Habitat Variability and Complexity in the Upper San Francisco Estuary
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Abstract
The San Francisco Estuary is a complex estuarine ecosystem. Variability in environmental conditions, especially in the Delta, once made it highly productive for native biota. Present conditions discourage desirable species, providing a rationale for restoring estuarine variability and complexity. 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 flows that create a tidally-mixed, upstream-downstream gradient in water quality; (2) create slough networks with natural channel geometry; (3) improve flows from the San Joaquin River; (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 mg/l) open water habitat in the Delta; (6) create a hydrodynamic regime in which salinities range from near-fresh to 8-10 mg/l on a regular basis to discourage alien species and favor desirable species; (7) create habitat conditions that support higher and more variable site-specific native species diversity; (8) establish abundant annual floodplain habitat, with large areas that flood in less frequent wet years; (9) reduce inputs of pollutants; and (10) improve temperature regimes in large areas so temperatures rarely exceed 20° C during summer and fall. These actions collectively provide a realistic approach to achieving flow and habitat objectives to benefit desirable species. Some of the goals are likely to be achieved as the result of sea level rise, climate change, and levee failures, but habitat, flow restoration and export reduction projects will enhance a return to a more variable and more productive ecosystem. This finding has widespread support in ecological theory and observations from other systems, but making quantitative predictions of change is not yet possible.

Introduction
The Sacramento-San Joaquin Estuary, especially the Delta, must be more variable in space and time than it is today if it is 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 River are key actions to push the estuary towards a more desirable state. The basic rationale for the preceding statements is that unmodified estuaries are highly variable and complex systems, renowned for their remarkable production of fish and other organisms (McLusky 1989). 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 estuary 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 paper has four objectives. The first objective is to characterize estuaries in general, describe how variability and complexity define them, and then discuss why these factors are so important. The second objective is to describe why salinity is such a useful and available indicator of estuarine heterogeneity. The third objective is to describe the variability and complexity of the San Francisco Estuary in the past, present, and future, in relation to adaptations...
of key fish species. The fourth objective is to recommend water and habitat management actions to re-establish variability and complexity and discuss policy implications of these actions.

**Estuaries**

Estuaries are places where fresh water from the land mixes with salt water from the coastal ocean within a semi-confined area (Pritchard 1967). Their natural history involves sustaining 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, such as Egypt, China, Mesopotamia, and most European countries, which established their major cities on estuaries. Arguably, declines of civilizations involved mistreatment of their 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). Estuaries also provide water access to the inland rivers and oceanic transport, and are convenient places to discharge wastes from human activities. 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 numerous efforts to restore some of the ecosystem services they once provided, especially fisheries (e.g., federal Estuary Restoration Act of 2000).

Restoration of estuarine ecosystem services requires re-establishing, at multiple scales, high physical and chemical variability in time and space (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, we dike and drain estuarine marshes to build cities and farms and then are surprised when extreme tides and high flows cause the dikes to fail. We dump wastes into rivers and then are surprised when the tides bring them back to us and the fish become toxic to eat. We simplify habitat, dredge channels, eliminate floodplains and marshes, divert inflowing water, and bring new species to the ecosystem, and then are surprised when food webs change in unfavorable ways, fisheries collapse, and endemic species become threatened with extinction. Estuaries worldwide have experienced similar changes and have lost many of their desirable natural attributes, especially sustainable fish populations. They also are increasingly the focus of restoration efforts.

**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 regularity can be further modified by changes in astronomical forcing, sea level, and strong winds. River flows also 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 is a key process promoting estuarine variability (Lucas et al. 2006). Caused by the interaction between river and tidal flows, tidal mixing establishes various water quality gradients between an estuary’s landward and seaward margins. 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 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 salinity 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 relatively narrow salinity range; they experience physiological stress only when forced to abandon the favored range due to other physical changes (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 because the range is optimal for 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 optimal conditions at specific times (e.g., seasons). Not surprisingly, fish species have adapted diverse life history strategies for using estuaries. 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). Not surprisingly, overall species richness is typically fairly high in 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). Freshwater flow brings in nutrients that promote primary production (photosynthesis by algae), while tidal energy and turbulence keep nutrients in circulation within the estuary. This mixing 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 mixed tidal water is distributed over a complex landscape, including areas of tidal marsh and floodplain, estuaries (Nixon 1988). This ecosystem “fertilization” process, is often cited as a mechanism underlying positive relationships between freshwater flow 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**

All species live in a highly variable landscape from their particular perspective. Accordingly, a vast ecological literature documents the significant roles played by habitat complexity and variability in promoting abundance, diversity, and persistence of species in a wide array of ecosystems1. 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 their fluctuations alter connectivity among patches and promote increased turnover of resources (productivity), enabling those resources to be available to a shifting array of species. The variability implies that different processes will interact at various spatiotemporal scales, but will result overall in more species being 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 (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 an example 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

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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).
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 population growth rates dominated deep-water (light-limited) habitat. Model simulations then showed that transport of phytoplankton to deep-water habitat, and 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 results in reduced phytoplankton-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.

Studies on the complex 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 current 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, undiked 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, carrying nutrients. In contrast, in adjacent sloughs that have been simplified and stabilized with dikes, water flows rapidly back and forth, increasing homogenizing water quality. The natural sloughs 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; complex slough geometry promotes higher variability in water quality across a landscape. This heterogeneous, variable estuarine landscape 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 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 system with inherent nonlinearities, feedbacks across scales, and stochastic behavior that will always be uniquely expressed at the landscape scale (Levins and Culver 1971). In other words, we cannot rebuild an estuary with desirable characteristics just by using numbers of desirable organisms as building blocks at some contracted price (e.g., fish from a hatchery) as one would construct a town. But we can enhance key processes that increase variability and complexity, to produce positive changes in the estuary.
Salinity: a key indicator

Given that major change is inevitable in the San Francisco Estuary, 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 characteristics usually co-vary with salinity, including water residence times, temperature, suspended sediment, and organism composition. Although humans typically appreciate change only at seasonal and annual scales, there are at least six attributes, or scales, at which salinity variability is important (Variable Salinity Workshop 2007):

• 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—defined as the reliability of gradient change on a tidal, seasonal or inter-annual scale
• Rate of change—a measure of 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 differ in their salinity requirements and time scales at which they respond to salinity changes. There is such large inherent uncertainty that searching for a single optimal set of conditions based on these attributes is unlikely to come up with a satisfactory solution. Nevertheless, three basic premises (assumptions) suggest that a focus on salinity variation is an appropriate (but not exclusive) direction for restoring variability and complexity to the estuary:

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

2. A more variable, heterogeneous estuary (especially the Delta) will also be more productive, increasing energy flow into desirable food webs and species.

3. Given some uncertainty in how species respond to conditions, more spatially variable conditions 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 and increased complexity and variability should provide more opportunities for native species to find conditions they need to survive.

An example of salinity variability that largely favors desirable fishes and discourages alien clams and aquatic plants can be found in Suisun Marsh (Figure 1). Compared to the Delta, the marsh has large annual ranges in salinity (and is usually fresh in winter) as well as large variation among years in mean salinity. There is also large variability in salinities within 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.
San Francisco Estuary: historic conditions.

The San Francisco Estuary is a young estuary, probably about 6,000 years old in its present location (Atwater et al. 1979; Healey et al. 2008). The Delta, misnamed from a geological perspective, was formed as a huge tule marsh through the interaction of the slow rise of sea level with the growth of the 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.’ 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 not particularly rich in native aquatic species because of its young age and relative isolation from other large estuaries. However, its high productivity and complexity attracted a high diversity and numbers of birds, especially waterfowl.

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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.
Figure 2: (a) The Delta in 1860, illustrating the highly complex and distributary pattern of river flows through the Delta and (b) in 1900s, illustrating the highly complex and distributary pattern of river flows through the 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 (Figure 3). The complex network of channels has been simplified into a series of ditches and canals, while the productive marshlands have been divorced from the estuary, mostly for agricultural and urban uses. In short, the complex landscape of the San Francisco Estuary has been greatly simplified.
Despite these changes, the San Francisco Estuary is still inherently complex at the landscape scale as the result of its structure with distinct regions (Delta, Suisun-Bay Marsh, San Pablo Bay, San Francisco Bay) and two major inflowing rivers (Sacramento, San Joaquin). This structure creates complex channels, combining the narrow, deep passages at Carquinez Strait and the Golden Gate with channels of variable depths that adjoin broad expanses of shallow shoals (Figure 4). As a result, tidal patterns and water quality gradients (especially salinity) are warped in complex ways so linear gradients are not maintained. The native aquatic fauna show adaptations to these complex 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 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.

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3 Residence time is essentially the length of time a particle (e.g., algal cell) 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.
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 generated by 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 (Healey et al. 2008). Because of such variability, San Francisco Bay could have surface waters that were largely fresh in some years, while brackish water could intrude into the western Delta in extremely dry years. 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 of waterfowl to overwinter in California.
Figure 5. Mean salinity (ppt) +/- SD for the 54 most common species of fish, shrimp, and crabs collected during CDFG's Bay Study, 1980-95. 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.

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 (*Arctoplites 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. As the estuary and inflowing rivers and their floodplains became developed, and as new species were brought in, 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, longfin smelt). Waterfowl populations have largely shifted away from the Delta to refuges and flooded rice paddies in the Sacramento and San Joaquin valleys.

The variability and productivity of the estuary also is reflected in life history adaptations of species that evolved within it, for example, delta smelt (*Hypomesus transpacifius*), splittail (*Pogonichthys microlepidotus*), and Chinook salmon (*Oncorhynchus tshawystscha*). The delta smelt is found only in the San Francisco Estuary, where it lives in the brackish parts of the estuary and spawns in fresh water (Bennett 2005). It was presumably once abundant in the upper estuary, but is 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, the delta smelt has evolved a primarily one-year life cycle, so it must spawn successfully each year to maintain its historically large populations. 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. 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. They have a fine-grained perspective of the estuarine environment and clearly have been able to follow gradients of salinity, turbidity, and temperature to find favorable conditions.

*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 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 the floodplains drain in the spring to the brackish marshes. Here they reside until migrating upriver to spawn again. The salinity tolerance of this species (up to 18 ppt for extended periods) is remarkably high for a member of family Cyprinidae, a freshwater group of fishes (Moyle 2002), reflecting their relatively coarse-grained perspective of the 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

\(^4\) The historic abundance of delta smelt is poorly understood because as a small midwater fish there was virtually no appropriate sampling for it (e.g., midwater trawling) 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 threadfish shad (*Dorosoma petenense*), American shad (*Alosa sadipissima*), and juvenile striped bass (*Morone saxatilis*) (Moyle 2002).
with diverse patterns of rearing and migration) and, probably, through use of the estuary and its adjoining floodplains for rearing. We know that today juvenile Chinook on floodplains grow faster and larger than those in the main river and this was probably once true of the estuary as well, with its diverse habitats and abundant food (Sommer et al. 2001; Jeffres et al. 2008). For migrating freshwater juveniles in the process of 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 clearly evolved an exceptionally coarse-grained perspective of the estuarine environment and maintained a complexity of life history strategies and habitat use that enabled them to persist through different climatic regimes, which is typical of salmon (Hilborn et al. 2003).

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

**San Francisco Estuary: present and future**

The estuary, especially the Delta, has recently 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 has resulted in relatively clear, fresh water and an assemblage of primarily freshwater alien species. Essentially, the Delta has been simplified and stabilized into a conveyance system to export fresh water from and through the estuary during summer and to reduce freshwater outflows at other times of year. With the Delta stabilized as a freshwater system, Suisun Bay and Marsh have been kept as an essentially brackish water system, with San Francisco Bay more constantly as a marine system (Figure 5). Such prolonged stabilization, combined with a relatively rapid influx of alien species, has caused a regime shift 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 low salinity standards (Figure 6) and altered hydrology (Figure 7) in support of 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 the Delta food web. These riverine and lake species include Mississippi silverside (*Menidia audens*), largemouth bass (*Micropterus salmoides*), and multiple sunfish (*Lepomis*) species.

The ecosystem, however, is likely to dramatically shift again within about 50 years as the result of 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. 2008). These significant changes will create large areas of open water, as well as new tidal and subtidal marshes. Other likely changes include

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\(^5\) Ecosystem engineers are organisms that regulate or change ecosystem functioning through their actions (e.g., Mosepele et al. 2009). 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.
reduced freshwater inflow during prolonged droughts, altered hydrology from reduced export pumping, and additional alien invaders (e.g., zebra mussel, *Dreissena polymorpha*). 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, these 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).

![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 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).](image-url)
Towards a more heterogeneous/variable estuary

So, what is needed to create a more heterogeneous estuary in time and space? Here we provide ten general directions for management of the San Francisco Estuary, especially the Delta and Suisun Marsh. 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.

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. Thus, water is released from reservoirs to hold back salinity intrusion and is moved, in a diffuse fashion, across the Delta. 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 an environment that can confuse 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. Current conditions favor resident freshwater invasive organisms such as largemouth bass and Brazilian waterweed. 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 historic extensive dendritic drainage patterns in sloughs and marshes is essential for re-establishing complex habitats and gradients in salinity, depth and other environmental characteristics important to desirable fish and other organisms. These shallow, complex 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 River.** 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 before it flows to the Delta. Consequently, San Joaquin River flows are greatly diminished and burdened with great salt loads from agricultural drainage. 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.

4. **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 duck hunting (Figure 3). Unfortunately, most such habitat in shallow water today is dominated by alien fishes, including highly abundant species such as Mississippi silverside that are competitors with and predators on native fishes (Moyle and Bennett 1996; Brown 2003). Such habitat might 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
higher abundance of 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 mg/l) 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, 2008; 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. 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 channels that run between islands today. 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 mg/l 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 ranges in this recommendation but the basic idea is that fairly high fluctuations in salinities would discourage freshwater organisms in the western Delta, especially Brazilian waterweed, 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. This would require changes in water management operations.

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 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 spawning streams).

c) **Creating more floodplain habitat**

8. **Establish abundant annual floodplain habitat, with large areas that flood in less frequent 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. 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 fairly easily 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.

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. Many sources of pollutants need to be reduced, including agricultural return water which has only recently seen regulation (Healey et al. 2008).

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.

**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 in particular 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 modifications. Depending upon 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 hard-fought water management policies, practices, and expectations and are likely to conflict with some 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 highly 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 significantly. 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 unavoidably involve experimentation. This experimentation might be unintentional as islands fail, legal verdicts are rendered, and mistakes are made. More useful and less expensive experimentation would take the form of more intentional, formal, and relatively controlled 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 export large volumes of water through the Delta. 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 an ecosystem that is much less heterogenous in structure and water quality, making it less productive than it was historically and resulting in declines of many fish species. 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 restoring its physical habitat variability, its variability in tidal and riverine flows, and its variability in water chemistry, especially salinity, over multiple scales of time and space. 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 enhance the return of the estuary to a more variable and more productive ecosystem.

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