the effectiveness of screening, especially at the population level. Also, fish screens are generally ineffective for larval and small postlarval fishes.

Flow Alteration

Given the number of reservoirs in California and the various purposes they serve—including flood control, water storage, power generation, and water supply—their effects on flow regime vary from stream to stream and from year to year. In general,

Table 2.—Number and percentage of fishes (in parentheses) observed at six sites in the Merced River drainage in 1994 between McClure Reservoir and Yosemite National Park (data from Brown and Short 1999). The elevation of the water surface in McClure Reservoir varies between about 210 and 250 m, depending on water level.

Size	Elevation (m)	Brown trout	Smallmouth bass	Spotted bass	Rainbow trout	Sacramento sucker	Sacramento pikeminnow	Riffle sculpin
Main-stem Merced River								
1	343	0 (0)	104 (79)	0 (0)	0 (0)	10 (8)	15 (11)	0 (0)
2	511	3 (2)	97 (49)	1 (1)	5 (3)	61 (31)	26 (13)	5 (3)
3	556	3 (1)	13 (2)	0 (0)	20 (4)	315 (59)	156 (29)	24 (5)
4	1177	23 (20)	0 (0)	0 (0)	23 (20)	70 (60)	0 (0)	0 (0)
South Fork Merced River								
1	434	0 (0)	76 (99)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)
2	1268	1 (1)	0 (0)	0 (0)	52 (49)	54 (50)	0 (0)	0 (0)

the larger Sacramento–San Joaquin drainage reservoirs are operated for flood control during the winter, maintaining sufficient storage capacity to moderate peak flows from large storms. In the spring, after the probability of large floods has declined, the reservoirs are allowed to fill, mainly capturing snowmelt runoff. The stored water is then used over the rest of the year. The results of these manipulations are moderated winter peak flows, infrequent inundation of floodplains, and a loss of elevated spring flows (Mount 1995; Bay Institute 1998; Gronberg et al. 1998). In dry years, large reservoirs can store almost an entire year's precipitation (Brown and Ford 2002).

Summer flow effects are different in the San Joaquin and Sacramento River drainages (The Bay Institute 1998). In the San Joaquin River drainage, most of the water is diverted for agriculture at foothill dams, so rivers below the dams are small, containing water from limited flow releases and from return of agricultural drainage water. In the Sacramento River drainage, the larger reservoirs are operated to deliver water at a relatively steady discharge through river channels to the Delta for export to agricultural and urban users via the state and federal pumping plants. In addition, cool water is released from Shasta Reservoir to maintain required water temperatures for maintenance of winter-run Chinook salmon in the Sacramento River. These operations result in much higher summer flows and cooler temperatures in the Sacramento River compared with the San Joaquin River.

Much of the recent research on California fish assemblages has focused on understanding the effects of these changes to the natural flow regime. A number of studies have recognized that high winter–spring discharges favor California native stream fishes over alien species (Baltz and Moyle 1993; Moyle and Light 1996a, 1996b; Brown and Moyle 1997). Brown (2000) noted that flow regime was important in the distribution of native fishes and several groups of alien species in the heavily regulated San Joaquin River drainage. Native species were more common in the lower Stanislaus, Tuolumne, and Merced rivers in a high flow year compared with two low flow years. The importance of flow regime was reinforced by analysis of a 10-year data set from the Tuolumne River, a large tributary to the San Joaquin River (Ford and Brown 2001; Brown and Ford 2002). These analyses indicated that flow regime was a key factor in determining the relative reproductive success of native and alien fishes. High flows favored native species adapted to the cooler water temperatures and more riverine habitat conditions. Alien species did better during low flows when water temperatures were warmer and flow conditions were more conducive to low water velocity nesting species. Marchetti and Moyle (2000, 2001) documented similar relationships in Putah Creek, a small, regulated tributary to the Sacramento River.

May and Brown (2002) observed that, except for agricultural drains, the streams and rivers they sampled in the Sacramento River drainage (not including Putah Creek) generally maintained populations of native fish species, even though alien species were present. They attributed this to minimal flow regulation of the smaller streams sampled and the use of larger rivers for delivery of water to the Delta, rather than diverting water into canal systems. Similarly, Baltz and Moyle (1993) found that the native fish assemblage of an unregulated tributary to the Sacramento River was resistant to invasion by alien species. Overall, the flow alterations in the San Joaquin River drainage appear to create habitat conditions more conducive to alien species and the flow alterations in the Sacramento River drainage are less conducive to alien species, allowing native species to remain common.

Water Quality

Another legacy of the California Gold Rush is contamination of California waters with mercury from mining activities in the Sierra Nevada and from the abandoned mines where the mercury was produced in the coast ranges (Davis et al. 2003). In addition, abandoned hard rock mines for other minerals contribute trace metals and acids. Mercury contamination of fish is a major human and wildlife health concern, especially in the Delta (Davis et al. 2003); however, there is no evidence that mercury accumulation is directly affecting the health of California fish populations. Similarly, much of the concern

about trace metals relates to human drinking water quality. A major exception is Iron Mountain Mine, an Environmental Protection Agency Super Fund site, which has been responsible for past fish kills (Finlayson and Wilson 1979). Mitigation work is ongoing, but accumulations of sediments in a debris pond below the mine and in Keswick Reservoir, where the mine discharges to the Sacramento River, are a particular concern. Mount (1995) cites estimates that over 500 kg of copper and 360 kg of zinc are contributed to Keswick Reservoir *per day*. Fish and aquatic insects bioaccumulate metals in the Sacramento River downstream of Keswick Reservoir (Saiki et al. 1995; Cain et al. 2000; Saiki et al. 2001b). Cutthroat trout have been shown to avoid high concentrates of dissolved copper and zinc in laboratory experiments (Woodward et al. 1997), suggesting that these discharges might affect populations of salmonids in the Sacramento River downstream of Keswick Reservoir. A mass movement of these sediment accumulations into the Sacramento River below Keswick Reservoir would likely have severe effects on downstream fish populations including the endangered winter-run Chinook salmon.

Central Valley irrigated agriculture makes extensive use of pesticides, including hundreds of compounds in the thousands of kilograms of active ingredient in any given year (California Department of Pesticide Regulation 2002). Erosion of agricultural soils continues to deliver long-lived organochlorine pesticides and their breakdown products to rivers and streams where they accumulate in biota (Saiki and Schmitt 1986; Brown 1997; MacCoy and Domagalski 1999). Despite this input of toxins, acute mortalities of fishes are rarely documented, with the exception of catastrophic spills (e.g., Cantara spill, Payne and Associates 1998). In many cases, the actual percentage of applied pesticide reaching a surface water body is quite small (Kratzer 1997); however, there is evidence for effects of these chemicals on fishes. Bailey et al. (1994) used bioassays to demonstrate that rice pesticides could account for declines in striped bass populations. Bennett et al. (1995) found histological evidence of liver deformities in striped bass larvae, consistent with pesticide exposure. Chronic effects of pesticides, such as disruption of antipredatory and homing behaviors

have been demonstrated (Scholz et al. 2000). Environmental estrogens have been detected in agricultural drains (Johnson et al. 1998) that could affect sexual and functional development of young (Leatherland 1992; Reijnders and Brasseur 1992). Such environmental estrogens might account for feminized male Chinook salmon observed in the Columbia and Sacramento–San Joaquin drainages; however other explanations are possible (Nagler et al. 2001; Williamson and May 2002). Indirect effects on fishes through toxicity to food organisms also seems possible given results of invertebrate bioassays (Foe 1995; Kuivila and Foe 1995).

Selenium in agricultural drainage water in the Central Valley has been a controversial topic for many years. Irrigation of soils derived from marine sediments on the west side of the San Joaquin Valley results in drainage water that is high in concentrations of dissolved salts and trace elements, including selenium. This selenium subsequently entered the food web and caused developmental abnormalities in birds (e.g., Ohlendorf et al. 1988a, 1989; Williams et al. 1989b). Selenium also reached high levels in other biota, and in fishes, reached concentrations known to affect reproduction in some species (Saiki and Lowe 1987; Ohlendorf et al. 1988b; Saiki and May 1988; Saiki et al. 1992a; Saiki and Ogle 1995). Changes in drainage water management have improved the situation to some extent, but selenium is still a management concern, especially in some small tributaries on the west side of the San Joaquin River. Selenium is also a concern in the Delta where the major sources are industrial. Filter-feeding clams accumulate high concentrations of selenium, which are then eaten by some fishes (Linville et al. 2002).

Agricultural drainage water may also contain several seemingly more mundane materials, including dissolved salts and sediment. Saiki et al. (1992b) found that agricultural drainage water from the west side of the San Joaquin Valley could affect survival and growth of juvenile Chinook salmon and striped bass. The effect was attributed to the unusual ionic composition of the drainage water resulting from irrigating soils derived from marine sediments. Although the effects of sediment in the Central Valley have not been well documented, such effects have

been recognized as important in many other areas (Waters 1995).

Changes in water quality, as documented above, are probably best viewed as chronic stressors on fish populations rather than causes of acute mortality. Saiki (1984), Brown (2000), and Saiki et al. (2001a) documented the dominance of introduced species over native species in the lower elevation rivers and agricultural drains of the irrigated San Joaquin Valley. May and Brown (2002) found that the principal habitats dominated by alien species in the lower elevation portion of the Sacramento River drainage were agricultural drains. Brown (2000) hypothesized that the harsh and fluctuating environmental conditions associated with agriculturally dominated water bodies favored introduced species from habitats with similar conditions over native species adapted for habitats that no longer exist or are extremely modified. Water clarity and its effects on predation risk and feeding efficiency may also be an important factor in determining the distribution of native and alien species (Brown 2000; Bonner and Wilde 2002).

Alien Invasions

Alien species can be regarded as an irreversible, self-replicating kind of pollution. Alien fishes are most likely to pollute environments already altered by human activity, although they can also invade relatively pristine systems if conditions are favorable (Moyle and Light 1996a, 1996b). In California, introductions of alien fishes have gone hand in hand with major disturbances of the landscape. Among the first successful introductions were American shad (1871), common carp (1872), and striped bass (1879)—species that thrived in the silty habitats created by hydraulic mining. Most of the subsequent 48 introductions were species that thrive in reservoirs, ponds, and stagnant river channels (Moyle 2002). Many of these species, once established, will invade less disturbed habitats and compete with or prey on native fishes. Other species, such as brown trout, brook trout, and redeye bass were introduced as sport fish because they *could* thrive in relatively undisturbed habitats such as mountain or foothill streams. Redeye bass, for example, are now the most abundant fish in long reaches of the Cosumnes River,

the last Sacramento–San Joaquin drainage river without a major dam on its main stem (Moyle et al. 2003). In addition, fishes native to various drainages in California have been introduced, often via aqueducts, into drainages to which they are not native. Some of these interbasin transfers have been deliberate, such as the planting of rainbow trout into high mountain lakes and streams. The result of all these invasions, combined with extirpations of native fishes, has been increased homogenization of the fish fauna of California (Marchetti et al. 2001). In some streams, the process of homogenization can be reversed by recreating a natural flow regime that favors native fishes, but even in these cases, the alien fishes are rarely eliminated; they just become uncommon.

Discussion

The decline of the native fish communities of the Sacramento–San Joaquin drainage cannot be attributed to any single change in habitat or water quality condition. Bennett and Moyle (1996) reached a similar conclusion about the fish communities of the San Francisco Estuary. Many species of California native stream fishes are actually quite tolerant of stressful physical conditions (Cech et al. 1990; Brown and Moyle 1993; Moyle 2002). However, invasion of new species in addition to loss and alteration of physical habitat, alteration of physical processes (e.g., flow regime), and changes in water quality have exceeded the ability of the native fishes to adapt. In essence, environmental conditions have been changed to the extent that they are now more suitable for alien species introduced from areas with similar conditions (Moyle and Light 1996a, 1996b; Brown 2000; Marchetti and Moyle 2001).

The changes in the fish assemblages are most obvious in the San Joaquin River drainage, where the physical and water quality changes have been most severe (Saiki 1984; Brown 2000; Saiki et al. 2001a). Of the three native fish assemblages historically present (Figure 2), the deep-bodied fish assemblage is completely gone, and the rainbow trout and pikeminnow-hardhead-sucker assemblages are highly disrupted (Figure 3). Alien species dominate most habitats downstream of the foothill dams. In

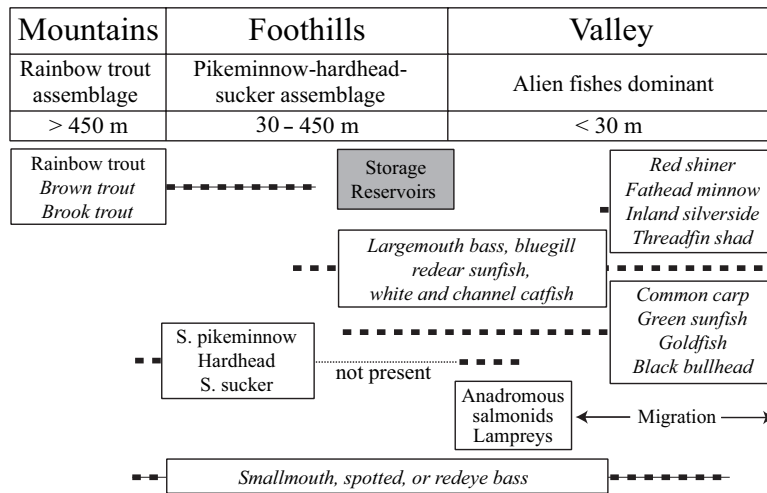| Mountains	Foothills	Valley
Rainbow trout assemblage	Pikeminnow-hardhead-sucker assemblage	Alien fishes dominant
> 450 m	30 – 450 m	< 30 m

Figure 3.—Distribution of species in the San Joaquin River drainage after European settlement (Brown 2000; Moyle 2002). The ranges of the historical fish assemblages are taken from Figure 2. The boxes indicate where the indicated groups of species are most abundant and the dashed lines indicate the approximate range of the species. Alien species are shown in italics. Only the most common species are included [S., Sacramento]. All the alien species except red shiner, fathead minnow, and inland silverside are commonly found in reservoirs.

the San Joaquin River drainage, the native species that have not disappeared entirely are now largely restricted to the areas just below the reservoirs. These areas resemble their native habitats, with regard to physical habitat and water temperature. The native species still present above the reservoirs are threatened by alien species moving upstream and alien species introduced into higher elevation waters. The situation in the Sacramento River drainage appears to be less severe. Native species still maintain healthy populations in many areas because of different water management practices on dammed streams, the presence of undammed tributaries, and less severe habitat loss and alteration, compared with the San Joaquin River drainage. Low abundances of alien species in many rivers and streams and the dominance of alien fishes in agricultural drains suggests that environmental changes resulting from changing water management operations or invasions of additional alien species could result in rapid changes in fish assemblage composition (May and Brown 2002).

The formal listing of multiple fishes in the drainage as threatened or endangered has stimulated numerous restoration efforts; however, these restoration efforts are generally not focused on native stream fishes. Concerns in the Delta focus on more estuarine species, such as delta smelt and splittail, and migratory anadromous salmonids. In the rivers, efforts focus mostly on threatened anadromous salmonids, although other native fishes are increasingly of concern (e.g., Moyle et al. 1995; Brown and Ford 2002). Management actions that are focused on anadromous salmonids may or may not aid other native fishes. In fact, management actions taken to restore Chinook salmon will not necessarily help restore steelhead in the same river (McEwan 2001). So, how can restoration efforts be directed toward communities rather than species? Moyle (1995, 2002) and Moyle and Yoshiyama (1994) suggest a plan to create a series of aquatic diversity management areas (ADMAs) throughout California. The series of ADMAs would be designed to protect all of California's native aquatic species, not just fishes, and would adopt a watershed approach to management and protection. However, there has been no movement in the management agencies to adopt the ADMA approach.

The largest restoration presently ongoing in the Sacramento–San Joaquin drainage is the Ecosystem Restoration Program (ERP) of the multibillion dollar CALFED Program (CALFED 2002). The purpose of the ERP is to restore ecosystem health of the Delta, its watershed, and northern San Francisco Bay as part

of the larger CALFED goals of protecting all beneficial uses of Delta waters, including drinking water quality, and agricultural and urban water supply. The ERP has been conceived as an ecosystem restoration program rather than as a species-specific restoration program. This approach is driven by the need to increase populations of multiple species of threatened and endangered fishes, plants, birds, and mammals. The difficulties of this approach in such an altered system are a major challenge for managers and scientists. For example, one of the initial ERP proposals was to increase populations of native fishes and other plants and animals by restoring tidal wetlands in the Delta. This proposal makes intuitive sense because tidal wetland habitat, once the dominant habitat type in the Delta, is now very limited. However, the benefits of tidal wetland restoration for fishes is complicated by the presence of a variety of alien fishes, other alien animals, and alien plants that interact with each other and native species in unexpected ways (Brown 2003a). There might also be effects on drinking-water quality because of production of organic carbon that can form disinfection byproducts (Brown 2003b) and on accumulation of mercury in food webs (Davis et al. 2003).

Similar complexities can be expected when ecosystem restoration in Central Valley rivers is addressed. For example, Sommer et al. (2001a, 2001b) document the benefits of an engineered seasonal floodplain of the Sacramento River. However, it is unclear if restoring natural floodplain features such as sloughs and oxbow lakes would be beneficial to native fishes. In the Willamette River, Scheerer (2002) found that populations of the endangered Oregon chub *Oregonichthys crameri*, a native floodplain minnow, were negatively affected by increased connectivity among floodplain habitats. Increased connectivity facilitated invasion of Oregon chub habitats by alien species, which apparently suppressed the chub populations. Similarly, Feyrer et al. (2004) found that Yolo Bypass perennial ponds were dominated by alien fishes. It seems likely that such complex interactions in the Sacramento–San Joaquin drainage will require managers and scientists to work closely to ensure that restoration efforts produce the desired outcome.

The need for developing cooperative and innovative approaches to native fish conservation has been made even more urgent by the recent predictions of climate change models. O'Neal (2002) determined that human-caused climate change will result in warming of mean annual temperatures in Central California of at least 3°C, with major consequences to precipitation and water temperatures. Basically, it is expected that there will be less snow and more rain, making run-off even more strongly seasonal than it is today and less predictable from year to year (Aguado et al. 1992; Dettinger and Cayan 1995; O'Neal 2002). In many respects, Sacramento–San Joaquin drainage streams will become more like coastal streams, in which flows rise and fall with rainfall rather than having a long extended period of gradually declining flows in the spring as the result of snowmelt. Because the snowpack in the Sierra Nevada essentially serves as a giant reservoir that slowly sends its water downstream, its depletion will reduce the ability of Californians to store enough water in artificial reservoirs to meet their needs. Increased demand for limited water in turn is likely to greatly decrease the flows of rivers below dams, especially during periods of extended drought. Reduced releases of water that is also warmer (from rain) will cause dramatic changes to the aquatic ecosystems. Without major changes to our water distribution system, we hypothesize some likely consequences to fishes, which in many ways are accelerations of trends caused by other factors:

1. Chinook salmon will likely decline in abundance. The spring-run, which requires coldwater year around, is especially vulnerable because some populations utilize unregulated tributaries. Rainfall runoff is warmer and less sustained than snowmelt runoff, resulting in diminished areas and duration of appropriate coldwater habitat in unregulated streams. The winter and late-fall runs, which also require cold water year around, may be less affected because they utilize the Sacramento River below Shasta Reservoir and reservoir releases are utilized to maintain appropriate temperatures. Declines may occur because the coldwater pool available for downstream release is likely to be smaller

and more variable in size and temperature from year to year. Wild fall-run Chinook salmon will presumably persist by shifting the peak of spawning to later in the season because adult upstream migrations will be delayed by low, warm fall flows. There may also be effects on fall-run juveniles if increased coldwater flows from reservoirs are needed to support juvenile rearing and migration; however, such flows may not be necessary. Connor et al. (2002) found that fall-run Chinook salmon emerged from the gravel sooner, grew faster, and emigrated sooner in response to warmer temperatures.

2. Alien warmwater fishes such as common carp, bluegill, and largemouth bass will become more abundant as warm, quietwater habitats become more widespread.
3. Common native fishes, such as Sacramento sucker and Sacramento pikeminnow, will likely persist. As downstream habitat for these species is lost because of reduced flows and warmer temperatures, the ranges of the species will extend into upstream areas of formerly coldwater habitat that previously supported the rainbow trout assemblage.
4. Resident populations of wild rainbow trout will be reduced in range and abundance with decreased flows and increased temperatures of high and mid-elevation streams (O'Neal 2002).
5. Floodplain dependent species, such as splittail, may benefit, assuming flooding during February–April is more frequent and longer in duration.

While many of these effects may be unavoidable, improved management of our water supplies can reduce them. Major changes that will need to be seriously considered include

1. Increase floodplain capacity in the Sacramento–San Joaquin drainage. Increasing the area of floodplain will provide greater flexibility in the management of flood flows and reservoir levels. In addition, flooding floodplains benefits native fishes, particularly Chinook salmon and splittail.
2. Conserve remaining coldwater streams and rivers specifically for fish and other aquatic biota.
3. Develop a system of ADMAs that can, through active management, provide refuges for native fishes likely to be negatively impacted by climate change and other factors.
4. Improve the efficiency of water use and transfer in order to reduce waste and leave more water instream for fishes.

The native fish assemblages of the Sacramento–San Joaquin drainage have already declined in both species richness and abundance. Failure to consider these assemblages in water management decisions will almost certainly result in further declines of native fishes.

Acknowledgments

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