Habitat Variability and Complexity in the San Francisco Estuary

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Abstract

In this essay, we describe estuarine variability in relation to the San Francisco Estuary, especially the Delta, describing the characteristics of the estuary which once made it so productive and to which the native fishes are adapted. We then show how present conditions and trends discourage desirable species and reduce desirable ecosystem attributes, providing a rationale for restoring estuarine variability and complexity. Ten desirable characteristics of a variable, more ecologically complex Delta and Suisun Marsh are: (1) internal Delta flows that basically create a tidally-mixed, upstream-downstream gradient, (2) increased tidal marsh habitat in both fresh water and brackish water, including shallow (1-2 m) subtidal habitat (especially in Suisun Marsh), (3) more slough networks with natural channel geometry and less diked, rip-rapped channel habitat, (4) salinities in the Delta and Suisun Bay and Marsh that range from near-fresh to 8-10 mg/l on a regular basis, (5) large expanses of low salinity (1-4 mg/l) open water habitat during summer-fall, (6) abundant annual floodplain habitat, with larger areas that flood in less frequent wet years, (7) improved flows from the San Joaquin River, (8) reduced inflow of agricultural and urban pollutants, (9) higher and more variable site-specific species diversity, including reduced abundance of non-native invasive species that alter ecosystem functioning, and (10) temperatures in large areas that rarely exceed 20 degrees C during summer and fall. These ideas may be useful in preparing water and habitat management actions to improve conditions for estuarine fishes in the Sacramento-San Joaquin Delta.

Introduction

Lund et al. (2007) and Moyle and Bennett (2008) suggest that the Sacramento-San Joaquin Estuary, especially the Delta, should be more variable in space and time than it is today if it is going to become a more favorable environment for desirable aquatic species, such as delta smelt and striped bass. In particular, they indicate that increased variability in salinity is a key factor that could drive the ecosystem towards a more desirable state. The underlying basis for this position is that unmodified estuaries are highly variable systems and yet are also remarkably productive of fish and other organisms (McLusky 1989). In this essay we first introduce estuaries as ecosystems along with the concept of estuarine variability. We then relate this background material to the historic San Francisco Estuary, describing the characteristics of the estuary which once made it so productive and to which the native fishes are adapted. Next, we briefly describe present conditions in the estuary and the environmental direction in which the estuary seems to be headed, based on Lund et al. (2007), Lund et al. (2008), Moyle and Bennett (2008), and Moyle (2008). We then show how present conditions and trends relate to the requirements of desirable species and desirable ecosystem attributes.

Finally, we will describe the ecological rationale for restoring estuarine variability, provide ten key characteristics of a variable estuary, and draw some brief policy implications and conclusions. This perspective is offered to help develop coherent water and habitat management actions to improve conditions for estuarine fishes in the Sacramento-San Joaquin Delta and Suisun Marsh.

Estuaries

Estuaries are places where large quantities of fresh water draining from the land mix with salt water in a semi-confined area (Pritchard 1967). Every place a river meets the sea there is usually an estuary, with important natural and human histories. Their natural history involves high productivity which sustains large populations of fish, invertebrates, aquatic birds, and mammals and benefits surrounding terrestrial systems as well. Their human history involves our tendency to locate cities on estuaries, to dike and drain their adjacent wetlands for farming, and to heavily harvest estuarine-dependent fish and invertebrates (Lotze et al. 2006). Estuaries provide water access to the inland rivers and are convenient places to discharge wastes from human activities. Not surprisingly, estuaries worldwide are both among the world's most valuable (to humans) 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).

However, restoration of estuarine ecosystem services requires re-establishing a key attribute of estuaries: their high physical and chemical variability in time and space, at multiple scales. This fundamental attribute of estuaries runs contrary to the dominant human approach to ecosystem management, which is to try to maximize yield of goods and services valuable to humans by reducing and simplifying the natural variability of ecosystems (Pahl-Wostl 1998). Estuaries worldwide have thus become channelized, dredged, and highly polluted systems which have lost many of their desirable natural attributes, especially for sustaining fish and fisheries. The widespread failure of ecosystem simplification is an indication that restoring estuarine ecosystems requires re-establishing variability and complexity.

Estuarine variability

The inherent variability of estuaries stems from being located where two dynamic systems, rivers and coastal oceans, meet in a confining 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. Tidal ocean forces, amplified in a confined space, have a regular pattern, waxing and waning in response to the pull of the moon and the sun. This tidal regularity, however, can be modified by changes in astronomical forcing, sea level, complex geographic features, and strong winds. The forces of river flow also vary seasonally, typically with an annual pattern of high and low flow, but inter-annual river flow also varies enormously, reflecting wet years and droughts. In addition, rivers supply sediment to estuaries, which is reworked by both the river and the tides to form the estuary's complex and shifting landscape. The most distinctive feature of estuaries, however, is the variability generated 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 gradients in salinity and temperature between the landward and seaward margins of estuaries. 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 that results from tidal mixing is then 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 shorter 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 the environment is physiologically stressful to most organisms. There can thus be a high energetic cost to living in estuaries. The variability also means it can be hard to stay in one place; tidal flows move individuals around and can expose them to wide ranges of salinity over short periods of time. Not surprisingly, given the physiological challenges of living in an estuarine environment, many organisms are adapted for living specifically 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 by it. Each species experiences estuarine conditions somewhat differently from other species in the same estuary. For some, the environmental variability they experience in space and time is large (i.e., coarse-grained) and for others it is small (i.e., fine-grained), relative 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 across it with the tides. These changes can be stressful or even lethal at times. In contrast, a small fish may experience the environment as fine-grained because it can swim to keep itself within a relatively narrow salinity range. It experiences physiological stress from salinity only when it is forced to abandon the favored range as the result of other physical changes, risk of predation, or lack of food.

Thus, the life history strategies of organisms vary according to how they encounter the environment, which in estuaries is typically 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 can tolerate a wide range of salinities often have a much narrower range that they mainly use because it is optimal for growth and survival. Consequently, organisms that are adapted for living specifically in estuaries tend to use only a particular subset of the variable conditions, or have life history stages that are adapted for using optimal conditions at specific times (seasons). This is reflected in the nature of estuarine fish faunas. Worldwide, different fish species present in estuaries have different strategies for using estuaries. Some move in and out on a seasonal basis, usually for spawning and rearing, while others are full-time residents, with a component of freshwater and marine species living at the landward and seaward margins (Moyle and Cech 2002). Not surprisingly, overall species diversity 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 point in space and time within the estuary. However, at any given time only a relatively small number of fish species (5-20) tend to dominant in terms of numbers and biomass.

Estuarine variability is also considered to be a primary factor promoting the high productivity typically observed in estuaries (Nixon et al. 1986). Freshwater flow brings in nutrients that promote primary production (photosynthesis by algae), while tidal energy and turbulence keep the nutrients in circulation within the estuary. This mixing effect promotes the growth of planktonic organisms, which form the base of food webs that include fish and other organisms of direct interest to humans. Thus when the tidal water is distributed over a variable landscape, including areas of tidal marsh and floodplain, estuaries become some of the most productive areas in the world for fish and other organisms (Nixon 1988). This ecosystem "fertilization" process, referred to as the Agricultural Model of production (Nixon et al. 1986), is often cited as a mechanism underlying positive relationships between freshwater flow and fish abundance in estuaries (Houde and Rutherford 1993). Thus, despite their relatively small geographical area, estuaries are often essential for supporting diverse marine, freshwater, and estuarine fisheries, especially because of their role as productive nursery areas for larval and juvenile fish (Beck et al. 2001).

Societal demands for stable, predictable physical systems, however, conflict with variable estuaries, despite the high benefits to fisheries. We dike and drain the marshes to build cities and farms and then are surprised when extreme tides and high flows cause the dikes to fail. We dump our wastes into the rivers and then are surprised when the tides bring them back to us and the fish become toxic to eat. We simplify the habitat, dredging channels, eliminating floodplains and marshes, and diverting inflowing water, and then are surprised when fisheries collapse and species become threatened with extinction. We bring in new species to live in the ecosystem and then are surprised when food webs change in unfavorable ways.

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[1], 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. The rising water 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 between the islands were historically shifting, winding distributaries of the entering river systems that moved inflowing water through the Delta and provided access to upstream areas for migratory fish (Figure 1).

[1] 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.

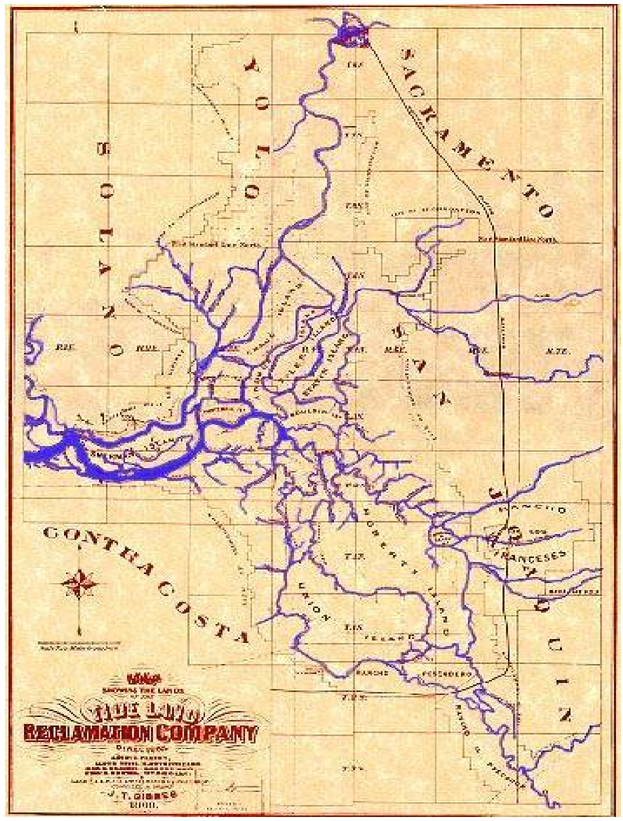

Figure 1a: The Delta in 1860, illustrating the highly complex and distributary pattern of river flows through the Delta.

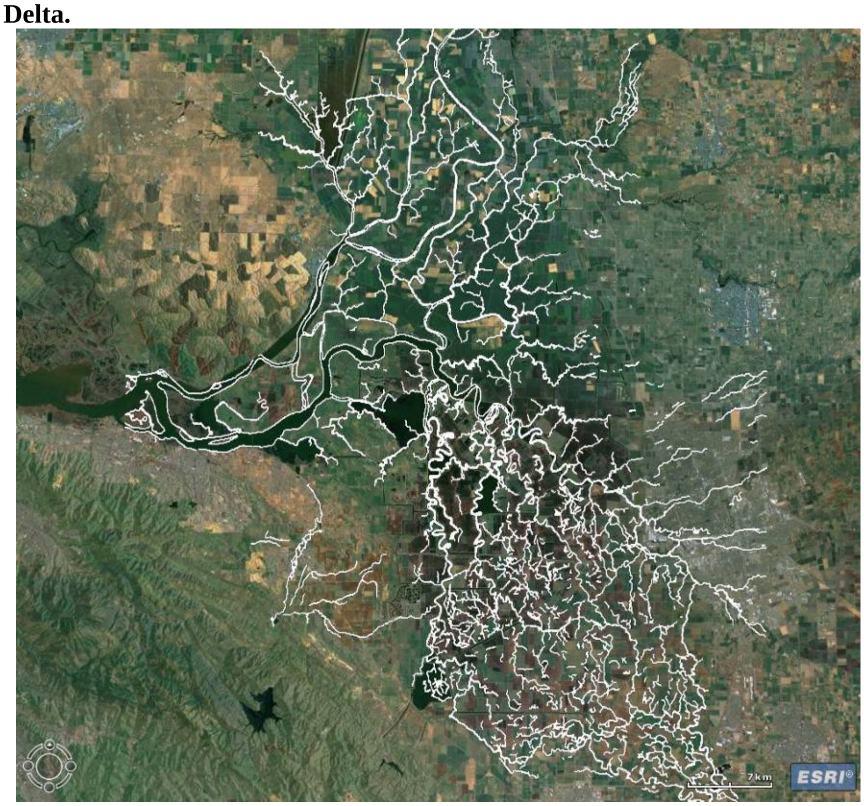

Figure 1b: The Delta in 1900s, illustrating the highly complex and distributary pattern of river flows through the Delta. (Courtesy, Chris Enright using Atwater data)

The historic configuration of the Delta, as well as the rest of the estuary, has been altered by the diking and draining of over 90% of its wetlands (Figure 2). The complex channels have been turned into ditches and canals, while the productive marshlands have been divorced from the estuary, many converted to agricultural and urban uses. In short, the complex landscape of the San Francisco Estuary has been greatly simplified.

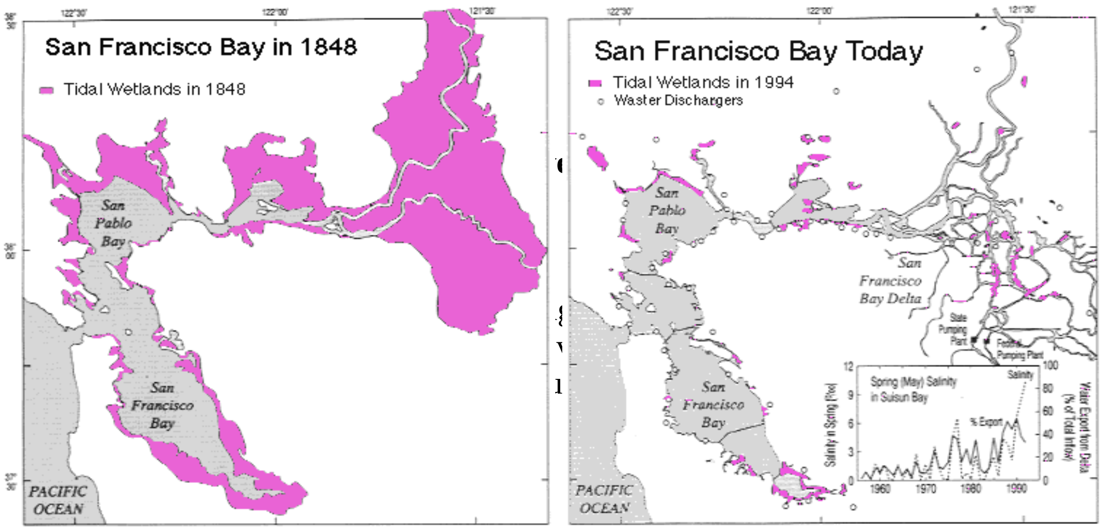

Figure 2: Extent of marshlands and wetlands in the San Francisco Estuary system in 1848 and present. (reprinted from http://sfbay.wr.usgs.gov/general _factsheets/change.html)

Because of the estuary's young age, the native aquatic fauna is not particularly rich in native species, but nevertheless there are endemic organisms that show specific adaptations to estuarine conditions, including tolerance of wide but specific salinity ranges (Figure 3).

The San Francisco Estuary may not be very old, but it is an extremely complex estuary, as the result of its unique structure, with distinct regions (Delta, Suisun-Bay Marsh, San Pablo Bay, San Francisco Bay) and two major inflowing rivers (Sacramento, San Joaquin). The estuary's hydrology also is complex, combining the narrow, deep passages at Carquinez Strait and the Golden Gate, with channels of variable depths adjoining broad expanses of shallow shoals (Figure 4). This complex and extensive structure tends to warp the tidal patterns and water quality gradients (especially salinity) in complex ways.

Historically, this complexity was enhanced by the extensive marshes that existed along the edges of the estuary, including Suisun Marsh, as well as by the marshes that are now Delta islands (Figure 2). 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[2] and quality. In addition, the Delta and Suisun Marsh once merged imperceptibly with floodplains and riparian forests along the inflowing rivers; flooded areas would have retained outflows and drained slowly through the spring season.

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[2] Residence time is essentially the length of time a particle (e.g., algal cell) in a body of water stays in a fairly limited area. The higher the residence time, the more likely that blooms of phytoplankton and zooplankton will develop in the open water that will be part of food webs leading to fish. Such blooms

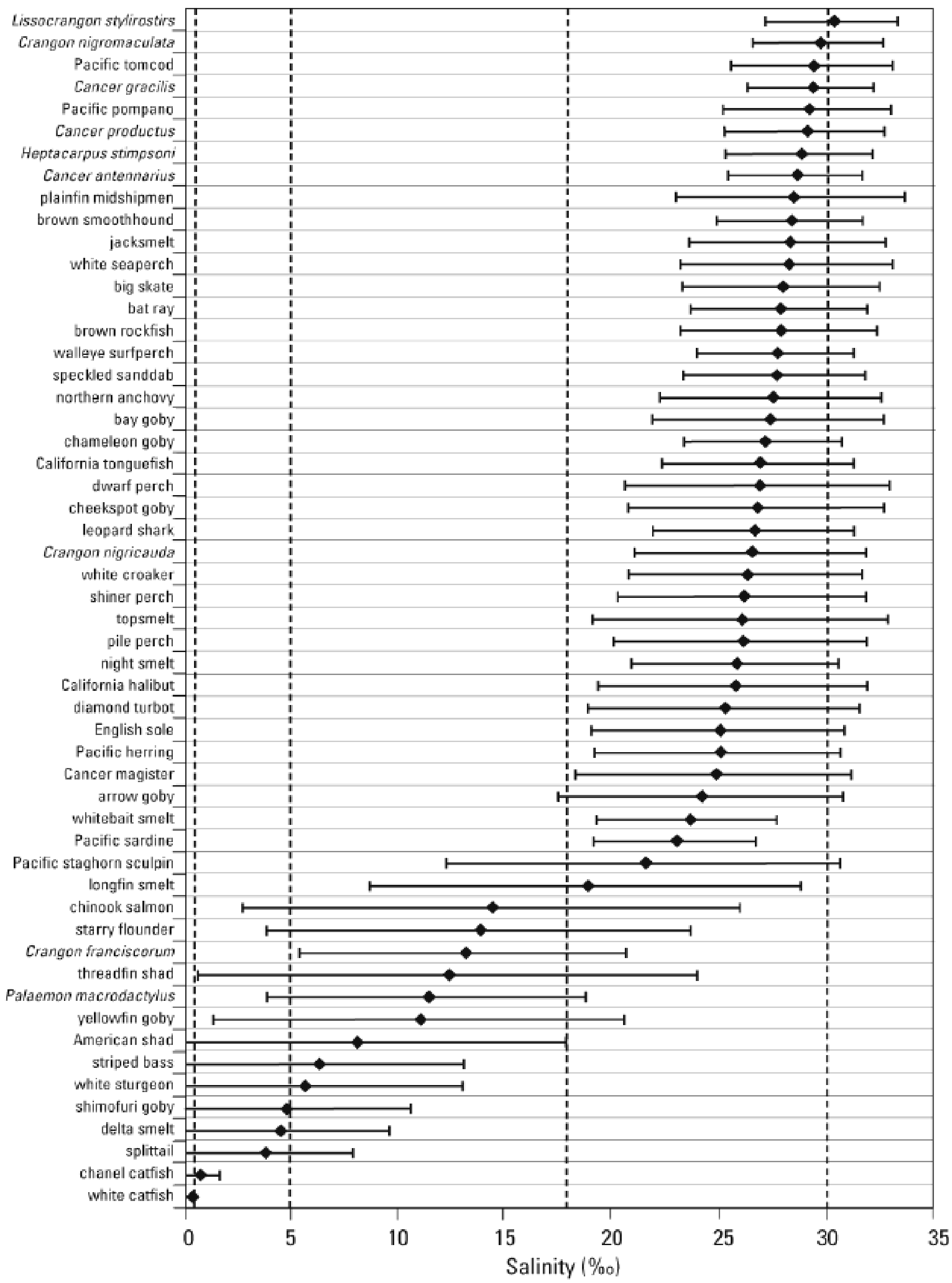

Figure 3. Mean salinity (ppt) +/- SD for the 54 most common species of fish, shrimp, and crabs collected during CDFG's Bay Study, 1980-95. From Baxter et al. 1999. All species are native except chameleon goby, *P. macrodactylus*, yellowfin goby, American shad, striped bass, shimofuri goby,

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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 and because organisms are carried downstream, out of area.

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.

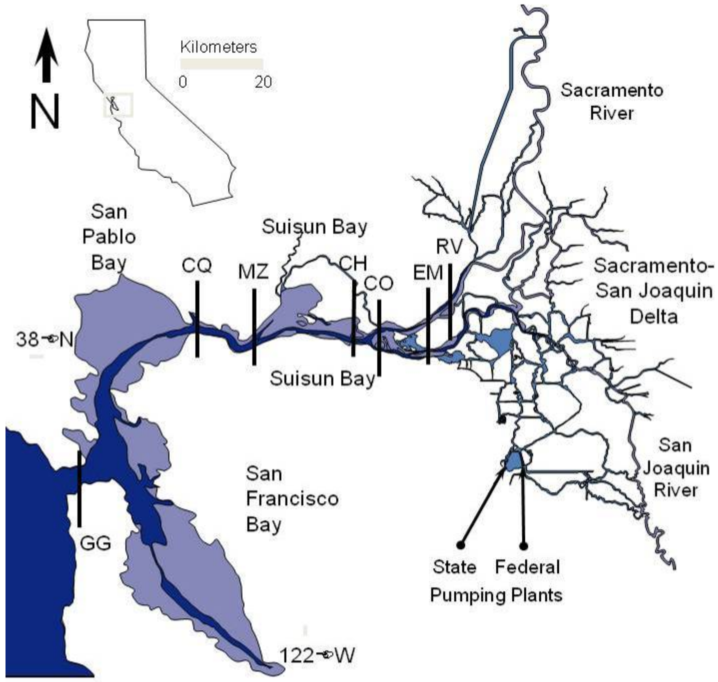

Figure 4. Map of San Francisco Estuary and Delta, showing major basins, channels, and shoals (10m depth contour). Paired letters indicate geographical landmarks. GG, Golden Gate Bridge; CQ, Carquinez Bridge; MZ, Martinez Bridge; CH, Chipps Island; CO, Collinsville; EM, Emmaton; and RV, Rio Vista.

Imposed on this complex, variable structure was a highly variable flow regime, both seasonally and across years. The basic seasonal pattern was 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 extremely high productivity likely generated by the nutrients from the extensive marshes and floodplains and the dispersion of these nutrients by the complex hydrology and tidal flows throughout the system and into the estuarine food webs. 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 every 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 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).

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

Smelt, splittail, and salmon

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 very abundant in the upper estuary, although it is now listed as an endangered species.[3] 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 low 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 has to spawn successfully every 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 periods of severe drought and extreme flood. It also means the smelt could easily find those conditions in the 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 the conditions they favor.

Sacramento splittail are now also largely confined to the estuary and rivers immediately upstream from it, 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. They apparently 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, among annual vegetation, but then move downstream, as the floodplains drain in the spring, to the brackish marshes where they reside until migrating upriver to spawn. The salinity tolerance of this species (up to 18 ppt for extended periods of time) is remarkably high for a member of family Cyprinidae, a freshwater group of fishes (Moyle 2002), and reflects 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, with diverse patterns of rearing and migration within each run) and, probably, through use of the estuary and its adjoining floodplains for

[3] 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).

rearing. We know that today juvenile Chinook on floodplains grow faster and larger than those in the main river and it is likely that this was 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 being saltwater fish, favorable conditions were presumably always present somewhere in the estuary. Chinook salmon clearly evolved an exceptionally coarse-grained perspective of the estuarine environment.

The fact that populations of these and other estuarine-dependent native fish are a small fraction of their historic abundance and are 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

Moyle and Bennett (2008) and Fleenor et al. (2008) present evidence that the estuary, especially the Delta, has been managed to limit its variability over the last half-century. As a result, it has recently shifted into a new regime characterized by an assemblage of alien species. Essentially, the Delta has been simplified and stabilized into a conveyance system to export fresh water from and through the estuary during the summer. With the Delta stabilized as a freshwater system, Suisun Bay and Marsh essentially have been kept as a 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 in the apparent loss of resiliency by pelagic fish populations that previously were able to rebound during periods of favorable environmental conditions (Sommer et al. 2007). The prolonged application of low salinity standards (Figure 5) and altered hydrology (Figure 6) in support of pumping operations has reduced variability in salinity during the critical summer months, favoring the expansion of alien 'ecosystem engineers'[4] 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 shift again, dramatically, within about 50 years from 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 result in the creation of large areas of open water, as well as new tidal and subtidal

[4] Ecosystem engineers are organisms that regulate or change ecosystem functioning through their actions (e.g., Mosepele et al. 2009). Thus the overbite clam has caused a major shift in the food web of Suisun Bay from centering on pelagic organisms to centering on benthic organisms, contributing to the decline of pelagic fish.

marshes. Other likely changes include 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 is 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).

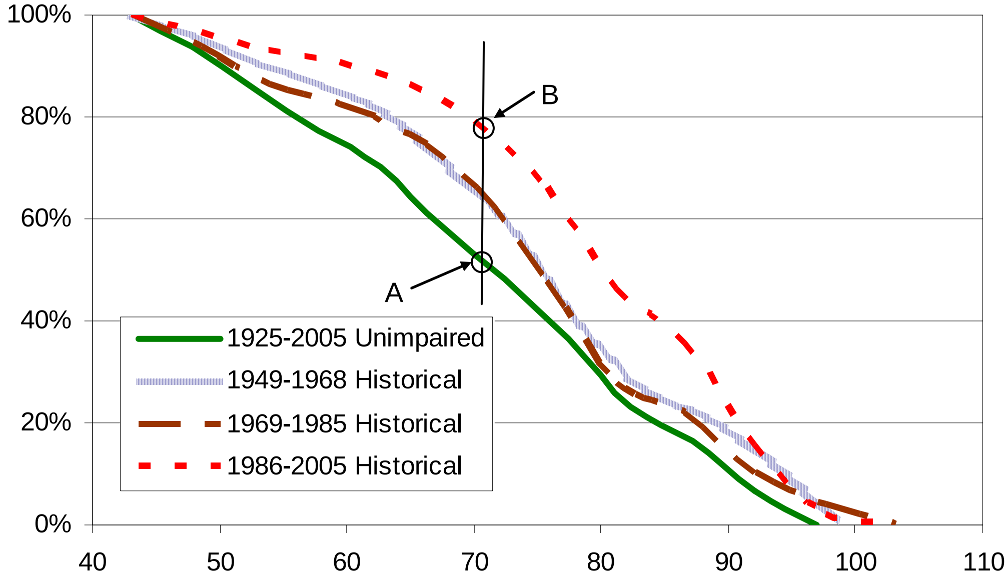

Figure 5. Cumulative probability distributions of daily X2 locations showing unimpaired flows (green solid line) and three historical periods, 1949-1968 (light solid blue line), 1969-1985 (long-dashed brown line) and 1986-2005 (dashed red line), illustrating progressive reduction in salinity variability (increase in freshwater conditions) from unimpaired conditions. X2 is the location of the 2 ppt salinity region of the estuary in terms of 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 boundary conditions from DWR and historical boundary conditions from Dayflow, analyzed by W. Fleenor

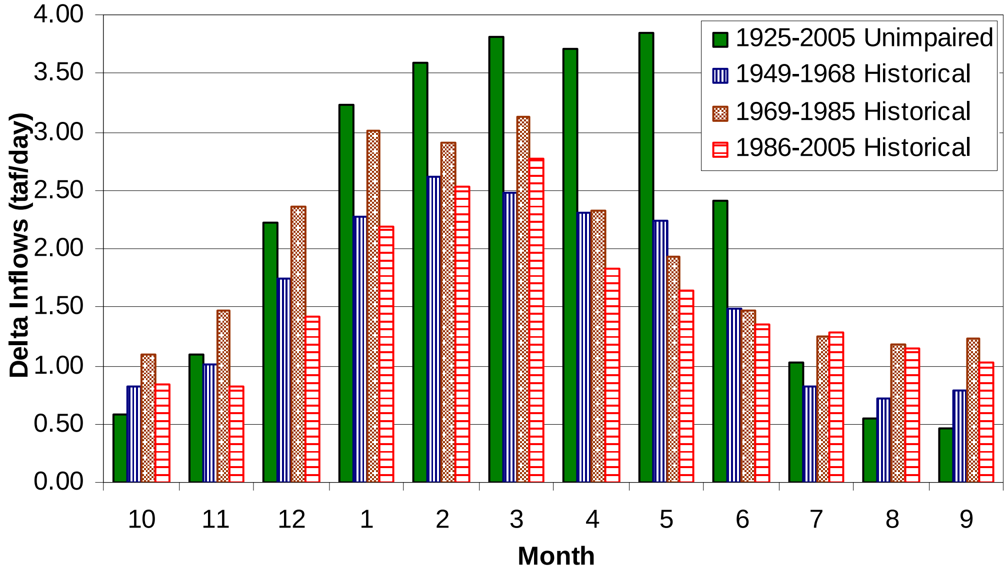

Figure 6. Sum of daily averaged inflows each month from Sacramento and San Joaquin rivers showing unimpaired flows (solid green bar) and three historical periods, 1949-1968 (vertically-striped blue), 1969-1985 (brown) and 1986-2005 (horizontally-striped red) , illustrating progressive changes to inflow from unimpaired conditions. Note the *increases* in summer inflow during recent decades. Data from unimpaired boundary conditions (DWR) and historical boundary conditions (Dayflow), analyzed by W. Fleenor.

Salinity: a key indicator

Given that major change is inevitable in the Delta, we have 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. 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 basis.
- 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 will promote 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 direction for restoring the variable 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 a more productive system, 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 more homogeneous Delta is not working very well for native species and increased variability should provide more opportunities for the natives 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 7). In comparison 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 the salinities at different places in Suisun Marsh at different times of year (not shown in Figure 7). Suisun Marsh also continues to support higher numbers of native fishes than the current Delta.

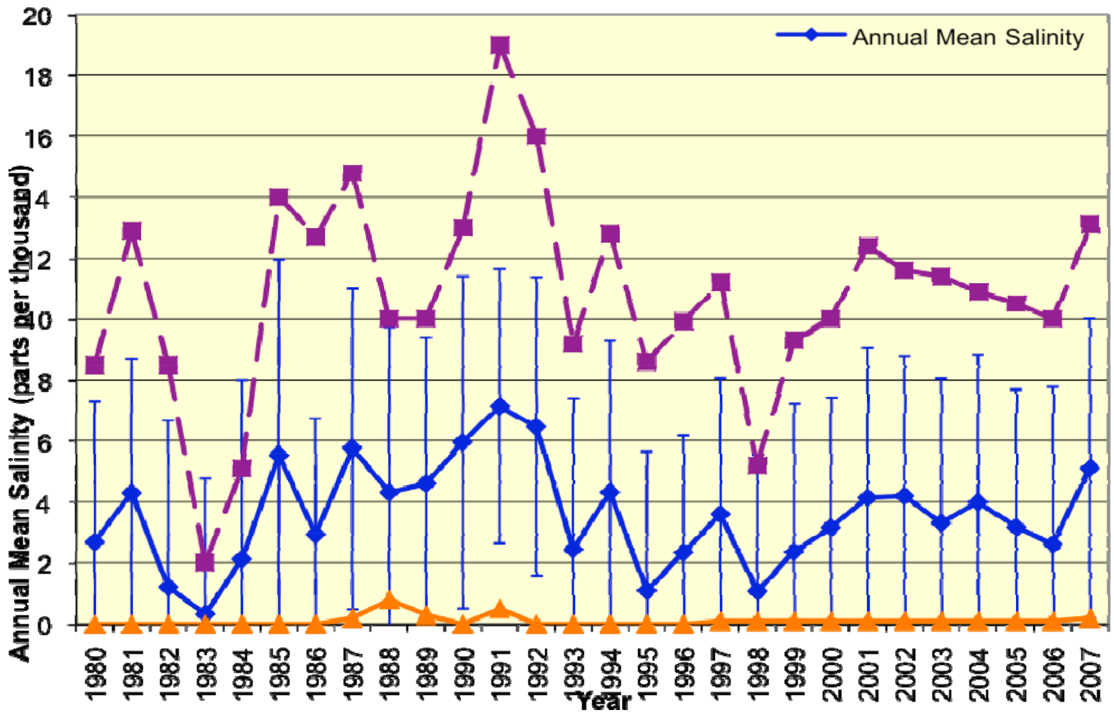

Figure 7. Mean annual salinity (with standard deviation, middle blue line), and annual minimum (bottom orange line) and maximum (top purple line) salinities for Suisun Marsh based on monthly measurements taken at 18-24 stations in the marsh (Moyle, unpublished data). Sea water is about 35 ppt.

Rationale: why is estuarine complexity and variability 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 the abundance, diversity, and persistence of species in a wide array of ecosystems[5]. This literature stresses the importance of connectivity among patches of favorable habitat for each species. However, landscapes are not stable in their configurations through time and their constant change alters connectivity among patches and promotes increased turnover of resources (productivity), enabling those resources to be available to a shifting array of species. The variability results in higher numbers of species being present overall 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 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 for phytoplankton growth in the shallow habitat and phytoplankton-food for zooplankton in the deeper habitat. Similarly, productivity rates are lowered 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 ways that water moves through the Delta and Suisun Marsh (Jon Burau, USGS; Chris Enright, CDWR; and others, 2009 DRERIP model)

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[5] The concepts of the *meta-population* (Levins 1969, Gilpin and Hanski 1991) and the *meta-community* (Levins and Culver 1971, Leibold et al. 2004) hold special promise for guiding our understanding of the importance of estuarine variability. 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 relative quality of each habitat patch (i.e., within-patch birth and death rates). This also holds true for meta-communities, or interacting sets of species (communities), that also move among isolated habitat patches at the landscape-scale (Levins and Culver 1971).

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, un-diked sloughs are considerably more variable in multiple water quality measures, because the water overflows onto the marsh plain on flood tides, whereas it flows rapidly through adjacent sloughs that have been stabilized with levees increasing mixing in the surrounding area. The natural sloughs also have higher abundances of desirable fishes (Moyle, unpublished data). Overall, this work shows that movement of water by tidal mixing homogenizes water quality in areas where tidal ebbs and flows can move water effectively among diked sloughs. Conceptually, estuarine physical forces (e.g., tidal and river flow) are filtered 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. Therefore, there is a substantial and growing scientific basis for promoting a heterogeneous estuarine landscape and for increasing variability overall to favor desirable species.

Ten characteristics of a more heterogeneous/variable estuary

What would a more variable Delta/estuary look like? We suggest the following as desirable characteristics:

1. **Internal Delta flows that create a tidally-mixed, upstream-downstream gradient (without cross-Delta flows)**. 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. This has led to an environment that can confuse migratory fish (e.g., juvenile salmon wind up in the middle of the Delta, where water temperatures are higher and water quality is otherwise unfavorable), and draw others such as delta smelt towards the South Delta pumps. These conditions, however, 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. **Increased 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 2). Unfortunately, most such habitat in shallow water today is dominated by alien fishes, including highly abundant species such as Mississippi silverside that are competitors

and predators with native fishes (Moyle and Bennett 1996; Brown 2003). It is possible that such habitat can become more favorable to 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 will become tidal marsh; this 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, in order to optimize habitat for desired fishes.

3. **More slough networks with natural channel geometry and less diked, rip-rapped channel habitat**. The simplified habitat in the channels between Delta islands is poor for most fishes. Many levees are maintained in a nearly vegetation-free state, providing little opportunity for complex habitat (e.g., fallen trees) to develop. Much of this habitat in the western and central Delta will disappear as islands flood, but remaining levees should be managed to increase habitat complexity (e.g., through planting of vegetation), especially in the cooler northern and eastern parts of the Delta.

4. **Salinities in parts of the Delta and Suisun Bay and Marsh that range from near-fresh to 8-10 mg/l on a regular basis (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 are needed to discourage freshwater organisms in the western Delta, especially Brazilian waterweed, and saltwater organisms in the brackish parts of the estuary, especially the overbite clam, (Suisun Bay and Marsh). 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.

5. **Large expanses of low salinity (1-4 mg/l) open water habitat during summer-fall.** Open water habitat is most likely to be created by the flooding of subsided islands in the Delta (Lund et al. 2007, 2008; Moyle 2008). The depth and managed 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 almost certainly likely to be better habitat for pelagic fishes than the rock-lined, steep-sided channels that run between the islands today. Helping to ensure these changes will favor desired species will require learning from experiments with controlled flooding of islands. 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 under unplanned flooding scenarios.

6. **Abundant annual floodplain habitat, with larger 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. 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.

7. **Improved 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. This will eventually be supplemented with San Joaquin River flows from the settlement agreement to restore Chinook salmon and other native fishes to the river. These flows need to be coordinated, and perhaps increased in some periods, to improve conditions in the south Delta for fish by (1) improving water quality through dilution, (2) increasing migration rates of juvenile salmon through the Delta, (3) reducing entrainment in the SWP and CVP pumps, (4) increasing net outflows during critical periods, and (5) improving habitat in the lower river through flooding of shallow areas. Of course, the best way to improve water quality for fish in the San Joaquin River would be to eliminate or greatly reduce pollution from agricultural return water, urban run-off, and sewage treatment plants or greatly reduce diversions of cleaner water from its tributaries.

8. **Reduced 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 at least four major sources (1) agricultural return water, (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).

9. **Conditions that support higher and more variable site-specific species diversity, including reduced abundance of non-native ecosystem engineers.** An increase in local biodiversity is likely to result if many of the above conditions are achieved, especially in combination, but diversity could be enhanced further by actions designed 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).

10. **Temperatures in large areas of the estuary that rarely exceed 20 degrees 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 a wider range in 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:

- First, most environmental and water management regulations for the Delta are intended to restrict variability. They therefore make it difficult to increase variability, which might be especially desirable for invasive species control. Salinity standards in particular would have to be changed to allow increased variability from water operations.
- Second, 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 of islands, setting back of levees, or breaching levees. These actions would require substantial revisions in current Delta levee policies.
- Third, the projected changes to the Delta as the result of sea level rise, island flooding, and other factors will likely 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.
- Fourth, 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.
- 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 fundamentally

inconsistent with the water quality and variability needs of desirable Delta species.

Conclusions

The San Francisco Estuary has become an ecosystem that is much less productive than it was historically, contributing to declines of many fish and invertebrate species. A major reason for the loss of productivity is likely to be the homogenization of habitat and water quality over large areas of the estuary, especially 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, flow restoration and export removal projects could enhance the return to a more variable and more productive ecosystem.

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