# The Future of Fish in Response to Large-Scale Change in the San Francisco Estuary, California

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Abstract.—The San Francisco Estuary is the largest estuary on the west coast of North America and one of the most altered. It supports a diverse fish fauna in which key species are in severe decline. The estuary is faced with catastrophic structural and ecological changes, especially in the Sacramento-San Joaquin Delta and Suisun Marsh, as the result of levee failure caused by the combination of earthquakes, land subsidence, sea level rise, and increased high outflows events (from climate change). The resulting flooding of Sacramento-San Joaquin Delta islands and Suisun Marsh is predicted to disrupt California's water supply system and, consequently, the state's economy. From a fish perspective, the changes seem likely to create conditions in which key native species and striped bass can persist at least at present low levels, after a period of possible high mortality created by the initial flooding events. Taking actions to regulate ecological changes in the estuary before a disaster occurs could actually improve conditions for desirable fishes while being highly compatible with delivering services the Sacramento-San Joaquin Delta provides, especially water supply. Specific actions include improving habitat for fish in Suisun Marsh, Cache Slough, the Yolo Bypass, and the San Joaquin River, while creating islands in which flooding can be managed. The key is increasing and maintaining habitat heterogeneity. The present situation in the estuary represents an unprecedented opportunity to reverse the impacts of more than 150 years of undesirable ecological change.

# Introduction

The San Francisco Estuary (SFE) is the largest estuary on the west coast of North America and one of the most altered (Nichols et al. 1986). It is highly urbanized but contains extensively diked agricultural lands and managed wetland habitats. It is also highly invaded by alien species, especially the aquatic habitats. Not surprisingly, the native species of plants and animals have declined in abundance; several are extinct and others are listed as threatened or endangered under state and federal laws (Herbold et al. 1992). Human-caused changes to the SFE are still taking place at an accelerated rate and there are strong indications that major, catastrophic

changes to the SFE are imminent (Mount and Twiss 2005; Lund et al. 2007). The changes are likely to be most dramatic in the upper part of the estuary, the Sacramento-San Joaquin Delta (the Delta), where large-scale levee failure can seriously disrupt local, regional, and state economies. A principal concern is disruption of California's water distribution system. Much of the freshwater used by San Joaquin Valley farms and the vast urban areas of Southern California originates directly or indirectly from the estuary's inflowing rivers. This water is removed from the Delta by the massive pumps of the State Water Project and the federal Central Valley Project. Additional water is removed to supply aqueducts to cities around San Francisco Bay and to irrigate farms in the Delta. Large scale levee failure could also eliminate farming on thousands of

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acres of Delta islands, threaten urban areas, and disrupt railroads, pipelines, and other infrastructure (Lund et al. 2007). Likewise, a sudden catastrophic change to the Delta and SFE will have substantial ecological impacts.

A major question being asked by management agencies and regional stakeholders is "how can we prevent large-scale change from taking place in the SFE, especially the Delta?" Answering precursors to this question (mainly, how do we protect endangered fish and fisheries?) was one of the reasons for the establishment of CALFED in 1996, a massive joint state-federal management and research effort (http://calwater.ca.gov/), which has been criticized for not quickly resolving problems of the SFE (Little Hoover Commission 2005). A report produced by the University of California, Davis and the Public Policy Institute of California (Lund et al. 2007) turned the original question on its head, asking instead "How can the Delta be managed to accommodate large-scale change before undesirable changes are forced by catastrophic events?" In this paper, key findings of Lund et al. (2007) are summarized in relation to aquatic organisms, especially fish. I first describe the SFE, provide a brief introduction to its fish fauna, and then discuss the major drivers of change. I then describe what is likely to happen to key fish species if present management trends continue, followed by suggestions for major actions that could be taken to improve the SFE for fishes even in the face of large-scale change.

# The San Francisco Estuary

The SFE is the outlet of the Sacramento and San Joaquin rivers, which in turn drain much of central California. The primary source of water for the rivers is the Sierra Nevada, which intercepts moisture-laden clouds coming off the Pacific Ocean. The estuary has three distinct segments, San Francisco Bay (including San Pablo Bay), Suisun Bay and Marsh, and the Sacramento–San Joaquin Delta (Figure 1). Each segment has a confined outlet through which the tides surge back and forth, creating complex hydrodynamics: the Golden Gate (San Francisco Bay), the Carquinez Strait (Suisun Bay), and the river confluence at Chipps Island (Delta), respectively. These narrows have allowed the three regions to have distinct identities, emphasized by human modifications to them. The Delta is perceived as a region where freshwater from the rivers tidally sloshes back and forth in leveed channels, flowing between islands of agricultural fields. The islands are highly subsided (many are 5+ m below sea level; Figure 2), surrounded by 1,800 km of fragile levees made of local materials, often peat, with some reinforcement with rip rap (Brown and Michniuk 2007). Historically, the Delta was a vast marshland that was flooded annually by undammed rivers (Lund et al. 2007).

In contrast, Suisun Bay was, and still is, a large area of open water that is transitional between the fresh waters of the Delta and the salt waters of San Francisco Bay; it is a shallow region of wind-stirred, brackish water, lined with tidal marshes. The largest of these marshes, nearly as large as Suisun Bay itself, is Suisun Marsh. This 30,000+ ha marsh is largely managed today as freshwater wetlands to support waterfowl hunting in both private clubs and public wildlife areas. The key for maintaining its freshwater character is inflow from the Sacramento River via Montezuma Slough. Montezuma Slough has large tidal gates on its upper end that control salinity in the marsh by allowing freshwater to flow in but preventing the tides from pushing it back out again. More than 360 km of levees separate marsh islands from the tidal channels, in which water is still seasonally brackish. The channels are highly productive of fish, which are a mixture of euryhaline freshwater and marine species (Matern et al. 2002).

The marine species in Suisun Marsh come from San Francisco Bay, which is largely a marine system, with variable but high salinities; the actual salinity depends on location and season. San Francisco Bay is ringed by cities, and its fringe marshes are fragments of its original tidal marsh system.

All three parts of the SFE were once more variable in their salinities and river-driven hydrodynamics than they have been for the past 50–60 years (Bay Institute 1998). Dur-

#### SAN FRANCISCO ESTUARY FISH

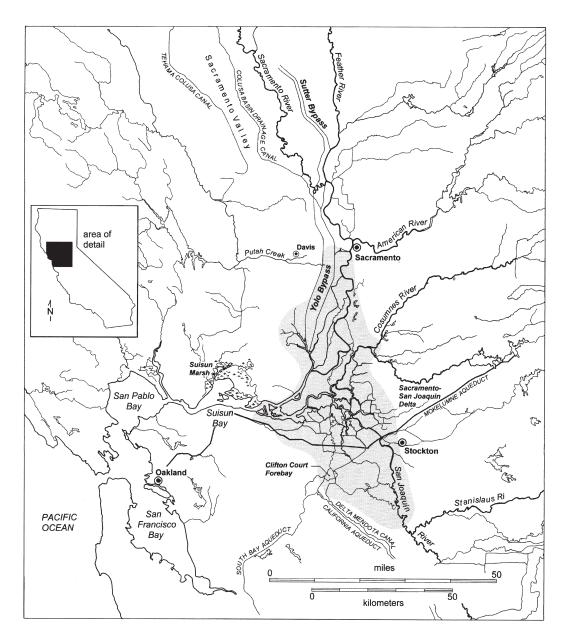


Figure 1. Map of San Francisco Estuary. (Moyle 2002)

ing wet years, the spring snowmelt from the Sierra Nevada could temporarily make fresh the surface waters of San Francisco Bay, while during late summer of drought years, ocean salt could be detected at the upper ends of the Delta, especially after upstream diversions became established (DWR 1993). The development of the federal Central Valley Project and the State Water Project, however, allowed freshwater inflows to be regulated, reducing variability in water quality so that, for the purposes of policy and public perception (if not always in reality), the Delta and Suisun Marsh became permanent freshwater systems, Suisun Bay became a brackish water system, and San Francisco Bay became an exclusively ma-

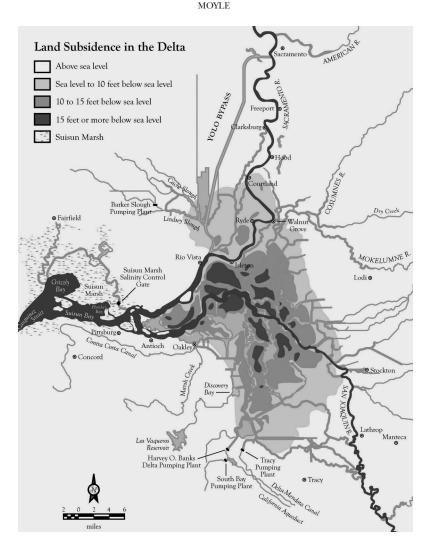


Figure 2. Map of the Sacramento–San Joaquin Delta showing land subsidence. Courtesy of Public Policy Institute of California, after DWR (1993). Recent surveys indicate that subsidence in most areas is 1–5 ft greater than shown. (Department of Water Resources, unpublished data)

rine system. The two water projects (and other related projects) constructed huge dams on the Sacramento and San Joaquin rivers and all their major tributaries in the 1930s–1960s, with consequences such as increasing summer flows of the Sacramento River and drying up part of the San Joaquin River. The dams also allowed for the regulation of salinity in the upper SFE. By releasing large quantities of freshwater, especially in the summer, the dam operators could both keep saltwater out of the Delta and Suisun Marsh and permit the pumping of freshwater from the southern edge of the Delta, for agricultural and urban use.

For further information on the environmental and ecological history of the SFE, see Herbold et al. (1992), Hollibaugh (1996), Bay Institute (1998), Lund et al. (2007), or http://www.deltavision.ca.gov. The rest of this essay focuses primarily on the Delta and Suisun Bay and Marsh because the lowermost part of the SFE, San Francisco Bay, has a whole additional set of issues related to its intense urbanization.

# The Fishes

The San Francisco Estuary has a high diversity of fishes, representing marine, freshwater, anadromous, and estuarine species, both native and alien (Matern et al. 2002; Moyle 2002). The total fish fauna is about 120 species that can be found in one environment or another on a fairly regular basis, of which about 30 (25%) are aliens, mostly in freshwater and brackish water. About 75 species, largely marine, have been recorded from San Francisco Bay in recent years, of which only 5 are alien species (Schroeter and Moyle 2006). In Suisun Marsh and Bay, 53 species are known, a mixture of euryhaline marine, freshwater, and anadromous species, plus a few more stenohaline species that appear during periods of high or low salinity. They represent 28 native species and 25 aliens (Matern et al. 2002). In the Delta, there are about 46 regularly occurring species, a mixture of freshwater and anadromous fishes, of which 27 are aliens.

The introduction of alien species has accompanied large-scale environmental change and the explosive invasion of many of the alien species has been a driver of declines of native species, including extinctions of native fishes such as thicktail chub Gila crassicauda and Sacramento perch Archoplites interruptus (Moyle 2002; Light and Marchetti 2007). Changes over the past 50 years, since the advent of the major water projects, contributed to severe declines of most native species, including four runs of Chinook salmon Oncorhynchus tshawytscha and the delta smelt Hypomesus transpacificus. The result has been that five fishes, including delta smelt and two runs of Chinook salmon, are currently listed as threatened or endangered by state and federal governments (Moyle 2002). In more recent years, declines in fisheries have also been a major concern, especially fall-run Chinook salmon, white sturgeon Acipenser transmontanus, and alien striped bass Morone saxatilis. Some of the fishes most likely to be affected by future large-scale changes to the SFE and also likely to drive policy decisions are listed in Table 1.

# **Drivers of Change**

The major drivers of change in the SFE that are likely to result in major shifts in environmental conditions, including catastrophic shifts, are earthquakes, island subsidence, sea level rise, climate change, and invasions of new alien species (Lund et al. 2007). Human land and water use could arguably be listed as another driver of change, but these uses are strongly affected by the first five drivers so will not be treated further as drivers here. The major catastrophic consequence of the five drivers is extensive levee failure in the Delta and Suisun Marsh. From an ecological perspective, the consequence is sudden change in the hydrodynamics of the two regions as the islands fill with water, creating new habitat conditions, followed by invasions of both desirable and undesirable species into the new habitat space.

### Earthquakes

There are at least five major faults in the SFE region, but there have been no major earthquakes in the region since the great 1906 San Francisco earthquake. This means that pressure is building on local faults, steadily increasing the probability that one will move as time goes by (Mount and Twiss 2005). The major impact likely from earthquakes is collapse of levees in the Delta and Suisun Marsh because of their poor foundation soils and weak construction.

### Island Subsidence

The islands of the Delta were originally marshlands on a thick base of peaty soils. More than 182,000 ha of islands were diked and drained for farming in the 19th and early 20th centuries, and soils were typically burned annually to release nutrients from the peat, causing the interiors of the islands to subside rapidly. Even after the practice of burning stopped, subsidence continued through oxidation of plowed soils and the loss of soil by wind erosion. As a result, all islands with peat soils used for farming have subsided, with subsidence greatest (3–7 m below sea level)

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Species	Native?	Why important	Comments
Delta smelt Hypomesus transpacificus	yes	Threatened species, endemic	Open water pelagic, near extinction
Longfin smelt Spirinchus thaleichthys	yes	Special concern species	Open water pelagic, anadromous
Splittail Pogonichthys macrolepidotus	yes	Special concern species, endemic	Spawns on flood plains, rears in brackish water
Tule perch Hysterocarpus traskii	yes	Native, declining	Represents complex of native fishes
Sacramento perch Archoplites interruptus	yes	Extirpated	Reintroduction program proposed
Striped bass Morone saxatilis	no	Estuarine sport fish declining	Anadromous, uses entire estuary
White sturgeon Acipenser transmontanus	yes	Sport fish, declining	Anadromous, rears in estuary
Green sturgeon A. medirostris	yes	Endemic, threatened	Anadromous, rears in ocean
Chinook salmon Oncorhynchus tshawytscha	yes	Four runs	Anadromous
Chinook salmon, spring run	yes	threatened	Appears in estuary mainly as smolts
Chinook salmon, winter run	yes	endangered	Appears in estuary mainly as smolts
Chinook salmon, fall run	yes	Sport and commercial fisheries, hatchery- driven	Large numbers of fry in estuary but survival low
Largemouth bass Micropterus salmoides	no	Alien predator, sport fish, increasing	Represents complex of alien pond fishes in Delta
Pacific herring Clupea pallasii	yes	Commercial fish	Represents euryhaline marine fishes

Table 1. Fish species of major importance for management in the San Francisco Estuary. (Moyle 2002)

in west and central Delta (Figure 2). Despite improved soil conservation practices, subsidence increases as long as farming continues. The effect of subsidence is to create a series of bowl-like depressions, into which water will pour in if it breaks through the levees.

# Sea Level Rise

Sea level is rising in the SFE and has been for at least 6,000 years (Lund et al. 2007). Because of global warming, the rate of rise is accelerating. There is scientific debate about how rapidly and how much sea level will continue to rise, but a 30–50 cm rise in the next 50 years is plausible (Mount and Twiss 2005). Higher mean sea levels result in higher high tide levels, increasing the probability that levees in the Delta and Suisun Marsh will overtop and then collapse, especially if combined with flood flows coming down the rivers.

### Climate Change

The climate of California is becoming significantly warmer, a trend that is likely to continue for some time (Dettinger 2005). While average precipitation is not expected to change much, more will fall as rain and less as snow in the high mountains, resulting in more periods of severe high run-off. Year-to-year variability in rainfall is also expected to increase, increasing the frequency of extended droughts and big floods (Dettinger 2005). One result of this change is increased hydrostatic pressure on levees during storms and floods and thus increased likelihood of failure.

# Invasive Species

The SFE has the reputation of being the most invaded estuary in the world and new invasions continue at a high rate (Cohen and Carlton 1998). Recent invaders (e.g., overbite clam Corbula amurensis, Brazilian waterweed Egeria densa) have already had major impacts on ecosystem structure and function (Kimmerer 2002; Nobriga et al. 2005). New invaders or expanding populations of existing invaders are likely to take advantage of the new habitats created by large-scale levee failure (Light and Marchetti 2007), further exacerbating the effects of levee failure and increasing the difficulty of protecting native species.

# Ecological Effects of Large-Scale Change

The likelihood is high that two or more of the above drivers of change will act together to create catastrophic levee failure within the next 50 years (Mount and Twiss 2005; Lund et al. 2007), assuming the SFE continues to be managed as it is today. The probability of such an event is high enough that it is presumably more a matter of when and how much rather than if. In recognition of this, the Delta Risk Management Strategy (DRMS) team of the California Department of Water Resources has modeled the effects of up to 50 simultaneous levee breaches on Delta islands (http://www.drms.water.ca.gov). Other signs of high levels of interest include (1) the appointment by Governor Arnold Schwarzenegger in February 2007 of the Delta Vision Committee with a Blue Ribbon Task Force to find ways to prevent or reduce the impacts of the likely disaster, (2) the recent passage of bond issues to fix levees and other infrastructure affecting urban areas, (3) the establishment of a Bay–Delta Conservation Plan process, and (4) numerous other actions and processes by agencies at all levels of government. The scenario of most concern is simultaneous and cascading failures of levees throughout the Delta because of the impact of such failures on Southern California's water supply, on agriculture and other uses of Delta islands, and on urban areas in and around the Delta (Lund et al. 2007). Here, however, I discuss mainly the impacts on the ecosystems of the Delta and Suisun Marsh, especially with respect to fish.

# Delta

For the central and western Delta, the basic disaster scenario is that following multiple levee failures, water would rush in, filling as much as  $2.5 \times 109 \text{ m}^3$  of space in the island basins. If the levee collapses occurred as the result of the combination of high outflows and high tides, the islands would likely fill mostly with freshwater. If the levee collapses occurred as the result of an earthquake during a low-flow period, much of the water filling the islands would be drawn up from Suisun Bay and even San Francisco Bay, creating lagoons with varying degrees of salinity.

The open-water habitat thus created would be up to 10 m deep and subject to strong tidal currents through the new levee breaches, as well as to mixing from frequent winds. The hydrodynamic and salinity regimes of each flooded island would depend on the number and location of levee breaches, closeness of the area to Suisun Bay (source of saltwater) and to inflowing rivers, and relationship to infrastructure such as the ship canal that goes through the system. As levees continued to erode, many of the flooded islands would presumably come to resemble Frank's Tract, a large island in the central Delta that flooded in the 1930s and was left that way. It is currently a freshwater lagoon with complex hydrodynamics that is dominated in summer by dense growths of alien Brazilian waterweed.

Presumably, the flood water would initially be highly turbid from the disturbance of peat and sediment on the islands (DWR 2007),

but once the suspended material had settled, there would likely be blooms of algae, especially when temperatures are warm, because of the release of nutrients from the soils and the increased water transparency. Depending on the species making up the algal blooms (diatoms versus green algae versus cyanobacteria), a bloom of zooplankton should quickly follow. Within a year, brackish island lagoons would be heavily colonized by the overbite clam, an alien species that currently dominates the benthos of Suisun Bay. Presumably, the clams would then consume much of the primary and secondary production of the new lagoons, as they do in Suisun Bay, reducing zooplankton populations. Island lagoons that contained fresh or low salinity water, would likely be colonized in 1-2 years with the species that dominate similar areas in the Delta: Brazilian waterweed and, in areas with sufficient flow, Asian clams Corbicula fluminea. The combination would result in lagoons choked with weeds and low zooplankton populations (similar to Frank's Tract today). It is possible that flooded islands located close to sources of both freshwater inflow (Sacramento River) and tidal sources of saltwater could maintain a pool of water that would fluctuate enough in salinity on either an annual or interannual basis to keep the overbite clam or Brazilian waterweed-Asian clam from becoming dominant. Biomass production in such lagoons could revert to a pelagic system of phytoplankton, zooplankton, shrimp, and fish, such as was the case of Suisun Bay before the invasion of overbite clams in the 1980s. Obviously, these scenarios can all be strongly affected by local conditions of wind, tide, and river, as well as the diverse configurations of the lagoons, which will change constantly as levees deteriorate after the initial breaches.

### Suisun Marsh

Suisun Marsh, for the most part, has not subsided as much as the Delta, although much of it is 0–2.3 m below sea level and parts of it (ca. 16%) are more than 2.3 m below sea level (C. Enright, Department of Water Resources, personal communication). Before European settlement, it was high marsh, mostly flooding on high tides and high river flows. A scenario of wide-scale levee failure in the Delta is likely to include levees protecting Van Sickle Island, located at the entrance to Montezuma Slough, the main artery of the marsh. Van Sickle Island is already subject to frequent levee failures, although failures are quickly repaired. The rapid repair response (by public agencies) occurs in good part because if the island floods, the entire freshwater distribution system of the central marsh (Roaring River Slough) ceases to work efficiently and the southern third of the marsh (between Montezuma Slough and Suisun Bay) becomes tidal and brackish. Future failures will likely make much of the central marsh tidally brackish. Less dramatically, increasingly high tides (from sea level rise) and increasingly large flood events (from climate change) are likely to cause levee overtopping and failures within the Marsh at increasing rates. Thus, broadly, the ultimate fate of much of Suisun Marsh is to become a tidal brackish marsh, with seasonally higher salinities in many areas than were historically present. Much of it is likely to be permanently inundated. The details of how the future marsh will actually look will depend on the interactions of a number of factors: (1) the rapidity and extent of sea level rise, (2) the depth of tidal and other flooding, (3) the residence time of the water in different areas (i.e., the hydrological relationship between the flooded areas and the deeper channels and sloughs that drain them), (4) the response of the natural vegetation to the inundation and salinity gradients, and (5) the influence of existing artificial dikes and channels, including railroad and road beds. This future marsh, however, will certainly have a mosaic of habitats centered around tidal brackish water marsh. Much of the new marsh will be drained by channels that should gradually recover their historic dendritic nature and be kept open by strong tidal action.

# Effects on Fishes of Large-Scale Change

In the broadest sense, the creation of more aquatic habitat in the Delta and Suisun

Marsh will result in a net increase in numbers and biomass of fish, once the initial flooding period is past. The important question is what will happen to the species that people care most about (Table 1). These are native species that are listed as threatened or endangered or are in severe decline or fishes that support fisheries. The effects suggested in the following accounts are highly speculative but based on extensive knowledge of the fishes, which are well studied (Moyle 2002; see also Moyle et al. 2004; Bennett 2005; Nobriga et al. 2005; Williams 2006).

### **Delta Smelt**

The single most important species from the viewpoint of affecting management of water in the Delta is the delta smelt, which is listed as threatened by both state and federal governments and is on the verge of extinction (Bennett 2005). It has a 1-year life cycle, is a pelagic planktivore, and is endemic to the SFE; it spawns in the Delta and rears in Suisun Bay and Marsh (Moyle 2002; Bennett 2005). Under multiple levee breach scenarios, most delta smelt will likely be sucked into the rapidly filling islands, whether they were upstream spawning in the Delta, downstream rearing in Suisun Bay, or moving between these habitats. A few delta smelt might be able to avoid displacement if they were located in the distant peripheral habitats such as the mouth of the Napa River, Montezuma Slough, or Cache Slough in the north Delta (Hobbs et al. 2007). The DRMS study (DWR 2007) predicts that many, if not most, fish sucked into the flooding islands will die of stress, especially that created by particulate matter in the water, which can abrade gills, and by high turbidity. The delta smelt, as a small (<9 cm total length [TL]) delicate, midwater, visual feeder, would seem especially vulnerable to these conditions. However, data are lacking to support the DRMS flood mortality hypothesis. Previous levee breaches on single islands have not been accompanied by reports of fish kills, but no one was looking in the haste to repair the levees and pump out the islands. It seems unlikely, however, that a complete fish kill would result from filling process, given the volumes of water involved and the nature of the matter (organic matter, mainly peat particles) most likely to be suspended. The filling could be most disastrous for delta smelt if they were spawning because it would draw them away from suitable spawning areas and would likely create hydrodynamic conditions (e.g., diminished tidal range in channels) that would make return difficult. Likewise, surviving larval smelt would likely find unfavorable conditions for feeding in the newly filled islands and could starve before large populations of microzooplankton (especially rotifers and copepods) developed.

Assuming massive blooms of toxic algae (e.g., Microcystis spp.) do not occur and that stockpiles of toxic materials have been removed before flooding, a month or so after island filling and hydrodynamic stabilization, conditions for plankton feeding fish such as smelt should start becoming favorable, with the development of blooms of one or more species of copepods and/or cladocerans. Delta smelt that survived up to this period in the islands should then find conditions extremely favorable for growth and survival, especially in islands that maintained salinities of less than 2 mg/L and temperatures of less than  $20^{\circ}$ C. Thus, the impact of a large-scale levee breach event on delta smelt depends in good part on the timing of the event. Presumably, a higher proportion of the population would be able to survive an event in July-November (when they are rearing in Suisun Bay) than in December-June (when they are spawning in the Delta).

In the long run, however, permanently flooded islands in the right place could increase the amount of favorable habitat for delta smelt. If a flooded island had conditions (such as those that exist in Nurse Slough in Suisun Marsh) that excluded dominant invasive benthic species, it would likely become highly productive pelagic habitat, habitat that is apparently in short supply for smelt at times today (Bennett 2005; Hobbs et al. 2006). Delta smelt would presumably also benefit from a flooded Suisun Marsh as rearing habitat, if flooding increased productivity of intersecting channels, especially Montezuma and Suisun sloughs, and salinity fluctuations at the right scale of time and space reduced the impacts of invasive species.

One indirect positive effect on delta smelt of large-scale island flooding would be that the large pumps of the State Water Project and the federal Central Valley Project in the south Delta would be shut down for long periods of time. This would happen because of salt water at their intakes as the result of flooding islands drawing in salt water from Suisun Bay and beyond. Because, in some years, pumping from the two plants can negatively affect delta smelt populations through entrainment and other effects (Bennett 2005), shutting down the pumps will remove one potential major source of mortality, perhaps compensating for some of the flooding mortality.

### Longfin Smelt

Longfin smelt have a 2–3-year life cycle, much of which is spent in San Francisco Bay and/or the Gulf of the Farallons, outside the Golden Gate (Moyle 2002; J. Rosenfield, Aquatic Restoration Consulting, unpublished analysis). They spawn in the western Delta in winter and often spend the first year of their life in Suisun Bay and Marsh. Being anadromous and iteroparous with up to three spawning age-classes, they are less vulnerable to extirpation by a large-scale event than delta smelt. Like delta smelt and other planktivores, however, longfin smelt have suffered a large decline in their population in recent years. Thus large-scale levee collapse in the Delta could initially harm longfin smelt, as indicated above for delta smelt, although at least some longfin smelt would have lower vulnerability because of their distance from the flooded islands. For more than half the year (May-November), most longfin smelt would be beyond the likely reach of a flooding event. Permanently flooded islands in the western Delta could ultimately become important rearing habitat for larval and juvenile longfin smelt, depending on whether large zooplankton populations develop. Increased productivity of sloughs/channels in

Suisun Marsh would presumably also benefit longfin smelt.

### Striped Bass

With high fecundity, iteroparity, large size, and a life span of 20+ years, nonnative striped bass have a high capacity to survive environmental disasters. Nevertheless, they have suffered a long-term decline in the SFE, although they still support a valuable fishery (Moyle 2002). In the SFE, striped bass migrate 125-200 km upstream to spawn in the Sacramento River in late April-early June. The embryos drift downstream and hatch about the time they reach Suisun Bay, where the larvae rear at low salinities. Juveniles rear throughout the estuary but seem to be most abundant in Suisun Marsh and Bay, where they feed on zooplankton and small fish. By the time they exceed 10 cm TL, they have largely switched to feeding on small fish (Feyrer et al. 2003). Adult striped bass are largely piscivorous. Adults will spend their entire life in the SFE, especially in San Francisco Bay, but when ocean conditions are right, some will go out into the ocean as well (Moyle 2002).

Overall, striped bass populations seem relatively immune to the negative effects of large-scale levee breaching. If breaching occurs in early summer, then large numbers of larvae and juveniles could die, but in following years, they would presumably benefit from increased pelagic habitat, especially if portions of it were highly productive of zooplankton and small fish. Larger juveniles and adults are strong swimmers and could presumably quickly leave a submerged island after the initial event, assuming they survived the flooding event itself. They could also remain in the vicinity of levee breaches to take advantage of the small fish moving through them, as they do now on existing flooded islands such as Frank's Tract.

### Sacramento Splittail

Splittail are largely confined today to the SFE, where they rear in Suisun Marsh and other places with fresh to brackish water sloughs (Moyle et al. 2004). Adults, which live up to 9 years, migrate up river to spawn on floodplains or edgewater habitat in or just above the Delta (Moyle et al. 2004). Timing of spawning depends on timing of natural flooding, usually intermittently between late January and early May. Juvenile splittail rear on the floodplain and remnant channel habitats for a month or so and then migrate rapidly downstream to brackish rearing areas, where they feed on zooplankton and benthos.

During a major island flooding event, many splittail are likely to be drawn in. However, many others would remain in place because of living in small sloughs distant from the Delta and also because they are strong swimmers. If the levee breaching occurred in conjunction with natural high flows in January-May, large numbers of migrating adult or juvenile splittail could be captured. Although sudden entrainment on the flooded islands could result in high mortality, the high tolerance of splittail for poor water quality (low dissolved oxygen, high turbidity, variable salinities, etc.) suggest adults and large juveniles are likely to survive the experience. The flooded islands are not likely to be great habitat for splittail until significant invertebrate fauna develops, especially amphipods and mysid shrimp. However, permanently flooded islands that remain brackish enough to exclude Brazilian waterweed should ultimately become suitable habitat for splittail, especially shallower areas.

### **Chinook Salmon**

Four runs of Chinook salmon pass through the SFE on their way upstream to spawn in the Sacramento River: fall run, late-fall run, winter run, and spring run (Moyle 2002). All runs are depleted from historic numbers, and the winter and spring run ESUs are listed as endangered and threatened, respectively. The fall run is supported in good part by hatchery production and occurs in tributaries to the lower San Joaquin River, as well as the Sacramento River. Fry and smolts of the salmon are found seasonally in the estuary, on their way downstream to the ocean. When the Delta was a giant tidal marsh, it was likely a major rearing area for fry before they moved out to sea as smolts. At the present time, rearing habitat for fry in the SFE is minimal and fry survival is low; higher returns of adults from hatchery fry generally occurs when the fry are planted in the SFE below the Delta (Brandes and Mc-Clain 2001; Williams 2006). Highest survival of fry and smolts in the SFE occurs in years of high outflow in both the Sacramento and San Joaquin rivers (Newman and Rice 2002), suggesting that it benefits the fish to move through the Delta rapidly. Survival of fry and smolts is also highest when the fish are largely confined to the main river channels and do not get moved into the central Delta (Brandes and McClain 2001). Although juvenile salmon can be captured in SFE at almost any time of year, most movement is in December through April.

As with other fish, the immediate effect of a major levee failure in the Delta depends on the time of year in which it occurs, with the greatest impact likely to be in February-April, assuming migrating juvenile salmon, especially fry, sucked into the flooded islands would mostly die. The effect would be greater for San Joaquin River salmon than for Sacramento River fish because there would more likely be a continuous river channel for the fish to follow on the Sacramento side, due to location and greater flows. Once island lagoons have become established, they would generally be unfavorable habitat for juvenile salmonids because they would contain little of the shallow water edge habitat preferred by juvenile salmon. Instead, they would be open-water or weed-choked and contain fairly high densities of predators such as striped bass or largemouth bass. The effect would be determined in large part by how easily it would be for juvenile salmon to be carried into the lagoons from the rivers and how easy it would be to escape from them. Once the lagoons were established, high outflows down both rivers would minimize their effects, while low outflows would increase the likelihood that juvenile salmon would wind up in them, especially on the San Joaquin side of the Delta. It is possible that Suisun Marsh will be heavily used by juvenile salmon once it floods because much of it will be productive shallow brackish-water habitat.

Effects on adult salmon would presumably be small because of their focus on swimming upstream through the Delta, although there would no doubt be some mortality and straying if breaches occur during a period of significant migration.

# Largemouth Bass

Largemouth bass are introduced piscivores that have greatly expanded their populations in the Delta following the invasion of Brazilian waterweed (Brown and Michniuk 2007). The waterweed provides habitat for the bass by creating cover for juvenile and adults, reducing flow rates through channels, and causing sediment to settle from the water, resulting in clearer water. It is the most visible species of a complex of alien pond species that thrive in waterweed-dominated freshwater sloughs, including redear sunfish Lepomis microlophus, bluegill L. macrochirus, white catfish Ameiurus catus, brown bullhead A. nebulosus, and common carp Cyprinus carpio. By and large, these are the same species that are dominant in upstream reservoirs (Moyle 2002). Largemouth bass and associated species will expand their populations further in flooded freshwater islands where Brazilian waterweed becomes established. While these species can survive in brackish water habitat, most of them avoid it and would thus be present in only low numbers in brackish lagoons without dense beds of waterweed.

# Marine Fish

San Francisco Bay supports a diverse fauna of marine fishes that includes most of the common species found along the central California coast. The abundances of different species fluctuate both in response to ocean conditions and to freshwater flows into the bay (Armor and Herrgesell 1985). Not surprisingly, some of the most abundant species are fairly euryhaline, such as Pacific herring, northern anchovy *Engraulis mordax*, Pacific staghorn sculpin *Leptocottus armatus*, yellowfin goby *Acanthogobius flavimanus*, and starry flounder *Platichthys stellatus*. Juveniles of the euryhaline forms frequently appear in the upper estuary, especially in Suisun Bay and Marsh, usually during periods of low river flows (Matern et al. 2002). Thus, the expanded brackish water habitat in the upper estuary is likely to increase habitat space for euryhaline marine species, especially during dry periods.

# **Overall Fish Responses**

It should be evident from the above descriptions that responses of fish species to large-scale island flooding will be highly variable, a reflection of the mixed assemblages of native and alien fishes interacting in a highly altered, complex habitat. Thus, it is likely that unanticipated responses to the changed conditions will also occur. For example, inland silverside Menidia beryllina are now abundant throughout the Delta and Suisun Marsh, so it is likely that they will colonize some of the newly flooded areas, depressing other fishes through predation and competition (Bennett and Moyle 1996). In addition, new alien invaders could cause major shifts in abundance of established species. For example, two piscivores are poised to invade the SFE: northern pike Esox lucius and white bass Morone chrysops (Moyle 2002; Lund et al. 2007). Despite these uncertainties, the general patterns of fish response to sudden large-scale flooding would roughly be the following:

- Fishes within the suction zone of Delta levee breaks (which could be a large, given the capacity of the islands to accept large volumes of water) would be sucked into the island with some mortality from sediment in the water column, sudden changes in water quality (salinity, temperature, pesticide concentrations, etc.), and/or other factors associated with the sudden movement of large volumes of water. The species affected would depend on time of year of flooding and the location of the flooded islands.
- 2. Once the waters had settled down, there would likely be a brief initial period of low

plankton densities, followed by blooms first of phytoplankton, then zooplankton, perhaps within a period of 1–3 months.

- 3. In the years following the floods (1-5 years), new lagoons formed from island flooding would assume the character of areas in the SFE with similar depths, flows, and salinities. Thus, those in the more eastern and central parts of the Delta would likely become dominated by Brazilian waterweed and alien freshwater fishes. Lagoons in the western Delta that maintained low (2–10 parts per thousand) salinities most of the time would have conditions similar to those in Suisun Bay. Planktonic productivity is greatly reduced in Suisun Bay by the filter-feeding overbite clam, but it still serves as an impor tant rearing area for pelagic fishes, at least in some areas (Hobbs et al. 2006). These areas would provide expanded habitat for euryhaline species such as striped bass, longfin smelt, and delta smelt, as well as additional feeding areas for sturgeon Acipenser spp., splittail, and other benthic feeders that consume clams and their associated faunas. A few deep lagoons that were created in intermediate locations, where salinities and other conditions were highly variable through the interactions of river inflow and tidal exchange, could become highly productive systems supporting dense populations of plankton and planktivores, including delta smelt and striped bass. Such areas could become a source for enhanced populations of euryhaline fishes.
- 4. Over the longer term (5+ years), conditions in the lagoons would change further as levees continued to erode, parts of the lagoons fill in with sediment, and islands not flooded previously give way to new hy draulic forces created by the lagoons (waves, changed current patterns, etc.), assuming that most levees were not repaired. Essentially, much of the central and south Delta could become one large embayment, similar to Suisun Bay but fresher on its upper end. By size alone,

this area would increase the amount of habitat for fishes. Presumably, the in creased habitat would increase popula tions of some of the desirable open-water species, although much of it would be dominated by waterweed and alien pond fishes or by relatively low productivity habitat depleted of nutrients by bivalve grazing. In this period, Suisun Marsh would probably also have become at least partially flooded, with the potential for large increases in tidal brackish water habitat, potentially favorable to desirable species such as longfin smelt, delta smelt, splittail, striped bass, and possibly juvenile Chinook salmon.

Thus the long-term overall effect of massive flooding would likely be to increase the populations of at least some desirable species while greatly increasing the abundances of less desirable aliens, such as largemouth bass and common carp. While there are fisheries for such species, they are deemed less desirable because the fish are not native and have large populations outside the SFE, unlike the species currently deemed more desirable.

# Improving the Estuary for Fish

The above speculative discussion is based on the scenario that California will continue on its present track of managing the Delta environment through a combination of applying temporary levee repairs, poorly regulating invasive species, removing large quantities of freshwater, managing Suisun Marsh as a lowsalinity system, and monitoring desirable species as they decline. In short, it is likely that management of the SFE will continue as usual until large-scale levee collapse forces largescale action, much of it likely to be poorly planned and futile in the long run (Lund et al. 2007). As indicated above, the massive collapse of levees in the Delta and Suisun Marsh would not be a long-term disaster for many fishes, and fisheries and could even be a benefit. Large-scale levee collapse could be a disaster for the California economy, however, mainly because it would disrupt the state's

water supply system and other infrastructure (Lund et al. 2007). Thus fixing the Delta and Suisun Marsh before an inevitable disaster is highly desirable, and several processes are underway at the state level to determine options. Lund et al. (2007) present nine scenarios for a future Delta and Suisun Marsh, five of which they regard as feasible. Four of the five protect water supply while allowing some portion of the Delta to remain as habitat for native fish and other desirable organisms. The five options provide suggestions for significantly improving the habitat in the Delta and Suisun Marsh for desirable species, provided that action is taken before large-scale levee collapse occurs. The options of Lund et al. (2007) are only a tiny fraction of the hundreds of permutations and combinations of actions that could be taken; they are designed to represent examples of the reasonable alternatives possible to provide a visualization of management options.

Here I will not discuss the alternatives, but instead discuss actions that will allow fishfriendly habitat to develop while not necessarily reducing most of the services to humans that the SFE provides. These actions could be part of any scheme that seeks to modify the Delta to improve or protect its water supply functions as well its ecological functions. The general approach towards creating an environment in the SFE that is more friendly to desirable fish species (and other biota) presented here is to increase habitat heterogeneity. The basic concept is as follows: as much area as possible should support conditions resembling those of the historic SFE, especially in the Delta and Suisun Marsh, because these are the conditions to which the native fishes are adapted. However, the improved habitats are likely to be in different locations than they were historically because of changed elevations due to subsidence and sea level rise. Thus habitats once present in the deeply subsided central Delta will have to be located in smaller patches in the less-subsided peripheries (Figure 2).

A key to increasing habitat heterogeneity is to have as much area as possible where fluctuations in salinity discourage freshwater and brackish water invaders (especially clams) while favoring desirable (mainly native) pelagic species. The exact extent, frequency, and range of salinity fluctuation needs to be determined by further studies of key organisms (both desirable and undesirable species), but present distributional limits of the organisms suggest that fluctuations required are likely to be in the range of 0–12 mg/L over 1–2 years, with high and low values sustained for 4–5 months at a time.

The following are some general, largescale actions that could improve habitat heterogeneity and create areas with desirable conditions of water quality, including fluctuating salinity. This list is neither complete nor inclusive (Lund et al. 2007).

Suisun Marsh.-This region of the SFE is 1. headed inexorably to becoming brackish tidal marsh, unless huge amounts of money are spent on raising and reinforcing levees; such action may not even be possible as a permanent solution, given the compressibility of the marsh soils underlying the levees. Most of Suisun Marsh is currently intensely managed in diked sections, principally as freshwater habitat for waterfowl. Even under these conditions, the intervening sloughs, especially in the few undiked areas, provide good habitat for desirable fish (Matern et al. 2002; R. E. Schroeter, University of California, Davis and P. B. Moyle, unpublished data). Improving the Marsh for fish will require systematically breaching or removing many levees, reconstruction of at least part of the original marsh drainage system, and removal of infrastructure. Models for the creation of new tidal (and subtidal) marsh areas can be found in the currently undiked section of Rush Ranch that is part of the San Francisco Bay National Estuarine Research Reserve (http://rtc.sfsu.edu/nerr/sf\_bay\_reserve) and by an ongoing experimental levee breach at Blacklock (http://www. iep.water.ca.gov/suisun/restoration). Even after restructuring the marsh, it may be desirable to continue to operate the large salinity control gates at the upstream

end of the Montezuma Slough to manage water quality. This slough and Suisun Slough are the deep (2–6 m) main arteries of the marsh and the principal habitats of pelagic fishes such as delta and longfin smelt, so it may be possible to operate the gates to increase the ranges of salinity that favor these species and discourage undesirable alien species.

- Cache Slough.-Cache Slough and adjoin-2. ing areas make up essentially the northwest corner of the Delta. The region is of high restoration potential as tidal freshwater marsh and slough habitat because (1) island subsidence is low compared to other parts of the Delta, (2) it maintains much of its original drainage pattern, even though most of the channels are leveed and some artificial cross channels exist, (3) it is a major spawning and rearing region for delta smelt, (4) it has strong tidal currents that move water from the Sacramento River in and out of its channels, (5) it drains the lower end of the Yolo Bypass (next section), and (6) it contains the large, recently (1998) flooded Liberty Island that is being used as an example of a passive restoration project (http://www.delta.dfg.ca.gov/ jfmp/libertyisland.asp). The region can be relatively easily converted into an expanded version of the favorable tidal habitat for desirable fishes (as well as for waterfowl and other biota) through levee breaches, elimination of cross channels, and other projects that improve circulation. It is also a region where it should be possible to create favorable habitats for delta smelt, mainly spawning beaches and productive rearing areas for larvae that also discourage their egg and larval predators, especially inland silverside.
- 3. *Yolo Bypass.*—To keep the city of Sacramen to from flooding, an artificial floodplain, the Yolo Bypass, was constructed in the 1930s. Essentially, when the Sacramento River reaches a certain stage, it spills over a low wall (Fremont Weir) into the 24,000-ha, 64-km-long bypass (Sommer at al. 2001a, 2001b). The flood waters flow

down the bypass and re-enter the Sacramento River via Cache Slough. The principal permanent water channel in the Yolo Bypass is the Toe Drain, which runs along the levee on the eastern side. About half the bypass is in the Delta, and the Toe Drain in this region is a leveed tidal slough, a branch of Cache Slough. The land in the bypass is a mixture of farmland and wildlife areas, but when it floods, it becomes high quality rearing habitat for Chinook salmon fry and splittail, as well as other fishes. The flood waters may also mobilize nutrients from the bypass, helping to support Delta food webs. From an ecological perspective, a problem with the Yolo Bypass is that is does not flood, even partially, every year. Construction of a gate on the Fremont Weir would permit limited controlled flooding from the Toe Drain every year, improving growth and survival of salmon and splittail and improving flows through Cache Slough.

- 4. San Joaquin floodplain.-The channel of the San Joaquin River above and through the Delta is highly channelized and provides little favorable habitat for desirable fishes: the water tends to be too deep and polluted in some places (e.g., Stockton Ship Channel) and dominated by invasive aquatic plants and invertebrates in others. One way to improve the habitat for fish is to create one or more bypasses like the Yolo Bypass. This would involve removing or breaching levees from islands (e.g., Stewart Tract) that border the river to promote periodic flooding. Such floodplain habitat may be especially beneficial as rearing habitat for juvenile salmon example of the benefits of restored floodplain in the Delta is provided by the small restored floodplain along the lower Cosumnes River, on the eastern fringe of the Delta, which has proved to be beneficial to several native fishes and provides experience in methods of modifying agricultural lands into fish-friendly floodplains (Moyle et al. 2007).
- 5. *Managed Delta islands.*—The previous four actions focused on areas at the edges of

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the upper estuary because of the assumption that subsided islands of the Delta will fill with water and will become a large open-water system over which little control can be exerted, aside from regulating freshwater inflow under some conditions (Lund et al. 2007). However, with some foresight, it may be possible to retain the levee integrity of some islands, by making them into islands of regulated aquatic habitat. Essentially, this concept follows the lead of Delta Wetlands, a private group that has sought to use Delta islands for water storage and wildlife habi-(http://www.deltawetlands.com/). tat The levees of habitat islands would presumably be reinforced on the inside by being gradually sloped towards the interior and planted with native vegetation to stabilize the soils. Gates on the upper and lower ends of the islands could be used to regulate water quality on the islands, including salinity. This concept might be especially useful for islands (e.g., Twitchell Island) in the western Delta located close the Sacramento River, so that salinity could be manipulated by trapping either river or tidal water as needed (as is currently done with tidal gates in Suisun Marsh). The islands of water could then be managed as nursery areas for desirable fishes. Ideally, the gates would also allow an island to be dried out or pumped out completely if necessary to control undesirable alien species.

Prevention of new alien species invasions.-6. A major stochastic factor that can negatively affect efforts to create a more desirable ecosystem in the Delta is the invasion of alien species that become agents of ecosystem change, such as overbite clam or Brazilian waterweed. Some known harmful invaders are likely to arrive in the near future (Lund et al. 2007). Thus, part of any program of ecosystem creation must include vigorous efforts to exclude new invaders from all sources, including the shipping, horticultural, pet, and aquaculture industries. There should also be in place a mechanism that allows quick action to eradicate a new invader before it spreads from the site of invasion.

# Conclusions

The San Francisco Estuary, especially the Delta and Suisun Marsh, is predicted to undergo drastic change in the next 50 years, with the probability of a major infrastructure disaster increasing through time, just on the basis of earthquakes and land subsidence alone (Mount and Twiss 2005). When sea level rise and increased frequency of flooding due to climate change are factored in, major change in the coming decades seems inevitable. The disaster scenario, however, is mainly for human goods and services, especially water supply to urban and agricultural areas. From a fish perspective, the ecological changes resulting from flooding of numerous Delta islands and Suisun Marsh are likely to create conditions that should be at least as favorable for desirable species at present conditions, after a period of possibly high mortality created by the initial flooding events. Potentially more favorable habitat will result from a disaster scenario simply because there will be increased area of open water and tidal marsh, some of it with enough fluctuation in salinity and other factors to be suitable habitat for delta smelt, striped bass, and other pelagic species now in decline. There is much uncertainty, however, about how much favorable habitat will be created under disaster scenarios because alien fish and invertebrates dominate so many current habitats. Thus, controlling where possible the way habitat changes, as suggested above and in Lund et al. (2007), could have major ecosystem benefits while being highly compatible with changing ways in which services provided by the Delta are delivered, especially water supply. The principal basis for action is to increase habitat heterogeneity over present conditions, as well as to increase the total amount of aquatic habitat. No matter what actions are taken, there will be a high degree of uncertainty in the ecological benefits. Nevertheless, the present situation in the estuary represents an unprecedented opportunity to reverse the impacts of more than 150 years of negative ecological change.

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# References

- Armor, C., and P. Herrgesell. 1985. Distribution and abundance of fishes in the San Francisco Bay Estuary between 1980 and 1982. Hydrobiologia 129:211–227.
- Bay Institute. 1998. From the Sierra to the sea: the ecological history of the San Francisco Bay– Delta Watershed. Bay Institute of San Francisco, Novato, California.
- Bennett, W. A. 2005. Critical assessment of the delta smelt population in the San Francisco Estuary, California. San Francisco Estuary and Watershed Science [online serial] 3(2), Article 1.
- Bennett, W. A., and P. B. Moyle. 1996. Where have all the fishes gone: interactive factors producing fish declines in the Sacramento–San Joaquin Estuary. Pages 519–542 in J. T. Hollibaugh, editor. San Francisco Bay: the ecosystem. American Association for the Advancement of Science, Pacific Division, San Francisco.
- Brandes, P. L., and J. S. McClain. 2001. Juvenile Chinook salmon abundance, distribution, and survival in the Sacramento–San Joaquin Estuary. Pages 39–137 in R. L. Brown, editor. Contributions to the biology of Central Valley salmonids, volume 2. California Department of Fish and Game Fish Bulletin 179.
- Brown, L. R., and D. Michniuk. 2007. Littoral fish assemblages of the alien-dominated Sacramento–San Joaquin Delta, California, 1980–83, 2001–2003. Estuaries and Coasts 30:186–200.
- Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555–557.
- Dettinger, M. D. 2005. From climate-change spaghetti to climate-change distributions for 21st century California. San Francisco Estuary and Watershed Science [online serial] 3(4), Article 4.

- DWR (Department of Water Resources). 1993. Sacramento–San Joaquin Delta atlas. California Department of Water Resources, Sacramento.
- DWR (Department of Water Resources). 2007. Delta risk management strategy report. Available: www.drms.water.ca.gov (January 2008).
- Feyrer, F., B. Herbold, S. A. Matern, and P. B. Moyle. 2003. Dietary shifts in a stressed fish assemblage: consequences of a bivalve invasion in the San Francisco Estuary. Environmental Biology of Fishes 67:277–288.
- Herbold, B., A. D. Jassby, and P. B. Moyle. 1992. Status and trends report on aquatic resources in the San Francisco Estuary. U.S. Environmental Protection Agency, San Francisco Estuary Project, Oakland, California.
- Hobbs, J. A., W. A. Bennett, and J. E. Burton. 2006. Assessing nursery habitat quality for native smelts (Osmeridae) in the low-salinity zone of the San Franscisco Estuary. Journal of Fish Biology 69:907–922.
- Hobbs, J. A., W. A. Bennett, J. Burton, and M. Gras. 2007. Classification of larval and adult delta smelt to nursery areas by use of trace elemental fingerprinting. Transactions of the American Fisheries Society 136:518–527.
- Hollibaugh, J. T. editor. 1996. San Francisco Bay: the ecosystem. American Association for the Advancement of Science, Pacific Division, San Francisco.
- Kimmerer, W. J. 2002. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages. Marine Ecology Progress Series 243:39–55.
- Light, T., and M. P. Marchetti. 2007. Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. Conservation Biology 21:434–446.
- Little Hoover Commission. 2005. Still imperiled, still important. The Little Hoover Commission's review of the CALFED Bay-Delta Program. Little Hoover Commission, Sacramento, California.
- Lund, J., E. Hanak., W. Fleenor, R. Howitt, J. Mount, and P. Moyle. 2007. Envisioning futures for the Sacramento–San Joaquin Delta. Public Policy Institute of California, San Francisco.
- Matern, S. A., P. B. Moyle, and L. C. Pierce. 2002. Native and alien fishes in a California estuarine marsh: twenty-one years of changing assemblages. Transactions of the American Fisheries Society 131:797–816.
- Mount, J. A., and R. Twiss. 2005. Subsidence, sea level rise, and seismicity in the Sacramento-

San Joaquin Delta. San Francisco Estuary and Watershed Science [online serial] 3(1), Article 5.

- Moyle, P. B. 2002. Inland fishes of California. Revised and expanded. University of California Press, Berkeley.
- Moyle, P. B., R. D. Baxter, T. Sommer, T. C. Foin, and S. A. Matern. 2004. Biology and population dynamics of Sacramento splittail (*Pogonichthys macrolepidotus*) in the San Francisco Estuary: a review. San Francisco Estuary and Watershed Science [online serial] 2(2), Article 1.
- Moyle P. B., P. K. Crain, and K. Whitener. 2007. Patterns in the use of a restored California floodplain by native and alien fishes. San Francisco Estuary and Watershed Science [online serial] 5(3), Article 1.
- Newman, K. B., and J. Rice. 2002. Modeling the survival of Chinook salmon smolts outmigrating through the lower Sacramento River system. Journal of American Statistical Association 97:983–993.
- Nichols, F. H., J. E. Cloern, S. N. Luoma, and D. H. Peterson. 1986. The modification of an estuary. Science 231:567–573.
- Nobriga, M. L., F. Feyrer, R. D. Baxter, and M. Cho-

thowski. 2005. Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies, and biomass. Estuaries 28:776–785.

- Schroeter, R. E., and P. B. Moyle. 2006. Alien fishes in California's marine environments. Pages 611–620 in M. H. Horn, L. G. Allen, and D. Pondella, editors. Ecology of California marine fishes. UC Press, Berkeley, California.
- Sommer, T. R., W. C. Harrell, M. Nobriga, R. Brown, P. B. Moyle, W. J. Kimmerer, and L. Schemel. 2001a. California's Yolo Bypass: evidence that flood control can be compatible with fish, wetlands, wildlife and agriculture. Fisheries 58(2):325–333.
- Sommer, T. R., M. L. Nobriga, W. C. Harrell, W. Batham, and W. J. Kimmerer. 2001b. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 58:325–333.
- Williams, J. G. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. San Francisco Estuary and Watershed Science [online serial] 4(3), Article 2.