Habitat Variability and Complexity in the Upper San Francisco Estuary

Peter B. Moyle, William A. Bennett, William E. Fleenor, and Jay R. Lund

Delta Solutions
Center for Watershed Sciences, University of California, Davis
http://deltasolutions.ucdavis.edu

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Abstract
The San Francisco Estuary is a complex estuarine ecosystem. High variability in environmental conditions in both space and time once made helped make the estuary highly productive for native biota, especially the Delta and Suisun Bay. Present conditions discourage native species, providing a rationale for restoring estuarine variability and habitat complexity, recognizing that restoration of variability and complexity is only a partial solution to all the estuary's ecological problems. Achieving a variable, more complex estuary requires establishing seaward gradients in salinity and other water quality variables, diverse habitats throughout the estuary, more floodplain habitat along inflowing rivers, and improved water quality. These goals in turn encourage policies which: (1) establish internal Delta flows that create a tidally-mixed, upstream-downstream gradient (without cross-Delta flows) in water quality; (2) create slough networks with more natural channel geometry and less diked rip-rapped channel habitat; (3) improve flows from the Sacramento and San Joaquin rivers; (4) increase tidal marsh habitat, including shallow (1-2 m) subtidal areas, in both fresh and brackish zones of the estuary; (5) create/allow large expanses of low salinity (1-4 ppt) open water habitat in the Delta; (6) create a hydrodynamic regime where salinities in parts of the Delta and Suisun Bay and Marsh range from near-fresh to 8-10 ppt periodically (does not have to be annual) to discourage alien species and favor desirable species; (7) take species-specific actions that reduce abundance of non-native species and increase abundance of desirable species; (8) establish abundant annual floodplain habitat, with additional large areas that flood in less frequent wet years; (9) reduce inflow of agricultural and urban pollutants; and (10) improve the temperature regime in large areas of the estuary so temperatures rarely exceed 20°C during summer and fall months. These actions collectively provide a realistic if experimental approach to achieving flow and habitat objectives to benefit desirable species. Some of these goals are likely to be achieved without deliberate action as the result of sea level rise, climate change, and levee failures, but habitat, flow restoration and export reduction projects can enhance a return to a more variable and more productive ecosystem.

Introduction

The San Francisco Estuary, especially the Delta, must be more variable in space and time than we have allowed it to be in recent years in order to support desirable aquatic species, such as delta smelt and striped bass (Lund *et al*. 2007, Moyle and Bennett 2008). Changes in water management, a more intricate network of channel geometry, as well as improved quantity and quality of inflows from the San Joaquin and Sacramento rivers are key actions needed to jolt the estuary into a more desirable state. The basic rationale for the preceding statements is that unmodified estuaries are highly variable and complex systems, renowned for their high production of fish and other organisms (McClusky and Elliott 2004). The San Francisco Estuary, however, is one of the most highly modified and controlled estuaries in the world (Nichols *et al.* 1986). As a consequence, the estuarine ecosystem has lost much of its former variability and complexity and has recently suffered major declines of many of its fish resources (Sommer *et al.* 2007). This reflects a very basic problem: when an estuary loses the connections and interactions between abundant stationary habitat, such as marshes and floodplains, and dynamic variables, such as salinity, its productivity declines (Peterson 2003).

The environmental variability that characterizes productive estuaries, and all other complex productive ecosystems can occur at various spatial and temporal scales (Kimmerer *et al.* 2008). The idea that physical variability at various scales (*i.e.*, disturbance) is key for maintaining ecosystem complexity and high biodiversity is widely accepted, and deeply imbedded in ecology textbooks as the fundamental factor influencing the evolution and ecological interrelationships among all levels of life from individuals to ecosystems (e.g., Krebs 2008). What is relatively new, however, is for landscape managers to recognize the value of incorporating such natural environmental variability into management practices and goals for ecosystems from forests to estuaries, and to recognize this may be essential for recovering for highly altered ecosystems. For example, the concept of the "natural flow regime" (Poff *et al*. 1997) is increasingly regarded as an important strategy for establishing flow regimes to benefit native species in regulated rivers (Postel and Richter 2003; Poff *et al*. 2007; Moyle and Mount 2007). For estuaries worldwide, the degree of environmental variability is regarded as fundamental in regulating biotic assemblages (McLusky and Elliott 2004). Many studies have shown that estuarine biotic assemblages are generally regulated by a combination of somewhat predictable changes (*e.g*., tidal cycles, seasonal freshwater inflows) and stochastic factors, such as recruitment variability and large-scale episodes of flood or drought (*e.g*., Thiel and Potter 2001). The persistence and resilience of estuarine assemblages is further decreased by various human alterations, ranging from diking of wetlands, to regulation of inflows, to invasions of alien species (McLusky and Elliott 2004, Peterson 2003). This paper reviews the importance of these patterns in the San Francisco Estuary to demonstrate why habitat complexity and variability should be considered in schemes to manage or change the estuary.

We have four objectives for this paper: 1) to briefly characterize estuaries in general, describe how variability and complexity define them, and then discuss why these factors are so important to native species; 2) to describe why salinity is such a useful and available indicator of estuarine heterogeneity; 3) to describe the past, present, and potential future variability and complexity of the San Francisco Estuary, in relation to adaptations of key fish species; 4) to recommend water and habitat management actions to re-establish variability and complexity and discuss policy implications of these actions.

Estuaries

Estuaries are generally recognized as places where fresh water from the land mixes with salt water from the coastal ocean within a semi-confined area (Pritchard 1967). From the perspective of the San Francisco Estuary, a somewhat better definition is that of Fairbridge (1980) who defines an estuary as "an inlet of the sea reaching into a river valley as far as the upper limit of tidal rise." This definition emphasizes the strong tidal nature of estuaries, even in areas that are primarily fresh water (such as the Delta). The natural history of estuaries involves large populations of fish, invertebrates, aquatic birds, and mammals, as well as interactions with the surrounding terrestrial systems. Their human history involves many centers of civilization origin, such as Egypt, China, and Mesopotamia, as well as many European countries, which established major cities on estuaries in part because they provide water access to the inland rivers and oceanic transport and in part because they were highly productive of edible organisms. Unfortunately, the rise of urban areas almost always results in mistreatment of estuaries through pollution, sedimentation, removal of water, diking and draining of adjacent wetlands for farming, as well as over-harvest of estuarine-dependent fish and invertebrates (Lotze *et al*. 2006). Not surprisingly, estuaries worldwide are both among the world's most valuable ecosystems and among the most damaged (Costanza *et al.* 1997; Lotze *et al.* 2006). The growing awareness of the value of estuarine systems is reflected in the many efforts to restore some of the ecosystem services they once provided, especially fisheries (e.g., the federal Estuary Restoration Act of 2000[PL 106-457 title 1]).

Restoration of estuarine ecosystem services requires re-establishing, at multiple scales, physical-chemical variability in time and space as well as habitat complexity and diversity (see next section). However, the value of variability in estuaries runs contrary to traditional resource management, which tries to *reduce* the natural variability of ecosystems to increase predictability and thereby maximize yield of goods and services valuable to humans (Pahl-Wostl 1998). Efforts to reduce variability often lead to unanticipated, and sometimes catastrophic, problems. Thus, diking and draining of estuarine marshes to build cities and farms leads to unanticipated dike failures and flooding, or fisheries declines due to loss of spawning and rearing habitat. Effluent released into estuaries can have the unintended consequence of being concentrated through tidal action and of fish becoming toxic to eat. Simplifying habitat, dredging channels, eliminating floodplains and marshes, diverting inflowing water, and bringing in alien species, cause food webs to change in unfavorable ways, fisheries to collapse, and endemic species to become threatened with extinction. Estuaries worldwide have experienced similar changes and have lost many of their desirable natural attributes, most noticeably sustainable fish populations. They also are increasingly the focus of restoration efforts (*e.g*., Henk et al 1995; NOAA 2002).

Estuarine variability and complexity

Estuarine variability and complexity arises because two dynamic systems, rivers and coastal oceans, meet in a confined geologic space. These opposing forces shape the estuarine basin through complex processes of erosion and deposition, creating a landscape of shifting channels, bays, and marshlands. Change in estuaries occurs on a continuum of space and time scales. Tidal energy from the ocean provides a regular cycle that changes water elevations and flows, with estuarine geometry and roughness governing local tidal amplitudes, flow patterns, and mixing with the inflowing fresh water. This tidal cycle can be further modified by changes in astronomical forcing, sea level, and strong winds. River inflows vary seasonally, typically with an annual high and low flow pattern, but with large inter-annual variation superimposed by climate (*i.e.,* wet years and droughts). Rivers also supply sediment to estuaries, which is reworked by river flows and tides to form the estuary's complex and shifting landscape. However, the most distinctive feature of estuaries is the variability produced by the mixing of salt water from the ocean with fresh water from the land.

Tidal mixing of fresh and salt water is a key process promoting estuarine variability (Lucas *et al*. 2006). The interaction between river and tidal flows establishes various water quality gradients between an estuary's landward and seaward margins, including gradients and mixing in freshwater portions of the estuary. Without this process, the heavier salt water would simply remain below the fresh water. Salt water mixing with sediment-laden river water also increases settling-out of clay particles by promoting particle aggregation (Krone 1979). The variability and complexity from tidal mixing is compounded by the degree to which estuarine geometry bends and shapes gradients in salinity, temperature, and other aspects of water quality. Moreover, these factors constantly change over various time scales in response to changes in river flow, sea level, barometric pressure, and winds, which together add further complexity.

For aquatic organisms, this variability can be both negative and positive. Variability in salinity, which carries with it variability in temperature, water clarity, and other water quality characteristics, implies a physiologically stressful environment for most organisms. Thus organisms living in estuaries often pay a high energetic cost to do so. The variability also means it can be hard to stay in one place; tidal flows move individuals around or expose stationary individuals to wide ranges of water quality over short time periods. Given the physiological challenges of living in an estuarine environment, many organisms are adapted specifically for living in estuaries, or have particular life history stages adapted to such variable conditions. How organisms encounter and perceive their environment determines how they are affected by it and how their life history strategy is shaped over time. Each species experiences estuarine conditions somewhat differently. For some species, environmental variability experienced by individuals is large in space and time (*i.e.*, the environment is coarse-grained), whereas other species experience relatively little variability as individuals (*i.e.*, the environment is fine-grained) with respect to their generation time and living space (Levins 1968). For example, a clam fixed to the bottom encounters the environment as coarse-grained with major shifts in water quality as the water sweeps back and forth with the tides. These changes can be stressful or even lethal. In contrast, small fish may experience the environment as fine-grained, because they can swim or adjust their buoyancy to keep themselves within a narrower water quality range; they experience physiological stress only when forced to abandon the favored range due to rapid change in physical variables (*e.g.*, temperature), risk of predation, or lack of food.

In estuaries, the life history strategies of organisms vary according to how they encounter the environment. Typically, this is dictated by how well they have adapted physiologically to withstand salt-stress over the course of their lives, or else to avoid it through behavioral adaptations. Even species that tolerate a wide range of salinities often occupy a much narrower range which is better for their growth and survival. Consequently, organisms adapted for living specifically in estuaries tend to use only a particular subset of the variable conditions, or have life history stages adapted for using different conditions at specific times (*e.g.*, seasons). Not surprisingly, estuarine fish species have diverse life history strategies. Some move in and out seasonally, usually for spawning and rearing, while others are full-time residents, with additional freshwater and marine species living at the estuary's landward and seaward margins (Moyle and Cech 2002). Because of this diversity in estuarine use, overall species richness is typically fairly high in relatively undisturbed estuaries (*ca.* 100-150 fish species for temperate estuaries), especially if measured over multiple years, because the inherent variability increases the likelihood that appropriate conditions for a wide array of organisms will always occur at some location and time within the estuary. However, at any given time only a relatively small number of fish species (5-20) dominate in terms of numbers and biomass.

Estuarine variability also is considered to be a primary factor promoting the high productivity typically observed in estuaries relative to other ecosystems (Nixon *et al.* 1986. Peterson 2003). Freshwater flow brings in nutrients that promote primary production (photosynthesis by algae), while tidal energy and turbulence circulate nutrients within the estuary. This general dispersive process promotes the growth of planktonic organisms, which form the base of food webs that include fish and other organisms of direct interest to humans. Productivity is enhanced further when the tidal water is distributed over a complex landscape, including areas of tidal marsh and floodplain within estuaries, because it picks up nutrients from flooded areas (Nixon 1988). This ecosystem "fertilization" process is often cited as a mechanism underlying *positive* relationships between freshwater flow, productivity, and fish abundance in estuaries (Nixon *et al.* 1986, Houde and Rutherford 1993). In the San Francisco Estuary, this process seems to be one of several reflected in fish-salinity relationships at the inter-annual time scale (Jassby *et al.* 1995, Kimmerer 2002). Thus, despite their relatively small geographical area, estuaries are often essential for supporting diverse marine, freshwater, and estuarine fisheries, especially because they are commonly used by larval and juvenile fish for nursery habitats (Beck *et al.* 2001).

Why variability and complexity are so important

A vast ecological literature documents the significant roles of habitat complexity and variability in promoting abundance, diversity, and persistence of species in a wide array of ecosystems[1]. This literature stresses the importance of both predictable and stochastic physical disturbances, timing and extent of resource availability, as well as the degree of connectivity among habitat patches, relative to the abilities of species to move between them. However, landscapes are not stable in their configurations through time and environmental fluctuations generally increase the duration and frequency of connections among patches of different kinds of habitat. This can increase turnover of resources, making the resources available to a shifting array of species. The variability implies that different processes interact at various scales in space and time, with the result that more species are present than would be characteristic of a hypothetical stable landscape (*e.g.,* an agricultural landscape). Therefore, ecological theory strongly supports the idea that an estuarine landscape that is heterogeneous in salinity and geometry (depth, the configuration of flooded islands, tidal sloughs, floodplains, *etc*.) is most likely to have high overall productivity, high species richness, and high abundances of desired species.

Cloern (2007) recently provided a model of how these concepts might translate to the Delta ecosystem. He extended a traditional model of an aquatic food web composed of nitrogen (N), phytoplankton (P), and zooplankton (Z) (NPZ model, Franks 2002) to represent two spatially-segregated habitats, a shallow-shoal habitat and an adjacent deep-water channel habitat. The model system was then used to explore how connectivity, or the transport of N, P, and Z between habitats, influenced overall productivity of the model food web. Given that the phytoplankton growth rate was light-limited in the model, primary production (growth of phytoplankton populations) dominated shallow-water habitat, whereas zooplankton populations dominated deep-water (light-limited) habitat. Model simulations then showed that transport of

[1] Several ecological concepts hold special promise for guiding our understanding of the importance of estuarine variability, including intermediate disturbance (Dayton 1971), contemporaneous disequilibrium (Richerson *et al.* 1970), time averaging of resource utilization (Levins 1979), the *meta-population* (Levins 1969, Gilpin and Hanski 1991) and the *meta-community* (Levins and Culver 1971, Leibold *et al*. 2004). Populations of organisms are often distributed over landscapes in isolated habitat patches, with connectivity limited by the dispersal abilities of each species. The ability of such meta-populations to persist over time at the landscape-scale is sensitive to the degree of connectedness among habitat patches and the frequency and magnitude of periodic disturbances and timing of resource availability, or the relative quality of each habitat patch (i.e., as reflected in within-patch birth and death rates). This also holds true for meta-communities (interacting sets of species) that shift among habitat patches at the landscape-scale (Levins and Culver 1971).

phytoplankton to deep-water habitat and transport of nitrogen (from excretion) back to shallow-water habitat markedly increased overall food web production. Moreover, productivity was optimized when the transport rates of phytoplankton and nitrogen between habitats were similar to the phytoplankton growth rate in the shallow-water habitat. Thus, slower transport rates (or reduced connectivity among habitats) decreased overall productivity by reducing nutrients available for phytoplankton growth in shallow habitat which resulted in reduced phytoplankton as food for zooplankton in deeper habitat. Similarly, productivity rates are reduced when transport rates are higher than phytoplankton growth rates. This results in phytoplankton being exported from shallow-water habitats faster than they can reproduce.

These model results are supported by a rich series of field studies and other modeling on the phenomenon of phytoplankton export from shallows to channel areas in the San Francisco Estuary, both in the south Bay and in the Delta (Lucas *et al.* 1999a,b; 2002, 2009; Lopez et al 2006). Curiously, the main constituent of the Delta food web is phytoplankton, primarily diatoms, even though there are flooded islands dominated by submerged vegetation, with epiphytic algae.

Studies on the complicated water movements through the Delta and Suisun Marsh (Jon Burau, USGS, Chris Enright, CDWR, pers. comm., 2009 DRERIP model) further illustrate the value of habitat diversity and interconnectedness. Detailed measurements of tidal currents indicate that the present network of channelized sloughs in the Delta causes water from different areas to mix rapidly, with low residence times in most areas. This reduces variability in water residence times, salinity, and temperatures. Similar work in Suisun Marsh indicates that natural, un-diked sloughs have a more complex geometry and are considerably more variable in multiple water quality measures, because the water overflows onto the marsh plain on flood tides, from which it drains slowly, presumably carrying nutrients, methylmercury, and other dissolved substances. In contrast, water flows rapidly back and forth in diked sloughs with simplified channels, homogenizing water quality. The natural sloughs of Suisun Marsh also have higher abundances of desirable fishes (Moyle, unpublished data). In general, estuarine physical forces (*e.g.,* tidal and river flow) are modified by slough geometry to produce gradients in various water quality and biological characteristics; dendritic slough geometry promotes higher variability in water quality across a landscape than does the interconnected geometry of channelized sloughs characteristic of the present Delta. The fact that sloughs of the present Delta are mostly open ended results in water quality and habitat being relatively homogenous through out the system, promoting alien freshwater species. In contrast, a heterogeneous, variable estuarine landscape (*e.g.,* see Figure 2) generally favors desirable estuarine species.

Although ecological theory and observational studies overwhelmingly support the argument for enhancing variability and complexity across the estuarine landscape, they cannot yet be used to determine the levels needed to assure the persistence of desirable species. Large-scale experiments designed to explore optimal levels of geometry or salinity variation can markedly improve our understanding of the problem; however, there are inherent disconnects among ecological processes working at more local scales and overall trends that emerge at the landscape-scale. In terms of ecological theory, the estuary is a self-organizing, complex, system with inherent nonlinear characteristics produced by feedback loops across scales, including the effects of stochastic events at the landscape and regional scales (Scheffer and Carpenter 2003). Thus a major flood event may scour submerged beds of aquatic vegetation, create new channels, break levees (both natural and human-made) and flood islands, as well as create temporary freshwater habitat in normally saline areas. The entire estuary may change temporarily or permanently in response to one large event, especially where human actions have created areas easily altered on a large scale (*e.g.*, subsided diked islands). In other words, we cannot rebuild an estuary with desirable characteristics just by adding desirable organisms (*e.g.*, fish from a hatchery) or scattered small pieces of habitat. But we can enhance key processes that increase variability and complexity that can produce positive changes in the estuary and that can adjust to large-scale stochastic events. Indeed, process-based restoration is likely to be more sustainable than structure-based restoration (*e.g.*, Simenstad *et al.* 2005).

Salinity: a key indicator

Given that major change is inevitable in the San Francisco Estuary in the next few decades, our society has an opportunity to help guide, or at least monitor, some of these changes by using salinity variability as an indicator of heterogeneity in the new estuarine landscape. Salinity variability is a convenient indicator because gradients in other important physical-chemical characteristics often (but not always) track salinity, including water residence times, temperature, suspended sediment, and organism composition. The relationship of salinity to other variables is affected by channel geometry and is therefore complex (*e.g.*, Monsen *et al.* 2007). Nevertheless, salinity has the advantage of being relatively easy to measure and of being physiologically important to most organisms and a major determinant of their distribution in the estuary. It also is extremely important as a water quality variable in relation to societal water uses. Although humans typically appreciate changes in salinity primarily at seasonal and annual scales, there are at least six important characteristics of environmental variability, including salinity variability. These attributes were developed largely for flow regimes of rivers by Richter *et al.* (1996) and Poff *et al* (1997) but have wide applicability:

- Magnitude—the amount of gradient change
- Duration—persistence, in time, of a shift in gradient
- Timing—the timing of changes in gradient magnitude and/or location
- Frequency—the reliability of gradient change on a tidal, seasonal or inter-annual scale
- Rate of change—the length of time it takes to establish a shift in gradients, how quickly a change occurs
- Spatial gradient — the salinity gradient perpendicular to the upstream-downstream salinity gradient at a given location and time.

Identifying the appropriate mix of these attributes that promotes the collective abundance of desirable species is a formidable challenge. Species naturally differ in their salinity and other habitat requirements as well as in the time scales at which they respond to change. This creates a great deal of difficulty in trying to establish an optimal mix of conditions for promoting desirable species assemblages in the estuary, even for a single variable such as salinity. Nevertheless, three basic premises (assumptions) suggest that a focus on estuarine variability, especially as reflected in salinity, is an appropriate but not exclusive direction for creating more desirable conditions in the estuary, especially the Delta:

1. Native species (and some desirable alien species, such as striped bass, *Morone saxatilis*) evolved under highly variable water quality conditions and so are more likely to thrive when variable conditions return; conversely, many undesirable alien species became established during times of reduced environmental variability.

2. A more variable, heterogeneous estuary (especially the Delta) may result in more productive open-water food-webs, because proportionally less energy would be captured by alien

submerged aquatic vegetation and, perhaps, benthic mollusks. This assumption rests on relatively poor information on the ability of alien pest species to tolerate variable conditions.

3. Given some uncertainty in how species respond to different conditions, higher spatial variability should provide a wider range of habitats in the Delta, some of which are more likely to support desirable species. The current rather homogeneous Delta is not working well for native species. Increased complexity and variability should provide more opportunities for native species to find conditions they need to survive, especially where favorable dynamic and stationary conditions are likely to coincide (Peterson 2003).

An example of variability that largely favors desirable fishes and discourages alien clams and aquatic plants can be found in the salinity gradients of Suisun Marsh (Figure 1). Compared to the Delta, salinity in the marsh typically has large annual ranges (and is usually fresh in winter) and considerable average variation among years. Salinity is also highly variable across Suisun Marsh at different times of year (not shown in Figure 1). Suisun Marsh continues to support higher numbers of native fishes than the current Delta, has few beds of submerged vegetation, and has areas that are relatively free of problem clams (*Corbula amurensis, Corbicula fluminea*).

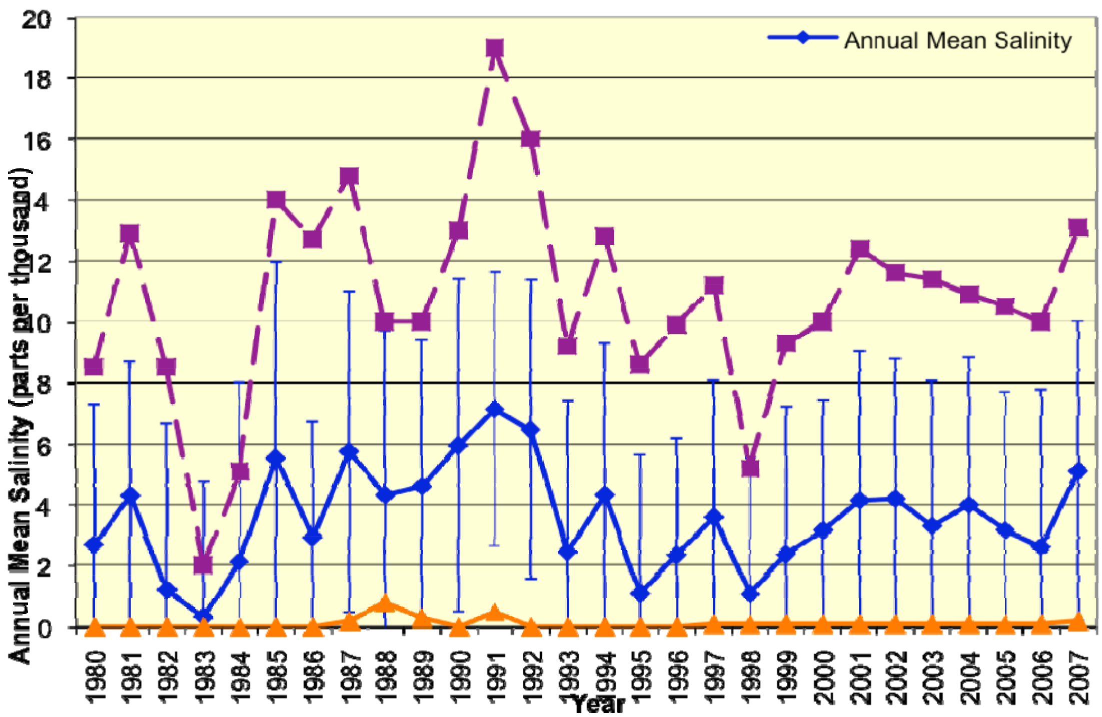
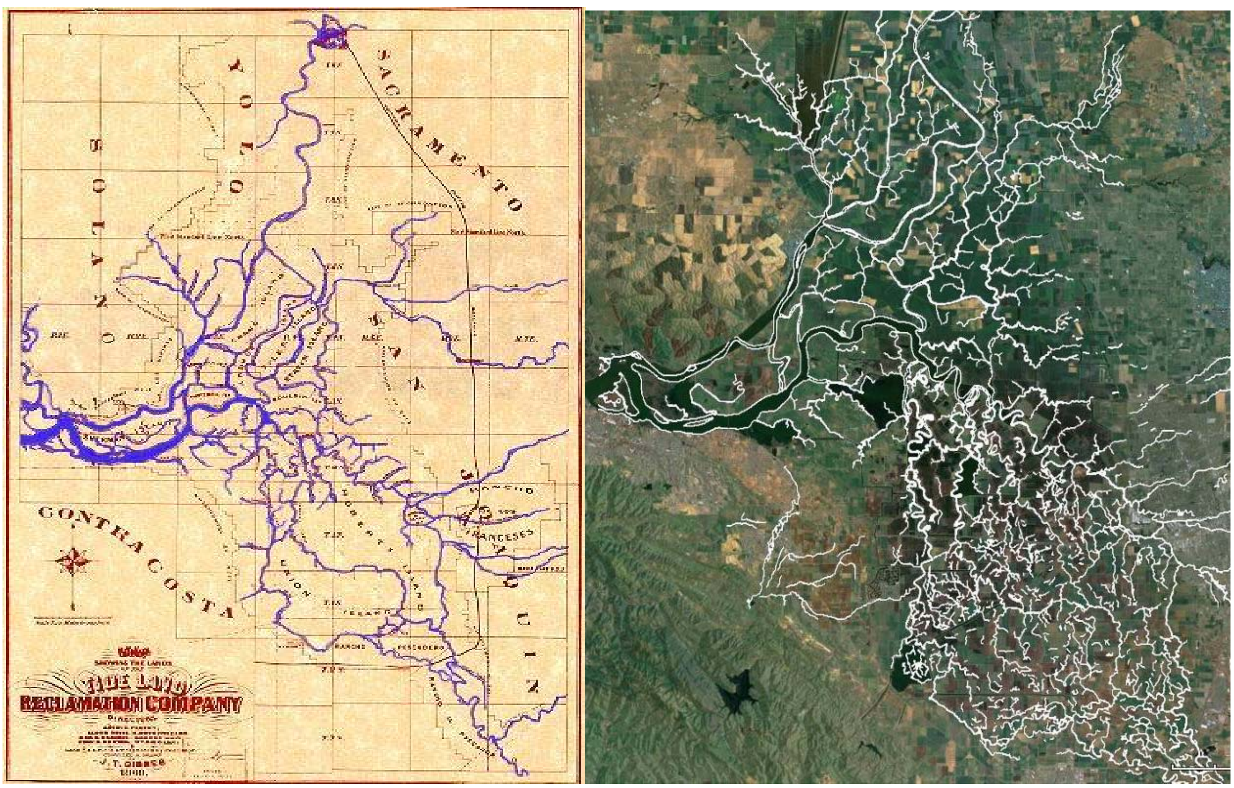


Figure 1. Annual mean (with standard deviation, middle line), minimum (bottom line) and maximum (top line) salinities for Suisun Marsh based on monthly spot measurements taken at 18-24 stations in channels throughout the marsh (Moyle, unpublished data). Sea water is about 35 ppt.

San Francisco Estuary: historical conditions.

The San Francisco Estuary is a young estuary, about 6-10,000 years old in its present location (Atwater *et al.* 1979; Malmud-Roam *et al*. 2007; Healey *et al.* 2008). The estuary became established during periods of extreme climatic variability (floods and droughts) compared to the situation in the past 150 years (Malmud-Roam *et al*. 2007). The Delta, misnamed from a geological perspective[2], was formed as a huge, largely freshwater marsh through the interaction river inflow and the slow rise of sea level with the growth of tules and other plants. Rising sea levels allowed for the deposition of large amounts of organic matter, creating layers of peat which formed the soils of present Delta 'islands', actually patches of floodable marsh. The channels among the islands were historically shifting, winding distributaries of the entering rivers that moved inflowing water through the Delta and provided access to upstream areas for migratory fish (Figure 2). The estuary was apparently not rich in native aquatic species because of its young age and relative isolation from other large estuaries (Cohen and Carlton 1998, Moyle 2002). However, its high productivity and complexity attracted a high diversity and numbers of birds, especially waterfowl.



(a) **(b)**

Figure 2: The Delta in 19th century. Map a shows the highly complex pattern of the main river channels through the Delta (*ca.* 1860) while map b shows a re-creation of the complex marsh distributary system that once existed, especially in the South Delta (Courtesy, Chris Enright, DWR, using Atwater data).

The Gold Rush resulted in the rapid transformation of the San Francisco Estuary in the latter half of the 19th century, starting with the urbanization of the San Francisco Bay region and the diking and draining of Suisun Marsh and parts of the Delta. The configuration of the estuary since then has been altered by the diking and draining of over 90% of its wetlands, as illustrated by the Delta (Figure 3) during one of the least variable climatic periods since the Pleistocene

[2] Deltas are technically alluvial fans at the mouths of rivers, large fan-shaped areas of sediment created when sediment loads of rivers are abruptly dropped as the river enters a larger water body or a broad flat valley, dissipating the energy which carries the sediment.

(Malmud-Roam *et al.* 2007). The complicated network of channels has been simplified into a series of ditches and canals, while the productive marshlands have been largely eliminated within the estuary, diked off for agricultural and urban uses. In short, the highly heterogeneous historical San Francisco Estuary has been greatly simplified.

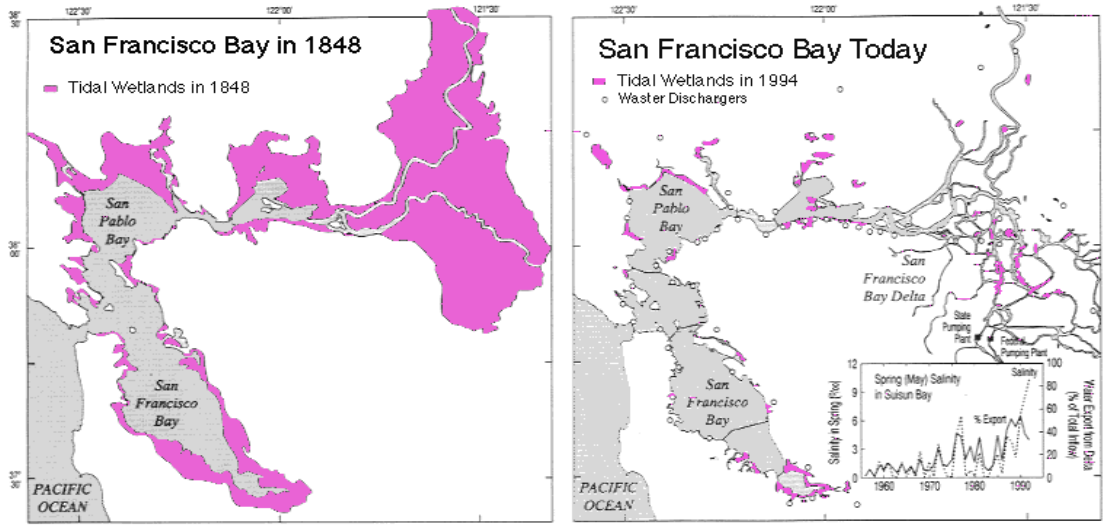


Figure 3: Extent of marshlands and wetlands in the San Francisco Estuary system in 1848 and present (reprinted from http://sfbay.wr.usgs.gov/general _factsheets/change.html).

Despite these changes, the San Francisco Estuary is still inherently complex at the landscape scale as the result of topographically diverse landscape with distinct regions (Delta, Suisun-Bay Marsh, San Pablo Bay, San Francisco Bay), two major inflowing rivers (Sacramento, San Joaquin), and numerous smaller streams. This overall physiographic structure creates diverse channel types from the narrow, deep passages at Carquinez Strait and the Golden Gate the shallow channels cutting through the broad expanses of shallow shoals and marshlands (Figure 4). As a result, tidal patterns and water quality gradients (especially salinity) are complex. The native aquatic fauna that has persisted through the past 150 years of change exhibit various adaptations to the complex, every-changing estuarine gradients, including wide but specific salinity ranges (Figure 5).

Historically, extensive marshes along the edges of the estuary enhanced this structural complexity, most notably Suisun Marsh and Delta islands (Figure 3). These marshes varied in the degree to which they retained and drained tidal and riverine waters, thereby creating considerable local variability in water residence times[3] and quality. In addition, the Delta and Suisun Marsh once merged imperceptibly with floodplains and riparian forests along the inflowing rivers. These flooded areas would have further retained outflows and drained slowly to support shallow water habitat through the spring. The wide expanses of marsh and floodplain also would have muted tidal energy, spreading it over wide areas rather than confining it into narrow channels, where it can move with considerable force (as is true today).

[3] Residence time is essentially the length of time water stays in a fairly limited area. The higher the residence time, the more likely blooms of phytoplankton and zooplankton will develop in the open water that will be part of food webs leading to fish. Such blooms have a hard time developing in flowing water (low residence times) because the phytoplankton cannot stay in surface waters long enough to grow and reproduce before being carried downstream and out of the area.

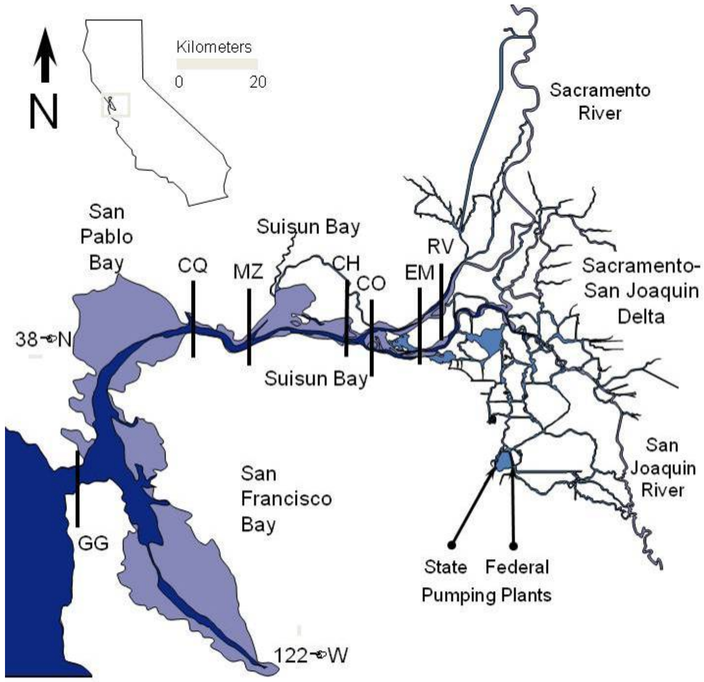


Figure 4. San Francisco Estuary and Delta, showing major basins, channels, and shoals (10m depth contour). Paired letters indicate geographical landmarks. GG, Golden Gate Bridge; CQ, Carquinez Bridge; MZ, Martinez Bridge; CH, Chipps Island; CO, Collinsville; EM, Emmaton; and RV, Rio Vista.

Imposed on this complex structure was a highly variable flow regime, both seasonally and across years. The basic seasonal pattern consisted of high flows in winter and spring, with variability from the timing of rain storms and snow melt from the Sierra Nevada, with the San Joaquin River more attenuated because of higher mountains in the southern Sierra. Inter-annual variability was generated by natural variation in precipitation along with long periods of drought and occasional years with huge floods (Malmud-Roam *et al*. 2007, Healey *et al.* 2008). By spreading out the tidal energy, the estuary's immense marshlands helped to keep the central Delta a freshwater system, by reducing saltwater intrusion. One result of such high seasonal and inter-annual variability was the extremely high abundances of organisms observed prior to significant human intervention. This abundance included not only fish, discussed below, but waterfowl, especially 26 species of ducks and geese (Herbold and Moyle 1989). Arguably, the historic Delta was the centerpiece of the Pacific flyway, allowing huge numbers (perhaps 10 million) of waterfowl to overwinter in California.

This abundance of life implies high productivity, which was likely generated by nutrients from the extensive marshes and floodplains and the dispersion of these nutrients by the complex hydrology throughout the system and into the estuarine food webs. Key indicators of this productivity were the large populations of fishes once supported by the system, especially Chinook salmon, Sacramento perch (*Archoplites interruptus*), and native minnows, as indicated by extensive 19th century and Native American fisheries (Moyle 2002) and the huge influxes of waterfowl that arrived each winter to feed and grow.

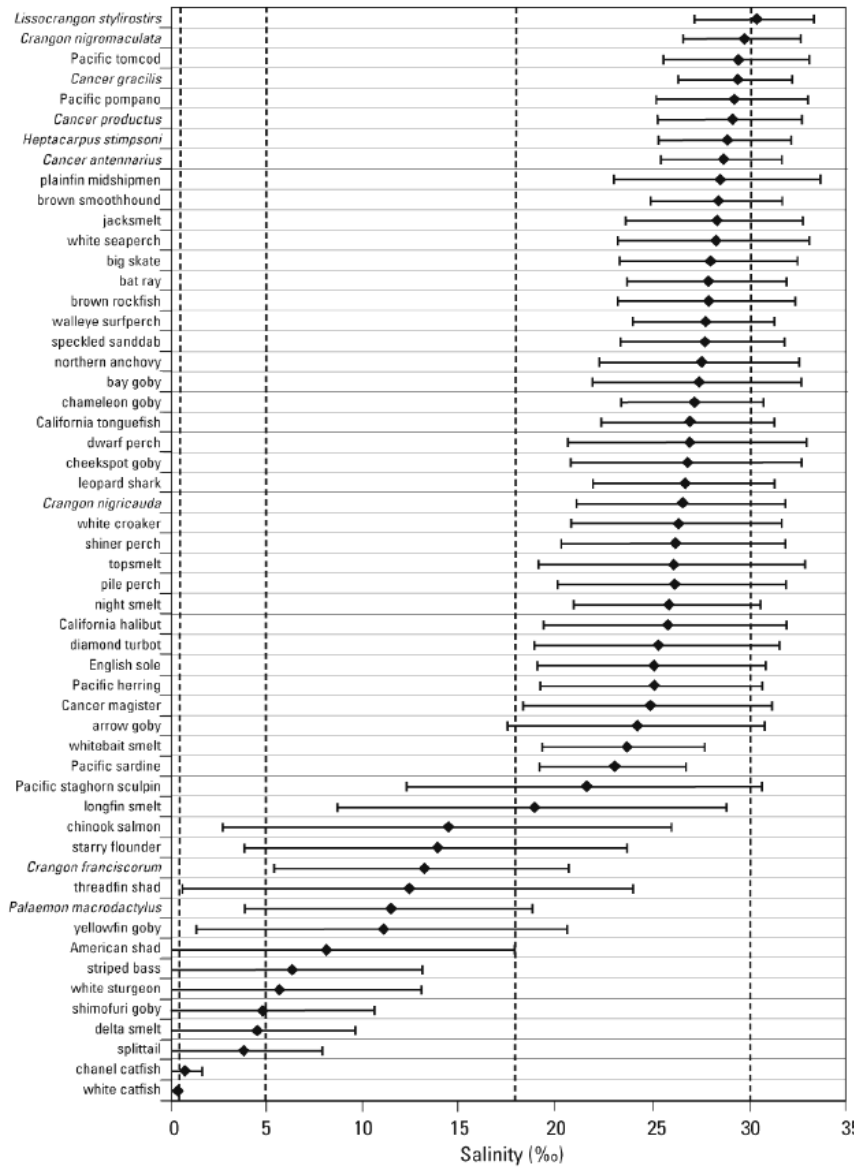


Figure 5. Mean salinity (ppt) +/- SD for the 54 most common species of fish, shrimp, and crabs collected during CDFG's Bay Study, 1980-1995. From Hieb and Fleming (1999). All species are native except chameleon goby, threadfin shad, *P. macrodactylus*, yellowfin goby, American shad, striped bass, shimofuri goby, channel catfish, and white catfish. The ranges shown here presumably represent optimal salinities; most species, especially those with mean salinities of <15 ppt, can be found within wider total ranges. The vertical dotted lines group the species into groups based on salinities (1) Delta, (2) Delta + Suisun Bay/Marsh, (3) San Francisco Bay, and (4) Pacific Ocean.

Once the marshes were diked and drained, and upstream water diversions in summer became large, tidal energy moved salt water further upstream during dry periods. As the estuary and inflowing rivers and their floodplains became developed, and as alien species invaded, the native fish fauna and waterfowl populations gradually declined. Some native species disappeared altogether (thicktail chub, *Gila crassicauda*; Sacramento perch) while others persisted in fairly large numbers until recently (*e.g.*, delta smelt, *Hypomesus transpacificus*, longfin smelt, *Spirinchus thaleichthys*). Both breeding and wintering waterfowl populations have largely shifted away from the Delta and Suisun Marsh to refuges and flooded rice paddies in the Sacramento and San Joaquin valleys (Herbold and Moyle 1989).

The variability and productivity of the estuary also is reflected in life history adaptations of species that evolved within it, for example, delta smelt, splittail *(Pogonichthys microlepidotus*), and Chinook salmon (*Oncorhynchus tshawystscha*).

Delta smelt are found only in the San Francisco Estuary, where they live in the brackish parts of the estuary and spawn in fresh water (Bennett 2005). They were presumably once abundant in the upper estuary, but are now listed as an endangered species.[4] Delta smelt feed entirely on zooplankton, mainly copepods, in open water. They have relatively narrow salinity preferences and thus have adapted their swimming mode to use tidal currents when possible to remain in lower salinity water. Rather than expending significant energy fighting tidal flows, smelt use the currents to carry them to where they need to go, including to spawning habitat (most likely beaches or similar shallow water substrates in the Delta). Remarkably, delta smelt have a primarily one-year life cycle, so they must spawn successfully each year to maintain their population. This means that the rather narrow range of conditions needed for spawning and rearing were always present somewhere in the estuary, even during years of severe drought and extreme flood. It also means the smelt could easily find those conditions somewhere in the historically dynamic estuary, until quite recently. Delta smelt are basically adapted to living in a highly variable system, including being able to find highly productive low-salinity areas of open-water where they feed and grow.

Sacramento splittail are now also largely confined to the estuary and rivers immediately upstream, although they were once more abundant and widespread in the Central Valley (Moyle *et al.* 2004). They basically live in brackish water marshes and migrate upstream to spawn in winter, preferably on floodplains just above the estuary. They are adapted to system variability by being able to spawn multiple times (they live 7-9 years) and in good times can produce large numbers of young. Apparently, splittail also maintain populations through long periods of adverse conditions by having both strong year classes and some spawning success in marginal conditions (Moyle *et al.* 2004). The juveniles rear briefly on the floodplain, in annual vegetation, but then move downstream as floodplains drain in the spring to the brackish marshes. They feed primarily on benthic invertebrates and detritus produced by the wetlands they inhabit (Moyle 2002). Here they reside until migrating upriver to spawn again. The salinity tolerance of this species (up to18 ppt for extended periods) is remarkably high for a member of family Cyprinidae, a freshwater group of fishes (Moyle 2002), reflecting their ability to live under a wide range of conditions in an estuarine environment.

Chinook salmon pass through the estuary on their way upstream to spawning areas and then downstream as juveniles on their way out to sea. They were once extraordinarily abundant (1-2 million spawners per year, Yoshiyama *et al*. 1998) and maintained this abundance during periods of extreme conditions through diversity in life history patterns (four distinct runs, each with diverse patterns of rearing and migration) and, most likely, through use of the estuary and its adjoining floodplains for rearing. Today juvenile Chinook on floodplains grow faster and larger than those in the main river (Sommer *et al.* 2001; Jeffres *et al*. 2008) and this was likely once true of the estuary as well, with its diverse habitats and abundant food. For out-migrating

[4] The historic abundance of delta smelt is poorly understood because as a small midwater fish there was virtually no appropriate sampling (*e.g.*, midwater trawling) for it until the late 1950s and 1960s. Even then it was one of the more common fish in the estuary, despite the abundance of introduced competitors for food and space, such as threadfin shad (*Dorosoma petenense*), American shad *(Alosa sadipissima*), and juvenile striped bass (Moyle 2002).

freshwater juveniles converting to becoming saltwater fish, favorable conditions were presumably always present somewhere in the estuary, with juveniles of different runs and ages using different parts of the estuary. Chinook salmon in the Central Valley evolved a complexity of life history strategies and habitat use that enabled them to persist through different climatic regimes and variable conditions of floods and droughts, which is typical of salmon (Hilborn *et al.* 2003). This ability made it likely that the historic Delta and estuarine marshes were major salmon rearing areas, because favorable conditions for different life history stages were always present somewhere in the system. Peterson (2003) notes that a consistent seasonal match between structural components of an estuary (*e.g.*, marsh habitats) and dynamic components (water quality variables such as salinity) are a key characteristic of estuaries that are important for rearing juvenile fishes.

The greatly diminished populations of these and other estuarine-dependent native fish and waterfowl from their historical abundance and their continuing decline indicates that the estuary no longer functions as the productive and variable system that it once was due to the combination of changed hydrology, highly altered landscape, contaminants, altered food webs, and invasive species (Peterson 2003).

San Francisco Estuary: present and future

The pre-modern estuary, with its extensive tidal marshes, especially in the Delta, presumably showed a strong gradient in salinity and other variables, from the freshwater Delta to the saltwater Bay. The marshes quite likely muted the effects of the tides, reducing short-term variability, although long periods of drought (decades, unlike any experienced in modern times) would presumably have favored extensive movement of salt water farther into the Delta. In the 19th and early 20th century, prior to construction of the major rim dams, Delta channelization and upstream freshwater diversions increased the frequency of saltwater intrusion, especially in drier years. The big rim dams, developed in the 20th century, release water in summer, allowing inflows to increase, shifting the Delta back towards a more freshwater system. Enright and Culberson (2009) indicate that in Suisun Bay and Suisun Marsh, just below the Delta, salinity variability on an annual scale has actually been higher in recent decades because of increased variability in precipitation. The water projects have nevertheless dampened this variability (Enright and Culberson 2009) and in the Delta have apparently reduced seasonal variability so export pumps in the South Delta can operate efficiently.

As a result, the estuary, especially the Delta, shifted into a new biological regime after a half-century of being managed to limit its variability (Moyle and Bennett 2008, Fleenor *et al.* 2008). The new regime in the Delta supports an assemblage of primarily freshwater alien species that live in fairly clear, fresh water with strong tidal fluxes. Essentially, the Delta has become simplified and stabilized into a channelized conveyance system to export fresh water from and through the estuary during summer and to reduce freshwater outflows at other times of year. Suisun Bay and Marsh became essentially a brackish water system, with San Francisco Bay a largely marine system as shown by fish distributions (Figure 5). Such prolonged stabilization, combined with a relatively rapid influx of alien species, has caused a *regime shift* (Scheffer and Carpenter 2003; Folke *et al.* 2004) that is also reflected in the overall low and declining productivity of the San Francisco Estuary compared with other estuaries worldwide (Nixon 1988; Anke Mueller-Solger, CDWR, personal communication) and the apparent loss of resiliency by pelagic fish populations that previously rebounded during periods of favorable environmental conditions (Sommer *et al.* 2007). The prolonged application of salinity standards

(Figure 6) and altered hydrology (Figure 7) to support pumping operations has reduced variability in salinity during the critical summer months, favoring the expansion of alien *ecosystem engineers*[5] such as overbite clam (*Corbula amurensis*) in Suisun Bay and Brazilian waterweed (*Egeria densa*) in the Delta. Similarly, alien freshwater fish species typically associated with aquatic vegetation have increased dramatically and currently dominate Delta food webs. These riverine and lake species include Mississippi silverside (*Menidia audens*), largemouth bass (*Micropterus salmoides*), and several sunfish (*Lepomis*) species.

The ecosystem, however, is likely to dramatically shift again within about 50 years due to large-scale levee collapse in the Delta and Suisun Marsh. Major levee failures are inevitable due to continued subsidence, sea level rise, increasing frequency of large floods, and high probability of earthquakes (Lund *et al.* 2007, 2010). These significant changes will create large areas of open water, as well as new tidal and subtidal marshes. Other likely changes include reduced freshwater inflow during prolonged droughts, altered hydrology from reduced export pumping, and additional alien invaders (*e.g.*, zebra and quagga mussel, *Dreissena spp.*). The extent and effects of all these changes are unknown but much will depend on how the estuary is managed in response to change. Overall, the major changes in the estuary's landscape are likely to promote a more variable, heterogeneous estuary, especially in the Delta and Suisun Marsh. This changed environment is likely to be better for desirable species; at least it is unlikely to be worse (Moyle 2008). Even if major changes were somehow avoided, examination of sea level rise for "unimpaired" flows (Figure 8) indicates that salinity would intrude an additional 5km for each foot of sea level rise creating a higher diversity of habitat in the Delta.

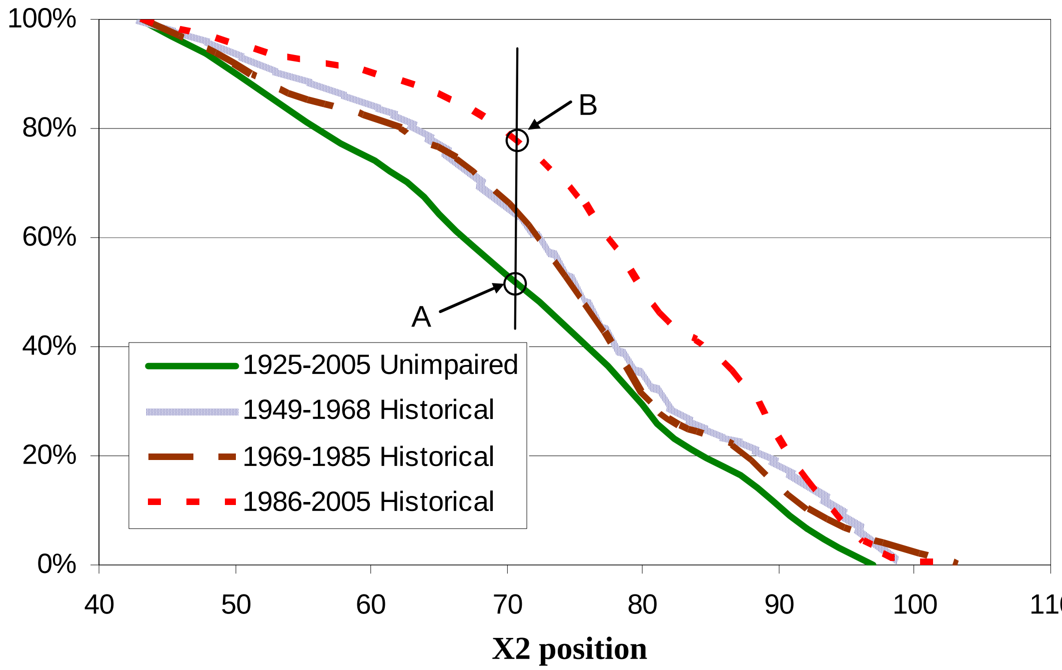


Figure 6. Cumulative probability distributions of daily X2 locations for unimpaired flows (green solid line) and three historical periods, 1949-1968 (light solid blue), 1969-1985 (long-dashed brown) and 1986-2005 (dashed red), illustrating progressive reduction in salinity variability from unimpaired conditions. X2 is the location of the 2 ppt salinity region of the

[5] Ecosystem engineers are organisms that regulate or change ecosystem functioning through their actions (Wright and Jones 2006). The overbite clam has caused a major shift in the food web of Suisun Bay from centering on pelagic organisms to benthic organisms, contributing to the decline of pelagic fish.

estuary in km from the Golden Gate. Thus a lower X2 value indicates that the low salinity zone is farther downstream in the estuary. Point 'A' demonstrates that for Unimpaired Flows the X2 salinity was equally likely to be upstream or downstream of the 71 km location (50% probability) while recent operations hold the X2 location upstream of the 71 km location nearly 80% of the time. Results from Water Analysis Module using unimpaired flow and historical boundary conditions (Fleenor *et al.* 2008).

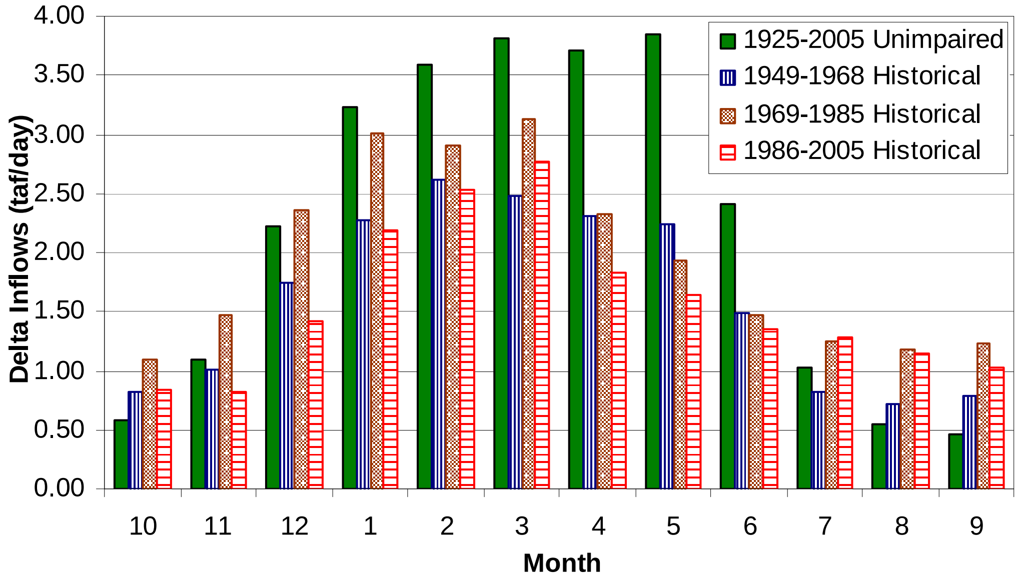


Figure 7. Averaged daily inflows in thousands of acre feet each month from Sacramento and San Joaquin rivers showing unimpaired flows (solid green bar) and three historical periods, 1949-1968 (vertically-striped blue), 1969-1985 (brown) and 1986-2005 (horizontally-striped red), illustrating progressive changes to inflow from unimpaired conditions. Note *increases* in summer inflow during recent decades. Data from unimpaired boundary conditions (DWR) and historical boundary conditions (Dayflow).

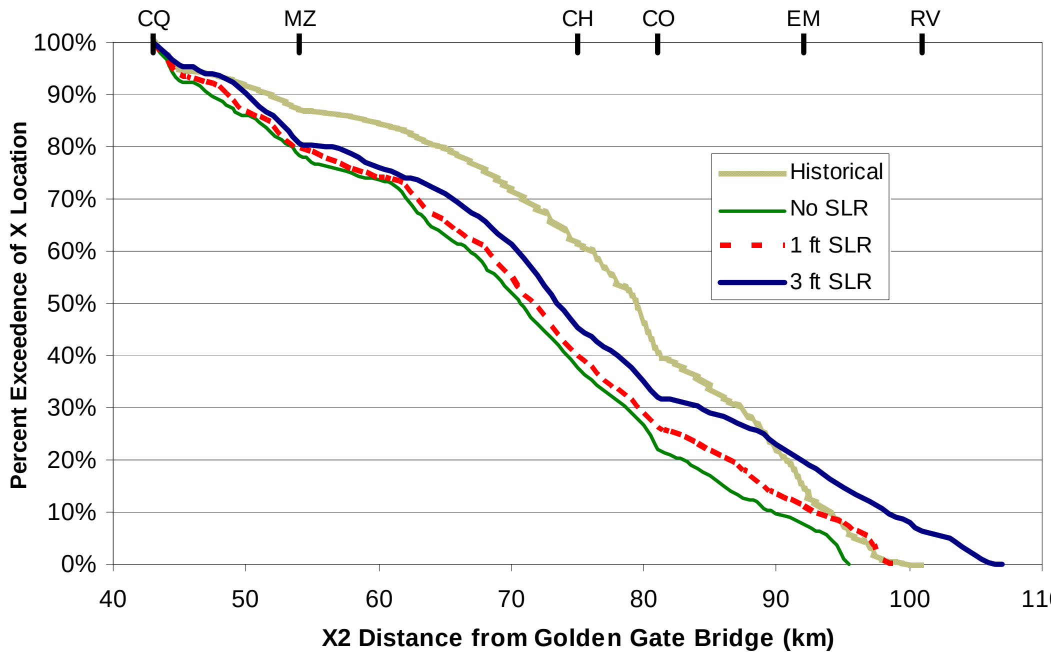


Figure 8. Cumulative probability distributions of daily X2 locations for unimpaired flows (thin green solid line) with 1-ft of sea level rise (red dashed line), 3-ft of sea level rise (thick solid blue line), and 1981-2000 historical condition (opaque brown line), illustrating progressive salinity variability for unimpaired conditions with sea level rise. X2 is the location of the 2 ppt salinity region of the estuary in km from the Golden Gate. Thus a lower X2 value indicates that the low salinity zone is farther downstream in the estuary. Results from Water Analysis Module using unimpaired flow and historical boundary conditions (Fleenor *et al*. 2008). Paired letters indicate geographical landmarks. CQ, Carquinez Bridge; MZ, Martinez Bridge; CH, Chipps Island; CO, Collinsville; EM, Emmaton; and RV, Rio Vista as shown on Figure 4.

Towards a more heterogeneous/variable estuary

So, what is needed to create a more heterogeneous estuary in time and space? The answer to this question reflects one basic truth: the estuarine ecosystem of the future will differ greatly from any ecosystem that has existed in the past. Here we provide ten general directions for management of the San Francisco Estuary, especially the Delta and Suisun Marsh, to create an ecosystem with attributes favorable to estuarine species. These directions fall into four broad categories: (a) establishing seaward gradients in salinity, temperature, turbidity, and various physical aspects of the environment, (b) establishing large expanses of diverse habitat, especially open water habitats close to tidal marshes, (c) increasing floodplain habitat area at the mouths of rivers flowing into the Delta and assuring that these habitats flood regularly, and (d) improving water quality in ways that favor desirable species and discourage undesirable alien species. We recognize that the recommended actions are not independent and may at times conflict. For example, creating a more natural, dendritic channel structure may increase residence time of water in the channels, reducing tidal-generated variability in salinity. Obviously, building an ecosystem is difficult!

a) Establishing seaward gradients.

1. **Establish internal Delta flows that create a tidally-mixed, upstream-downstream gradient (without cross-Delta flows) in water quality**. One current problem with the Delta is that flows are manipulated to draw fresh water into the pumps of the SWP and CVP in the south Delta and to provide fresh water for Delta farmers, especially in late summer. Water is released from reservoirs to hold back salinity intrusion and is moved, one way or another, across the Delta for export. While the tides are powerful enough to create an impression of normal land to seaward movement, the net flow is often across the Delta and daily tidal patterns, which direct seaward movement of fish, can be overwhelmed by movement of water towards the pumps in the south Delta. This has led to a confusing environment for migratory fish (*e.g.*, juvenile salmon may end up in the central and southern Delta, where water temperatures are higher and water quality is otherwise unfavorable) and draw others, such as delta smelt, towards the south Delta pumps (Kimmerer 2008; Grimaldo *et al.* 2009). Current conditions favor resident freshwater invasive organisms such as largemouth bass and Brazilian waterweed (Brown and May 2008). Recreating tidally driven, landward-seaward flow patterns should favor estuarine fishes, such as striped bass, longfin smelt (*Spirinchus thaleichthys)*, and delta smelt.
2. **Create more slough networks with natural channel geometry and less diked, rip-rapped channel habitat**. Re-establishing the historical extensive dendritic sloughs and marshes is essential for re-establishing diverse habitats and gradients in salinity, depth and other environmental characteristics important to desirable fish and other organisms (*e.g.*, Brown and May 2008). These shallow drainages are likely to increase overall estuarine productivity if they are near extensive areas of open water, because they can deliver nutrients and organic matter to the more open areas. Dendritic slough networks will develop naturally in Suisun Marsh after large areas become inundated following dike failures and they can be recreated fairly readily in the Cache Slough region by reconnecting existing networks. In the Delta, the present simplified habitat in the channels between islands needs to be made more suitable as habitat for desirable species. Many levees are maintained in a nearly vegetation-free state, providing little opportunity for complex habitat (*e.g*., marshes and fallen trees) to develop. Much of the low-value channel habitat in the western and central Delta will disappear as islands flood, but remaining levees in submerged areas should be managed to increase habitat complexity (*e.g.*, through planting vegetation), especially in the cooler northern and eastern parts of the Delta.
3. **Improve flows from the San Joaquin and Sacramento rivers.** Inflow to the Delta from the San Joaquin River currently comes mainly from the regulated tributaries, the Merced, Tuolumne, and Stanislaus Rivers, and from agricultural drainage to the main river. Most fresh water is diverted upstream of the Delta. Consequently, San Joaquin River flows are greatly diminished and burdened with salt loads from agricultural drainage (Lund *et al.* 2007; Fleenor *et al.* 2008). A seaward gradient should be established with greater flows to improve conditions in the south Delta for fish. While difficult to achieve in this water scarce region, increased San Joaquin River outflows would (1) improve water quality through dilution, (2) increase migration rates of juvenile salmon through the Delta, (3) reduce entrainment in the SWP and CVP pumps, (4) increase net outflows during critical periods, and (5) improve habitat in the lower river through flooding of shallow areas.

   The Sacramento River is the major source of freshwater for the estuary and the need to transfer its relatively high quality water to the pumps in the South Delta is the major reason the hydrodynamics of the estuary are so altered. However, much of the Sacramento River is diverted for agricultural use *before* it reaches the Delta, which also affects flows and water quality in the Delta (Lund *et al.* 2007). Improving flows through the estuary by either reducing pumping or increasing inflows would have the same general effects noted for the San Joaquin River.

b) Increasing habitat diversity

4. **Increase tidal marsh habitat, including shallow (1-2 m) subtidal areas (especially in Suisun Marsh), in both fresh and brackish zones of the estuary.** Part of variability is having diverse habitats available to fish, especially tidal marshes containing natural tidal channels and large expanses of subtidal habitat. This type of habitat has been greatly depleted because marshes in the Delta and throughout the estuary have been diked and drained, mostly for farming and hunting (Figure 3). Unfortunately, most such habitat in shallow water today is dominated by alien fishes, including highly abundant species such as Mississippi silverside which are competitors with and predators on native fishes (Moyle and Bennett 1996; Brown 2003). Such habitat could become more favorable for native fishes with increased variability in water quality, especially salinity. In particular, increasing the amount of tidal and subtidal habitat in Suisun Marsh should favor native fishes, given the natural variability in salinity and temperature that occurs there. The few areas of the marsh with natural tidal channels tend to support the highest diversity of native fishes, as well as more striped bass (Matern *et al.* 2002; Moyle, unpublished data). With sea level rise, many diked areas of Suisun Marsh currently managed for waterfowl (mainly dabbling ducks and geese) will return to tidal marsh and will likely favor native fishes such as splittail and tule perch (*Hysterocarpus traski*), as well as (perhaps) migratory fishes such as juvenile Chinook salmon. Experimental (planned) conversions of some of these areas would be desirable for learning how to manage these inevitable changes to optimize habitat for desired fishes.
5. **Create/allow large expanses of low salinity (1-4 ppt) open water habitat in the Delta.** Open water habitat is most likely to be created by the flooding of subsided islands in the Delta, as well as diked marshland 'islands' in Suisun Marsh (Lund *et al*. 2007, 2010; Moyle 2008). The depth and hydrodynamics of many of these islands when flooded should prevent establishment of alien aquatic plants while variable salinities in the western Delta should prevent establishment of dense populations of alien clams (Lund et al. 2007). Although it is hard to predict the exact nature of these habitats, they are most likely to be better habitat for pelagic fishes than the rock-lined, steep-sided and often submerged vegetation-choked channels that run between islands today (Nobriga *et al.* 2005). Experiments with controlled flooding of islands should provide information to help to ensure that these changes will favor desired species. Controlled flooding also has the potential to allow for better management of hydrodynamics and other characteristics of flooded islands (through breach location and size) than would be possible with unplanned flooding.
6. **Create a hydrodynamic regime where salinities in parts of the Delta and Suisun Bay and Marsh range from near-fresh to 8-10 ppt periodically (does not have to be annual) to discourage alien species and favor desirable species.** There is a high degree of uncertainty in the specific salinity ranges in this recommendation but the basic idea is that fairly high fluctuations in salinities may discourage freshwater organisms in the western Delta, especially Brazilian waterweed and largemouth bass, and saltwater organisms in the brackish parts of the estuary(Suisun Bay and Marsh), especially the overbite clam. Reducing

the abundance of these ecosystem engineers could (in theory) improve food supplies for pelagic fish and other organisms and reduce habitat that favors alien species such as largemouth bass and sunfishes. Variability in salinity in the western and central Delta may have to be significantly greater now than it was in the past to suppress invasive species that are now well established. The weakness of this recommendation is our lack of adequate knowledge as to how various alien species will react to a more variable regime. It possible that reduction of one species may simply allow another equally obnoxious species to take its place.

7. **Take species-specific actions that reduce abundance of non-native species and increase abundance of desirable species.** An increase in local biodiversity is likely to result if many of the above (1-6) conditions occur, especially in combination, but diversity could be enhanced further by large-scale actions to reduce abundance of alien ecosystem engineers (*e.g.,* actively controlling clam or aquatic weed populations) and to enhance populations of desirable species (*e.g.,* improvement of salmon streams through improved flow regimes). Species-specific actions always should be done as carefully-monitored experiments, to avoid becoming dependent on continuous programs such as salmon hatcheries, which can create as many problems as they solve in the long run (*e.g.,* Williams 2006).

c) Creating more floodplain habitat

8. **Establish abundant annual floodplain habitat, including large areas that flood in wet years (e.g., Yolo Bypass, San Joaquin floodplain).** Most floodplains in the Central Valley have been isolated from their rivers by levees. Recent studies demonstrate that floodplains are good for desirable fishes, as well as for waterfowl of all types (Opperman *et al.* 2009). Many fishes rear opportunistically on floodplains (Moyle *et al.* 2007) and juvenile salmon grow faster and become larger (Sommer *et al.* 2007, Jeffres *et al.* 2008). Splittail require such habitat for spawning (Moyle *et al.* 2007). Floodplains also can generate nutrients for downstream areas (Jassby and Cloern 2000). Increasing the amount of regularly flooded seasonal habitat, with large expanses flooded during wetter years, will have large benefits to fishes, especially if the physical structure of flooded areas is taken into account and perhaps modified (Feyrer *et al*. 2006). Flooding large expanses of habitat during winter and spring on an irregular basis (frequencies of every 2-7 years) can produce large year classes of some species, to help carry their populations through dry periods. This can be done by improving management of the Yolo Bypass for fish, by increasing floodplain areas along other rivers (*e.g.,* Cosumnes and Mokelumne rivers), and by developing floodplain habitat along the lower San Joaquin River, including a bypass in the Delta. It is worth noting that improving floodplain management for native fish is highly compatible with agricultural use of flooded lands (*e.g.,* by keeping it in annual vegetation) and mosquito control (*e.g.,* by having abundant juvenile fish and rapid drainage).

d) Improving water quality

9. **Reduce inflow of agricultural and urban pollutants (especially from the San Joaquin River).** Despite the positive effects of the Clean Water Act, the Delta still receives abundant pollutants from (1) agricultural drainage, (2) wastewater treatment plants, (3) urban storm drains, and (4) airborne pesticides. These pollutants have the potential to produce significant effects on fish and invertebrate populations which may mask larger-scale effects, such as diversions, or negate the effects of habitat improvements. While we have not discussed

10. **Improve the temperature regime in large areas of the estuary so temperatures rarely exceed 20°C during summer and fall months.** Diversions, drainage water, and other factors are combining with climate change to increase water temperatures in the Delta. Summer temperatures in many areas may become lethal to delta smelt and less favorable for other native species, suggesting that higher temperatures may be bad for some desirable species and favor less desirable alien species. Thus finding ways to keep part of the Delta cool in summer is likely to be important. Flooding western islands and re-flooding of intertidal marsh may be one way to do this through greater mixing and evaporative and radiative cooling over tidal cycles (C. Enright, personal communication).

Policy Implications of Variability

Restoring habitat complexity and variability to the Delta imposes major policy challenges. Among them are:

1) Most environmental and water management regulations for the Delta are intended to restrict variability. They therefore make it difficult to increase variability as recommended here. Salinity standards and the operations of water export projects and some other in-Delta diversions would have to be changed to allow increased variability from water operations.
2) Restoring complexity and variability in physical habitats in the Delta will require significant physical landscape modifications. Depending on the location within the Delta, these changes may involve flooding islands, setting back levees, or breaching levees. These actions would require substantial revisions in current Delta levee policies.
3) Water management and flow changes to improve Delta habitat complexity and variability will challenge existing water management policies, practices, and expectations and are likely to conflict with other flow objectives, including perhaps some environmental flows correlated with desirable species in the past.
4) Substantial improvements of outflows and water quality from the San Joaquin River, which are of particular importance for habitats in the southern and central Delta, will be difficult. Upstream diversions in the San Joaquin basin are valuable economically, and drainage to the San Joaquin River is the major way the basin reduces accumulations of salts and other pollutants.
5) Inevitable changes to the Delta from sea level rise, island flooding, and other factors will increase habitat and water quality variability in the Delta, which is likely to improve conditions for desirable fish species. These changes will have to be incorporated into future land and water use decisions.
6) Improvements from increased complexity and variability can be negated or reduced if pollution from surrounding urban and agricultural areas is not reduced or better controlled. This means, in part, reducing "non-point source" pollution from agriculture and reducing inputs from sewage treatment plants.

7) Restoring complexity and variability for future conditions in the Delta will necessarily involve experimentation. Experiments might be unintentional as islands fail, legal verdicts are rendered, and mistakes are made. More useful and less expensive experimentation could consist of intentional, formal, and relatively controlled manipulative research supported by preparatory modeling studies. Some management activities will fail, even with more formal experimentation. Policy difficulties will arise in establishing scientific capabilities to undertake experiments which more efficiently guide the transition of the Delta. Resources in terms of land, water, funding, expertise, leadership, and responsible political insulation will be needed to allow formal experimentation and exploratory modeling to go forward and be useful.

8) Finally, restoring environmental variability in the Delta is fundamentally inconsistent with continuing to move large volumes of water through the Delta for export. The drinking and agricultural water quality requirements of through-Delta exports, and perhaps even some current in-Delta uses, are at odds with the water quality and variability needs of desirable Delta species.

Conclusions

The San Francisco Estuary has become a heavily invaded ecosystem that is less heterogeneous in structure and water quality, resulting in declines of many fish species that depend on estuarine conditions. This is especially true of the Delta. A key to returning the estuary to a state that supports more of the desirable organisms (*e.g.*, Chinook salmon, striped bass, delta smelt) is increasing variability in physical habitat, tidal and riverine flows, and water chemistry, especially salinity, over multiple scales of time and space. It is also important that the stationary physical habitat be associated with the right physical-chemical conditions in the water at times when the fish can use the habitat most effectively (Peterson 2003). To combat the problems with invasive species, short-term (monthly, annual) variability in some factors, such as salinity, probably has to be higher than it was historically. Some of this variability is likely to return naturally as the result of sea level rise, climate change, and levee failures, but habitat improvement, flow restoration and export reduction would push the estuary toward a more variable and presumably more productive ecosystem, or at least one with higher abundances of desirable species. While these findings are speculative, our findings have widespread support in ecological theory and observations from other systems, so making quantitative predictions of change should become a high priority for research.

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