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Will Tidal Wetland Restoration Enhance Populations of Native Fishes?

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Abstract:
Restoration of tidal wetlands might enhance populations of native fishes in the San Francisco Estuary of California. The purpose of this paper is to: (1) review the currently available information regarding the importance of tidal wetlands to native fishes in the San Francisco Estuary, (2) construct conceptual models on the basis of available information, (3) identify key areas of scientific uncertainty, and (4) identify methods to improve conceptual models and reduce uncertainty. There are few quantitative data to suggest that restoration of tidal wetlands will substantially increase populations of native fishes. On a qualitative basis, there is some support for the idea that tidal wetland restoration will increase populations of some native fishes; however, the species deriving the most benefit from restoration might not be of great management concern at present. Invasion of the San Francisco Estuary by alien plants and animals appears to be a major factor in obscuring the expected link between tidal wetlands and native fishes. Large-scale adaptive management experiments (>100 hectares) appear to be the best available option for determining whether tidal wetlands will provide significant benefit to native fishes. Even if these experiments are unsuccessful at increasing native fish populations, the restored wetlands should benefit native birds, plants, and other organisms.

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Introduction

In the last 150 years, approximately 80% of the tidal wetlands in San Francisco Bay (hereafter "Bay") (Figure 1) have been lost, as have 95% in the Sacramento-San Joaquin Delta (hereafter "Delta," Figure 2) (TBI 1998). Concurrent declines in many native fishes could suggest a cause and effect relationship; however, many other environmental changes may have also contributed to the declines (Bennett and Moyle 1996). Water storage and diversions have modified the natural hydrologic and sediment regimes of the upper watersheds (Mount 1995) and consequently of the Delta and Bay. Delta hydrology and ecology have been altered by water diversions within the Delta, primarily the state and federal export pumps (see Figure 2) (Jassby and Powell 1994; Arthur and others 1996). Agricultural, industrial, and urban land uses in upstream areas and in the Delta have contributed potentially toxic concentrations of human-manufactured chemical compounds or increased concentrations of naturally occurring chemicals (Kuivila and Foe 1995; Hornberger and others 1999). Intentional and unintentional introductions of alien species may have fundamentally altered the structure and processes of the ecosystem (Carlton and others 1990; Nichols and others 1990; Alpine and Cloern 1992; Kimmerer and Orsi 1996). Bennett and Moyle (1996) observe that it is difficult to isolate the relative magnitude of any one of these multiple factors and that it is likely that the relative importance of any one factor will fluctuate annually or seasonally depending on environmental conditions. In addition, there have been few studies of the importance of tidal wetlands to the fishes of the San Francisco Estuary, (hereafter "Estuary," the combined Bay and Delta). Therefore, there is a high degree of uncertainty regarding the benefits of tidal wetland restoration for native fishes, including special status species such as delta smelt (*Hypomesus transpacificus*), chinook salmon (*Oncorhynchus tshawytscha*), steelhead rainbow trout (*O. mykiss*) and splittail (*Pogonichthys macrolepidotus*).

The established importance of tidal wetlands habitats to fishes of the Atlantic and Gulf coasts (Kneib 1997; Kruczynski and Ruth 1997) appears to support the idea that tidal wetland restoration will enhance native fishes in the Estuary. In eastern tidal wetlands, vegetated, shallow, near-shore habitats, including tidal wetlands, are widely recognized as important nursery areas for fish (Boesch and Turner 1984; Baltz and others 1993). Emergent and submerged vegetation can provide cover for smaller organisms, including fish, from larger predators (Kneib 1982, 1987; Kilgore and others 1989). Despite this increased probability of predator avoidance by prey, vegetated areas also supply rich feeding grounds for larger organisms, including predatory fish (Rozas and Odum 1987; Heck and Crowder 1991; Olmi and Lipcus 1991; Orth 1992). Vegetation provides substrate and food resources for invertebrate species (Van Dolah 1978; Gleason 1986; Gleason and Wellington 1988) that are important food resources for fish and other wildlife. Lubbers and others (1990) found that abundances of many fish species in Chesapeake Bay were positively correlated with plant biomass.

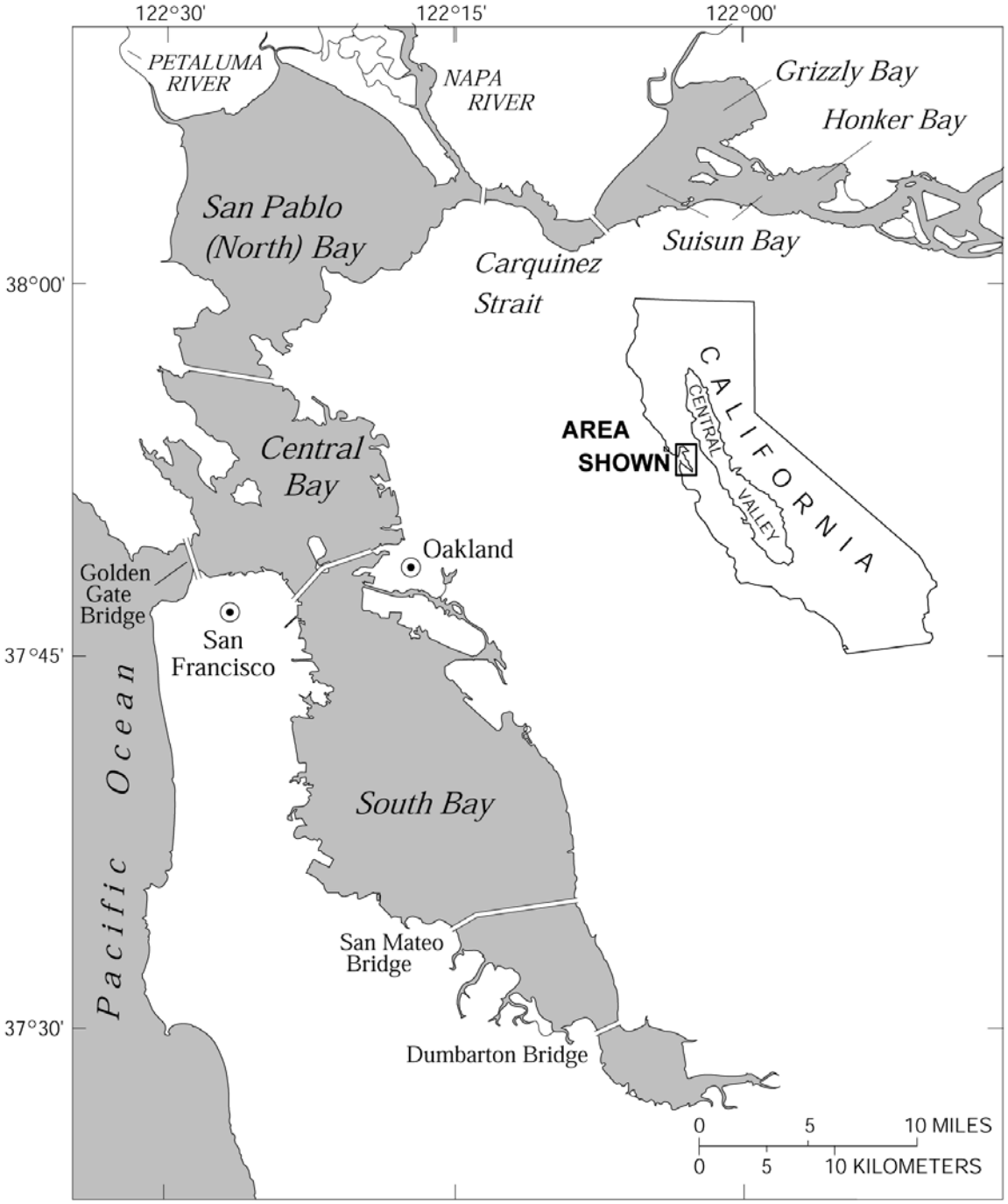

Figure 1 Areas and features within San Francisco Bay

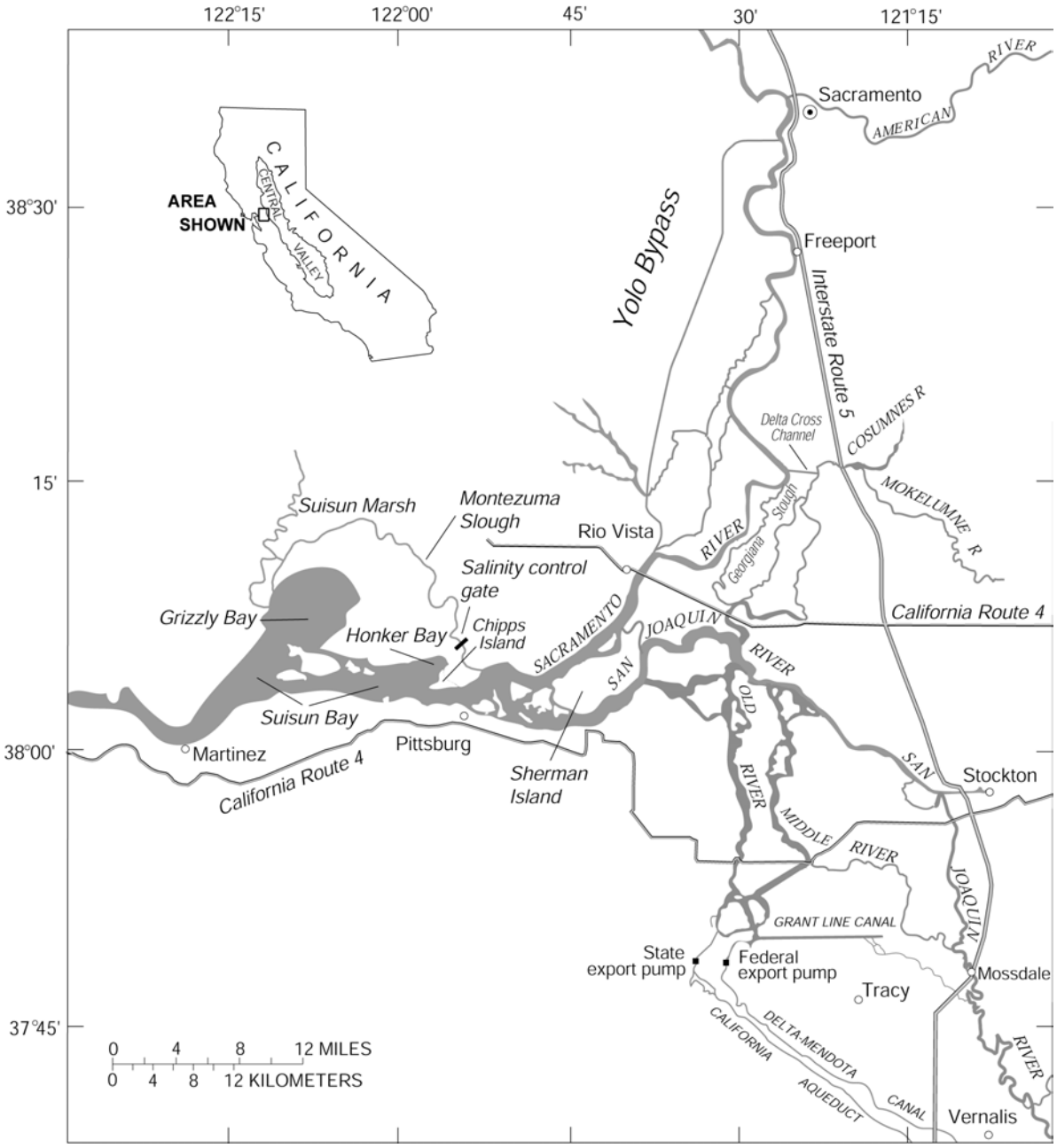

Figure 2 Areas and features within northern San Francisco Bay (west of Chipps Island) and the Sacramento-San Joaquin Delta (Delta). The Delta is approximately defined by Chipps Island to the west, Sacramento to the north, and the river confluence near Vernalis to the south.

The value of emergent and submerged vegetation in tidal wetlands can be dependent on vegetation density and species habitat preferences. Stem density is an important variable affecting the ability of predatory fish, such as largemouth bass (*Micropterus salmoides*), to detect and capture prey. Minimum predatory effectiveness occurs at some intermediate density (Savino and Stein 1982; Hayes and Wissing 1996). In the tidal Lake Pontchartrain, Louisiana, different fish assemblages are associated with shallow-water areas with and without submerged aquatic vegetation (Duffy and Baltz 1998). Emergent vegetation can also provide food (seeds, leaves, and stems) and habitat for birds, mammals, and other vertebrates.

Despite the importance of tidal wetlands to fish and invertebrate populations on the Atlantic and Gulf coasts (Kneib 1997; Kruczynski and Ruth 1997), information on Pacific Coast estuaries provided little evidence that tidal wetlands are important to native fishes. This apparent difference in importance is likely the result of two factors. First, coastal marshes are a relatively minor habitat type along the Pacific Coast, contributing only 7% of the coastal wetlands in the contiguous United States (Mitsch and Gosselink 1986). Second, the fishes of Pacific Coast estuaries are largely mixtures of freshwater, marine, and anadromous species that are not dependent on tidal wetlands for completion of their life cycle. In the San Francisco Estuary, only delta smelt is a true estuarine resident (Moyle 2002). Therefore, preservation of tidal wetlands may not have been perceived as critical for conservation of native fishes or fishery production. Conversely, eastern estuaries include many resident tidal marsh fishes and fishes that are dependent on tidal marsh or other estuarine habitats for completion of their life cycle, many of them important to commercial and recreational fisheries. Recent evidence from the Pacific Northwest indicates that estuarine and tidal wetland habitat can be important for rearing of juvenile anadromous salmonids (Shreffler and others 1990; Healey 1991; Simenstad and others 1993); however, evidence for other fishes is still lacking.

This article assesses the current evidence regarding the importance of tidal wetlands to populations of native fishes in the San Francisco Estuary. The concept of migration corridors for migratory fish moving through the Delta is also assessed because such corridors are often conceived as channels fringed by tidal wetland and riparian habitat. The assessment of migration corridors does not address the relative merits of different migration pathways through the Estuary, but only the possible benefits of such pathways being bordered by tidal wetlands. Available data and interpretations are combined into conceptual models. On the basis of the data assessment and the resulting conceptual models, the following question is evaluated: Will tidal wetland restoration enhance populations of native fishes? Constructing the conceptual models and evaluating the question identify important areas of scientific uncertainty. These uncertainties suggest an array of methods to reduce uncertainty in assessing the benefits of wetland restoration to native fishes.

Table 1 Common and scientific names of native and alien fishes commonly encountered during studies of tidal wetlands in the San Francisco Estuary

Common name	*Scientific name*	*Residency*[a]	*Life style*[b]	*Tidal wetland type*[c]
Native species				
Arrow goby	*Clevelandia ios*	R	M	S
Bay pipefish	*Syngnathus leptorhynchus*	R	M	S
Chinook salmon[d]	*Oncorhynchus tshawytscha*	M	AN	F
Delta smelt[e]	*Hypomesus transpacificus*	M	E,F	F
Dwarf surfperch	*Micrometrus minimus*	R?	M	S
Jacksmelt	*Atherinopsis californiensis*	T	M	S
Lampreys	*Lampetra* spp.	juvenile–R, adult–M	AN	F
Longjaw mudsucker	*Gillichthys mirabilis*	R	E	S
Northern anchovy	*Engraulis mordax*	T	M	S
Pacific staghorn sculpin	*Leptocottus armatus*	T	E,M	B,S
Prickly sculpin	*Cottus asper*	R	E,F	F,B,S
Sacramento pikeminnow	*Ptychocheilus grandis*	T	F	F
Sacramento sucker	*Catostomus occidentalis*	T	F	F,B
Shiner perch	*Cymatogaster aggregata*	R?	E	S
Splittail[f]	*Pogonichthys macrolepidotus*	T or R?	E,F	F,B
Steelhead rainbow trout[g]	*Oncorhynchus mykiss*	M	AN	F
Threespine stickleback	*Gasterosteus aculeatus*	R	E,F	B,S
Topsmelt	*Atherinops affinis*	T	E	S
Tule perch	*Hysterocarpus traski*	R	E,F	F,B
Alien species				
American shad	*Alosa sapidissima*	T	AN	S
Black crappie	*Pomoxis nigromaculatus*	R	F	F
Bluegill	*Lepomis macrochirus*	R	F	F
Common carp	*Cyprinus carpio*	R	F	B
Golden shiner	*Notemigonus crysoleucas*	R	F	F
Inland silverside	*Menidia beryllina*	R	E,F	F,S
Largemouth bass	*Micropterus salmoides*	R	F	F
Rainwater killifish	*Lucania parva*	R	E	S
Redear sunfish	*Lepomis microlophus*	R	F	F
Shimofuri goby	*Tridentiger bifasciatus*	R	E	B,S
Striped bass	*Morone saxatilis*	T	E	F,B,S
Threadfin shad	*Dorosoma petenense*	R	F	F
Western mosquitofish	*Gambusia affinis*	R	E,F	S
White catfish	*Ameiurus catus*	R	F	F,B
Yellowfin goby	*Acanthogobius flavimanus*	R	E	B,S

Notes: (a) Residency: R, resident; T, transient; M, migrant; (b) Life style (primary habitat of species): F, freshwater; E, estuaries; M, marine; AN, anadromous; (c) Tidal wetland type (as classified in this article): F, freshwater; B, brackish water; S, salt water; (d) Winter-run is state and federal endangered. Spring-run is state and federal threatened. (e) state and federal threatened; (f) federal threatened; (g) federal threatened.

This assessment is timely because the Ecosystem Restoration Program (ERP) of the CALFED Bay-Delta Program (hereafter “CALFED”) includes tidal wetland restoration as one method for increasing populations of fishes of concern (see Table 1 for fishes listed under state or federal endangered species acts). In response to growing conflicts between the need to manage the Delta to aid in the recovery of ecosystems and species of concern and the need to provide high quality water for agricultural and urban uses, CALFED was formed in 2000, after a preliminary 5-year planning phase (CALFED 2001). CALFED is a collaborative effort among 23 state and federal agencies with the basic mission of developing and implementing a long-term comprehensive plan to restore ecological health and improve water management for the beneficial uses of the Bay-Delta. Four interdependent program areas are presently being pursued, including water supply reliability, water quality, ecosystem restoration, and levee system integrity. In addition, the CALFED Science Program was established to guide and oversee the tasks of scientific review and adaptive management that have been identified as two of the implementation priorities of the program. The mission of ERP is to implement ecosystem restoration actions to help restore and improve the health of the Bay-Delta system for all native species while reducing water management constraints within the system.

Review and Conceptual Models

For this article, the term “tidal wetland” includes areas subject to inundation during the natural (lunar) tidal cycle. Passively or actively managed wetlands, such as duck club ponds, are not explicitly included, but such habitats will be discussed as necessary for the understanding of tidal marsh processes. Floodplains are also not explicitly considered, except as necessary to discuss their interactions with tidal wetlands. This article will consider nearshore aquatic habitat types, including intertidal and subtidal areas of submerged aquatic vegetation and open water. In general, this aquatic zone includes the area referred to as “shallow water habitat” and can be roughly defined as water less than 2 m deep at mean lower low water. Discussion of such areas is necessary in understanding the connections of tidal wetlands to the larger channels and bays.

Tidal wetlands are often classified according to salinity. Mitsch and Gosselink (1986) provide the following classifications: freshwater (0‰ to 0.5‰), oligohaline (0.5‰ to 5‰), mesohaline (5‰ to 18‰), and polyhaline (18‰ to 30‰). For this article, a simpler classification is adopted, which facilitates division of the Estuary into three geographic areas that are based roughly on salinity regime. These salinity regimes are characterized as freshwater (seasonally varying over a range of about 0‰ to 2‰), brackish (seasonally varying over a range of about 0‰ to 17‰), and saltwater (seasonally exceeding 17‰). The seasonal ranges also incorporate annual variability in freshwater inflow. For example, freshwater tidal marshes as defined here would only approach the 2‰ maximum during an extreme drought. The freshwater regime is typical of the Delta. The brackish-water regime is typical of the Suisun Marsh (see Figure 2) and presumably the tidal wetlands fringing on Suisun, Grizzly, and Honker bays (see Figure 2). The saltwater regime is typical of the tidal marshes surrounding San Francisco Bay. It is important to realize that this description is general, and the application will vary with environmental circumstances.

For example, the brackish and freshwater models (or variations on them) may need to be applied in the upper Petaluma and Napa river systems (see Figure 1) to fully understand tidal wetlands in those areas. Also, the geographic location and extent of the three general types in the larger Bay-Delta system will change in response to annual discharge conditions. For example, during a dry, low outflow year, the saltwater model could apply in parts of Suisun and Grizzly bays. The brackish water model could be applied in parts of the western and central Delta. The geographic area where the freshwater model could be applied would be reduced to the remaining areas of the northern, central, and southern Delta. Each type of tidal wetland supports a unique combination of native and alien fishes (Table 1) and other organisms. Migration corridors are considered in the context of freshwater tidal wetlands in the Delta because the concept has little meaning within the more open waters of the North and Central bays. Finally, these salinity regimes reflect present-day conditions, which are likely different from historical conditions (TBI 1998), when annual variability in flow was not moderated by water management activities.

The native and alien fishes commonly using tidal wetlands in the Estuary can be classified on the basis of residency (Table 1). “Resident” species include those that are capable of completing their entire life cycle within tidal wetlands, including nearby open water habitats. “Transient” species most likely do not complete their entire lifecycle in the local area, but may spend an extended period of time in the area as juveniles or adults. “Migratory” species occur in tidal wetlands on a seasonal basis as part of well-defined migratory cycles.

Delta Freshwater Tidal Wetlands

Explicit studies of the relations between fish populations and freshwater tidal wetlands in the Delta are rare. The best example is a study of the habitats that develop in breached islands. The study included fish sampling from nearshore habitats of breached islands in the central Delta (Simenstad and others 2000; Grimaldo and others, personal communication, see “Notes”). Databases on the distribution and abundance of fishes in near-shore, shallow water habitats are available including the U.S. Fish and Wildlife Service (USFWS) Beach Seine Survey (1976-present), the California Department of Fish and Game (CDFG) Resident Fishes Monitoring Survey (1980-1984, 1995, 1997, 1999), and electrofishing data collected by the California Department of Water Resources as part of an evaluation of temporary rock barriers in the southern Delta. Chotkowski (1999) summarized the USFWS beach seine data and CDFG resident fishes surveys. Feyrer and Healey (2003) analyzed the electrofishing data collected as part of the South Delta project. Studies of ecological processes (e.g., food web dynamics) are limited to the breached island study (Simenstad and others 2000).

Freshwater tidal wetlands in the Delta provide, or are associated with, a variety of habitat types available to fishes and other aquatic organisms. Habitats for fishes include marsh plains, usually vegetated by tules (*Scirpus* spp.) and other emergent vegetation (*Typha* spp., *Phragmites* spp.) when tidal elevation is sufficient to cover the marsh. When

present, permanent and tidal channels within wetlands are also available to fish; however, many Delta tidal wetland areas do not have sufficient area or the proper geomorphic conditions to develop extensive channel networks. In fact, much of the tidal wetland habitat in the Delta is restricted to a narrow band between steep levees and deep water within channels or flooded islands. Tules may extend into the subtidal zone. In many areas, the subtidal zone is vegetated by a variety of submerged macrophytes. The most common species is *Egeria densa*, Brazilian waterweed, an alien species that tends to form dense monocultures in near-shore shallow waters (Grimaldo and Hymanson 1999). The factors determining the distribution of *Egeria* and other submerged macrophytes in the Delta have not been locally researched but likely include salinity regime, presence of suitable rooting substrate, water velocities, turbulence, and light regime, as influenced by shading and turbidity. In a Chilean estuary, *Egeria* could be found growing at up to 5‰, but growth was greatly inhibited at salinities greater than 2‰ (Haunstein and Ramirez 1986). *Egeria* has been found growing in depths of up to 3.5 m in the Delta, and the dense monocultures seem to have local effects on water clarity because the reduced water velocities within the vegetation allow suspended sediment particles to settle out of the water column (Grimaldo and Hymanson 1999). Other near-shore habitats that occur in association with tidal wetlands include bare mud and sand beaches and mudflats. Other Delta near-shore habitats usually not associated with extensive freshwater tidal wetland include both vegetated and unvegetated rip-rap.

Most of the resident fishes in freshwater tidal wetlands are also alien (Table 1). The only resident native fishes commonly encountered in recent studies of nearshore Delta fishes are tule perch (*Hysterocarpus traski*) and prickly sculpin (*Cottus asper*) (Grimaldo and others, personal communication, see “Notes”; Feyrer and Healey 2003). Several of the resident alien fishes are known or suspected to be predators on larval, juvenile, or adult fishes. Adult largemouth bass are well known predators, and even juvenile largemouth bass are primarily piscivores (Moyle 2002).

The transient fishes are primarily native riverine fishes but include the alien striped bass (*Morone saxatilis*). These fishes spawn in nontidal upstream reaches of rivers and streams tributary to the Delta, but the juveniles and adults use a variety of nearshore shallow water habitats as rearing or feeding areas. There is some question about the status of splittail. During wet years, splittail spawn extensively on inundated floodplains upstream of the Delta (Sommer and others 1997). The adult and young-of-year splittail then move downstream, perhaps in response to increasing water temperature. The assumption has been that the young splittail then rear in various parts of the Delta, Suisun Marsh, and Suisun Bay (Moyle and others 1995; Sommer and others 1997; Moyle 2002); however, recent observations indicate that splittail appear to leave freshwater tidal wetland areas in the central Delta as water temperatures increase above about 20 °C (Grimaldo and others, personal communication, see “Notes”; Simenstad and others 2000).

The migrant fishes include the native anadromous salmonids and delta smelt. Juvenile salmonids (steelhead rainbow trout and chinook salmon) must pass through the Delta and Bay on their seaward migration, but little is known about the habitats they use while doing so. Young salmon are regularly caught in the Delta during their seaward migration, especially in the USFWS beach seine survey (Brandes and McLain 2001). Much of the speculation regarding the importance of tidal wetlands and associated nearshore habitats to anadromous salmonids revolves around differences in survival of chinook salmon fry rearing in the Delta compared with tributary streams or survival of smolts taking different migration routes through the Delta (Brandes and McLain 2001). Survival of fry in the Delta appears to be lower than in the tributary streams. Nevertheless, the relative contribution of Delta-reared fry to adult production is unknown and may have been substantial under natural conditions. Studies of smolt migration through the Delta generally reveal decreased survival of migrating smolts when they enter the central Delta rather than migrating directly along the Sacramento or San Joaquin rivers. The hypothesis is that smolts diverted into the central Delta are exposed to sources of mortality, such as predation, toxics, entrainment by diversions, or elevated water temperatures, for a longer period; however, the relative importance of possible sources of mortality has been difficult to establish (Newman and Rice 1997; Baker and Morhardt 2001; Brandes and McLain 2001).

Increased areas of freshwater tidal wetlands may provide increased rearing and refuge habitat for fry, resulting in greater survival and hence greater production of adult fish. The limited sampling in existing habitat has not revealed large numbers of salmonid fry; however, the most intensive survey (USFWS beach seine survey) samples at easily seined locations rather than in tidal wetland vegetation. Similarly, improving tidal wetland and riparian habitat along juvenile salmonid migration corridors might improve smolt survival by providing a refuge from predation and feeding habitat. There are no data to assess the idea of predator avoidance, but migratory juvenile salmon do feed on a variety of food items in the Delta. Sasaki (1966) found insects to be the most frequent food item ingested by juvenile salmon collected from the river channels; however, in flooded islands the mysid shrimp, *Neomysis*, and the amphipod, *Corophium*, were the most frequent items ingested. Kjelson and others (1982) found cladocerans, copepods, and dipterans to be the important food items and noted rapid growth of salmonid fry in the Delta compared with their growth in the river. In general, estuaries appear to provide good rearing habitat for chinook salmon from Washington to California (Healey 1991). The migration corridor concept has also been suggested for splittail and delta smelt. As already mentioned, splittail migrate through portions of the Delta and improved tidal wetlands habitats might facilitate increased survival during such movements. Young-of-year delta smelt also move (or move with water currents) from Delta spawning areas through the Delta to Suisun Bay; however, delta smelt are associated with open waters rather than tidal wetlands (see below). Defining a migration corridor for improvement is difficult because the cues the different fishes use to choose a particular route through the structurally and hydrodynamically complex Delta are unknown even for the comparatively well-studied chinook salmon (Baker and Morhardt 2001).

The importance of freshwater tidal wetlands to the native delta smelt is largely speculative. Recently hatched larval delta smelt are generally captured in shallow, nearshore habitats and in channels associated with freshwater tidal wetlands, but larval delta smelt have never been captured from within a tidal wetland or from areas of emergent wetland vegetation (Bennett, personal communication, see “Notes”). Although, tidal wetland vegetation seems an obvious substrate for deposition of the type of adhesive eggs produced by delta smelt, this has never been observed in the wild or in the laboratory. There is a correlation of spawning events with spring tides suggesting that spawning occurs at depths lower than spring-tide low water (Bennett, personal communication, see “Notes”). Juvenile and adult delta smelt are pelagic, and any benefits of restored freshwater tidal wetlands would be indirect in the form of export of primary or secondary production to the open water habitats occupied by these life stages. Bennett (1995) has noted that the alien inland silverside (*Menidia beryllina*) is an efficient predator on larval fish and has hypothesized that it might be an important predator on larval delta smelt under some circumstances. Inland silverside is found both nearshore and offshore of freshwater tidal wetlands (Grimaldo and others, personal communication, see “Notes”).

It is interesting to note that many of the alien fishes commonly found in Delta freshwater tidal wetlands are the same species found in freshwater tidal wetlands on the Atlantic and Gulf coasts (Odum and others 1984; Peterson and Meador 1994). The mixture of freshwater, estuarine, marine, and anadromous fishes is also typical of eastern tidal freshwater marshes. Peterson and Meador (1994) found that most eastern freshwater species cannot survive chronic exposure to salinities of greater than 9‰ and successful reproduction is limited to salinities of less than 3‰ to 4‰. Structure and function of freshwater fish communities in brackish water were found to depend on the rate of change and stability of salinity.

Patterns in Distribution and Abundance

The fish communities of freshwater tidal wetlands and associated near-shore habitats are dominated by alien species. Chotkowski (1999) showed that 59.3% of the total number of fish captured in the USFWS beach seine surveys were alien. Thirty of 61 fishes captured were alien. Inland silverside and chinook salmon dominated the catch (59.5%). The other six relatively abundant species included two native fishes (Sacramento sucker, *Catostomus occidentalis*; and Sacramento pikeminnow, *Ptychocheilus grandis*) and four alien fishes (threadfin shad, *Dorosoma petenense*; red shiner, *Cyprinella lutrensis*; western mosquitofish, *Gambusia affinis*; and striped bass). These eight species contributed 90.9% of the fishes captured in the seining survey. Red shiner is only abundant in the lower San Joaquin River system (Brown 2000). It is also notable that few of the fishes generally associated with vegetated habitats, such as tule perch, largemouth bass, or bluegill (*Lepomis macrochirus*) were captured in the seining surveys. The seining survey emphasizes the use of boat ramps, beaches, and other locations accessible under a variety of flow conditions and thus emphasizes water-column-oriented fishes rather than vegetation-oriented fishes.

CDFG electrofishing surveys showed that alien centrarchids, including largemouth bass, bluegill, and redear sunfish (*Lepomis microlophus*), with lesser numbers of golden shiner (*Notemigonus crysoleucas*) and other alien fishes, dominated vegetated habitats including emergent, submerged, and mixed vegetation and shoreline with riparian vegetation (Chotkowski 1999). In all, 23 of 35 fishes and 94.2% of total individuals captured by electrofishing were alien.

McGowan and Marchi (1998) sampled in dense *Egeria* beds using popnets and by sorting through plant material collected by a mechanical harvester and found only alien species, including bluegill, redear sunfish, largemouth bass, warmouth (*Lepomis gulosus*), black crappie (*Pomoxis nigromaculatus*), goldfish (*Carassius auratus*), western mosquitofish, golden shiner, threadfin shad, and inland silverside.

Alien fishes dominated in boat electrofishing surveys in the southern Delta (Feyrer and Healey 2003). Analysis of eight years of data from 11 sites in the south Delta documented 33 fish taxa, of which only eight were native. None of the native fishes contributed more than 0.5% of the total number of fish captured. In total, native fishes made up less than 5% of the catch. Bluegill, redear sunfish, white catfish (*Ameiurus catus*), and largemouth bass were the most common species and each occurred in 79% or more of the total samples collected. These species also constituted over 65% of the total catch. The abundances of native tule perch and Sacramento sucker, were positively associated with high river flow and turbidity. *Egeria densa* was not a significant variable in this analysis because it was common at all sites and there was no effort to sample it separately from other habitats.

Alien fishes also dominate breached island tidal wetlands and associated nearshore habitats in the central Delta (Grimaldo and others, personal communication, see “Notes”). Of 32 fishes captured, only 10 were native. Of the total juvenile and adult fish collected, over 98% were resident species. Migratory and transient fishes included four natives (chinook salmon, steelhead rainbow trout, delta smelt, and splittail) and two aliens (striped bass and American shad, *Alosa sapidissima*). Pacific staghorn sculpin (*Leptocottus armatus*), a more saltwater-adapted species, was also captured and would be considered a transient.

Grimaldo and others (personal communication, see “Notes”) found differences among fishes in use of vegetated habitat types. Juvenile chinook salmon, inland silverside, and threadfin shad were more abundant in unvegetated habitats than in vegetated ones as was found in the electrofishing studies (Chotkowski 1999). Tule perch, prickly sculpin, brown bullhead (*Ameiurus nebulosus*), and centrarchids were more abundant in vegetated habitats than in unvegetated ones. Adult largemouth bass and splittail had peak abundances in areas with low densities of submerged aquatic vegetation. There were some differences among species related to distribution of larvae among habitat types. American shad, inland silverside, bigscale logperch (*Percina macrolepida*), and

centrarchid larvae were more abundant in inshore shallow water, and delta smelt larvae were more abundant in offshore open shallow water (Simenstad and others 2000).

Bare mud banks and sand beaches were dominated (62% and 69% of fish captured, respectively) by native lampreys (*Lampetra* spp., probably ammocoetes, the larval form which burrows into soft substrates) and chinook salmon, as determined by boat electrofishing (Chotkowski 1999). Twelve of 24 species captured in these habitats were alien. In contrast, bare mudflats were dominated by bluegill and redear sunfish accounting for 57% of the fish captured by boat electrofishing (Chotkowski 1999). Twelve of 24 species captured in mudflats were alien. The data for mud banks and sand beaches are consistent with the results from the USFWS beach seine with regard to the large proportions of chinook salmon captured. However, given the seasonal nature of chinook salmon migration through the Delta, large proportions of chinook salmon would only be expected during the winter and spring.

Spatial and Temporal Variability in Distribution and Abundance

There appears to be a spatial component to fish distributions within the Delta. The northern and western Delta tend to have larger proportions of the transient native riverine fishes, such as Sacramento pikeminnow and Sacramento sucker (Urquhart 1987). This presumably occurs because the Sacramento and Mokelumne rivers and their tributaries serve as sources for these species. The southern Delta tends to be more heavily dominated by alien fishes (Urquhart 1987; Feyrer and Healey 2003). This may be partially due to differing environmental conditions in the two regions, but the southern Delta also lacks a significant nearby source of native riverine fishes. In the San Joaquin River system, native riverine fishes tend to predominate in the more upstream portions of tributary rivers, but the mainstem San Joaquin River is dominated by alien fishes (Brown 2000). The central Delta is intermediate and may represent a mixing area for species from the north and south.

There also appears to be a seasonal component to fish abundances, which is likely linked to the relative reproductive success of species under different environmental conditions. Similar patterns have been found in California stream fish communities (Marchetti and Moyle 2000, 2001; Brown and Ford 2002). Grimaldo and others (personal communication, see “Notes”) observed peak abundance of golden shiner, juvenile largemouth bass, yellowfin goby (*Acanthogobius flavimanus*), black crappie, and threadfin shad during the summer when temperatures were high and freshwater outflow was low. Juvenile chinook salmon, splittail, redear sunfish, adult largemouth bass, and rainwater killifish (*Lucania parva*) were most abundant when water temperatures were low and freshwater outflow was high. On the basis of abundances of larval and juvenile fishes, adult native fishes spawned in April and May when water temperatures were low (10 to 18°C) and adult alien fishes spawned in later months when water temperatures were warmer (15 to 25°C) (Simenstad and others 2000).

Feyrer and Healey (2003) found that the abundances of most alien fishes were associated with warmer water temperatures and lower river flows compared with native fishes. Striped bass and white catfish were the major exceptions and were associated with high river flow. Striped bass spawning is most successful during moderate and high-flow years. White catfish are most susceptible to electrofishing gear during high flow summer periods when they inhabit shallow flooded areas.

Trophic Processes

Studies of ecological processes in relation to fish production in Delta freshwater tidal wetlands are sparse. Simenstad and others (2000) presented some preliminary data on food web structure. Juvenile chinook salmon fed predominantly on chironomid larvae and pupae (associated with emergent marsh vegetation) and the amphipod, *Hyalella azteca*. However, the sample size for salmon was small (n = 29). Tule perch and splittail fed on a variety of organisms, typical of different habitats including cladocerans (associated with water column), *Hyalella azteca* (associated with submerged aquatic vegetation), and chironomid larvae and pupae (associated with emergent marsh). Inland silversides collected in open water habitats during the spring consumed planktonic prey items, but inland silversides collected in association with floating or submerged vegetation consumed items more typical of emergent marsh (ostracods and chironomid larvae and pupae). Bluegill were opportunistic feeders who consumed a wide variety of organisms from all of the habitats available. Field examinations of the gut contents of large piscivorous largemouth bass, white catfish, and striped bass revealed several species of fish, including splittail, threadfin shad, and inland silverside.

The limited food habit data for large piscivorous fish suggest that predation by alien piscivores on native fishes might be a factor in the decline of native fishes. Preliminary analyses suggest a decline in the abundance of tule perch in the Delta over the last several decades as centrarchids have increased (Nobriga and Chotkowski 2000). The close association of all of these fishes with *Egeria* might suggest that interspecific interactions among these species would be likely. Nobriga and Chotkowski (2000) further suggest that predatory interactions are more likely than competitive interactions given the life histories of the species.

Grimaldo and others (2000) tethered hatchery fall-run chinook salmon in areas with and without submerged aquatic vegetation and compared predation rates from each habitat. Prey fish were tethered using hooks so that predators could be captured and identified. Predation rates were high in both vegetated and unvegetated habitats (79% and 95%, respectively), but predation in unvegetated habitats was statistically higher. Sacramento pikeminnow were the most frequently identified predators (11 captures) with white catfish (2 captures) and white crappie (1 capture) also identified; however, most of the predation events were not attributed to specific predators because of bent hooks or broken tethers (39 cases). These predation events were attributed to larger more powerful predators, such as largemouth bass and striped bass. It should be noted that chinook salmon have not been collected within submerged aquatic vegetation within the Delta and

that such habitats are generally inhabited by juveniles of alien fishes and native tule perch and prickly sculpin (Simenstad and others 2000; Grimaldo and others, personal communication, see “Notes”).

The Delta population of largemouth bass may be especially significant. Largemouth bass support an extensive fishery in the Delta (Lee 2000). Largemouth bass tend to grow slowly in slightly saline estuarine environments (Meador and Kelso 1990), and growth rates of Delta largemouth bass are relatively low compared with most California reservoirs (Schaffter 1998). However, there is an increasing level of catch and release fishing (Schaffter 2000), which promotes a large population of large piscivorous fish despite low growth rates.

It is worthy of note that Sacramento pikeminnow is a native piscivore that has been shown to influence prey habitat selection in riverine systems (Brown and Moyle 1991; Brown and Brasher 1995; Brown and Moyle 1997). Predation has always been a part of the Delta ecosystem; however, habitat conditions now seem to favor alien predators over native predators. The food web data, including the probable importance of predation, in combination with the different fish communities found in areas with and without *Egeria* (Grimaldo and others, personal communication, see “Notes”), suggest a major role of this submerged aquatic plant in determining the outcome of habitat manipulations.

Fishes Responses to Tidal Wetland Restoration

Few studies have focused on evaluating the “success” of restored tidal wetlands in the Delta and those studies completed have been limited in scope and duration. Lindberg and Marzuola (1993) documented the presence of delta smelt near levee breaches in a flooded island restoration project in the northern Delta. All of the delta smelt captured were described as sexually mature or recently spent suggesting spawning activity in the area. However, delta smelt contributed only 11% of the catch with alien inland silverside and threadfin shad contributing 58% and 18% of the catch, respectively.

England and others (1990) documented fish use of islands created with dredge material within two flooded islands in the central Delta from 1987 to 1989. Fish use appeared to increase during the study, especially from 1987 to 1988. This increase was linked to enhanced habitat heterogeneity associated with the establishment of aquatic vegetation. The fish assemblage was dominated by alien fishes, primarily inland silverside. Only 33% of the species and 16% of the individuals captured were native. The native fishes included chinook salmon, splittail, Sacramento pikeminnow, threespine stickleback (*Gasterosteus aculeatus*), tule perch, and starry flounder (*Platichthys stellatus*). Chinook salmon and splittail were only captured in the spring (April, May, June). Notably, catches of all species except inland silverside decreased in July and August, when only one native fish was captured.

Simenstad and others (2000) do not address the functions of restored tidal wetlands directly, but compare functions of breached island freshwater tidal wetlands of various ages with reference sites. There were statistically higher densities of native fish (all species combined) at the reference site compared with the three breached island sites in 1998 (Simenstad and others 2000; Grimaldo and others, personal communication, see "Notes"). Densities of alien fish were highest at the deepest, most lake-like breached island site. These data suggest that the habitat at the reference wetland, which provides more intertidal habitat, favored native fishes and the habitat at the deepest, most subsided site, providing the most subtidal habitat, favored alien fishes. Total catch over the entire study (1998 and first half of 1999) was dominated by alien fishes at all sites. The highest percentages of native fishes occurred at the reference site.

Summary

Although a fair amount is known about the distribution of fishes among some of the aquatic habitats associated with Delta freshwater tidal wetlands, the various studies reviewed above used many different collecting techniques. Of those collecting techniques, few are effective in the vegetated habitats for which there are the fewest data. We do not know the extent to which gear biases are influencing the relative importance of different habitat types within the conceptual model. The data are inadequate to infer anything about population sizes of native and alien fishes and the effects of populations on one another. For example, largemouth bass and striped bass are known to be predators on juvenile and adult fishes of many species, and such predation is likely an important source of mortality to chinook salmon fry rearing in the Delta and smolts migrating through the Delta. However, without knowledge of predator population sizes, predation rates in response to seasonal shifts in water temperatures, and compensating benefits of freshwater tidal wetlands, such as increased growth rate and improved predator avoidance, it is difficult to infer much about the net benefit to chinook salmon populations.

Conceptual Model for Delta Freshwater Tidal Wetlands

The simple conceptual model (Figures 3 and 4) is primarily intended to organize the concepts likely important in determining the benefits of freshwater tidal wetland restoration for the common fishes. The conceptual model is not inclusive of all fishes (benthic fishes in particular are ignored), life stages, or other aquatic species (e.g., crayfish). The conceptual model also does not attempt to integrate the available food web data, although the model assumes that feeding is an important activity. Although some diet data are available, the data are not sufficient to construct credible food webs for all of the habitat types and species interactions. The model also suggests that the smaller fishes are balancing feeding opportunities against predation risk. The model is presented in two versions, one without submerged aquatic vegetation (Figure 3) and one with submerged aquatic vegetation (Figure 4).

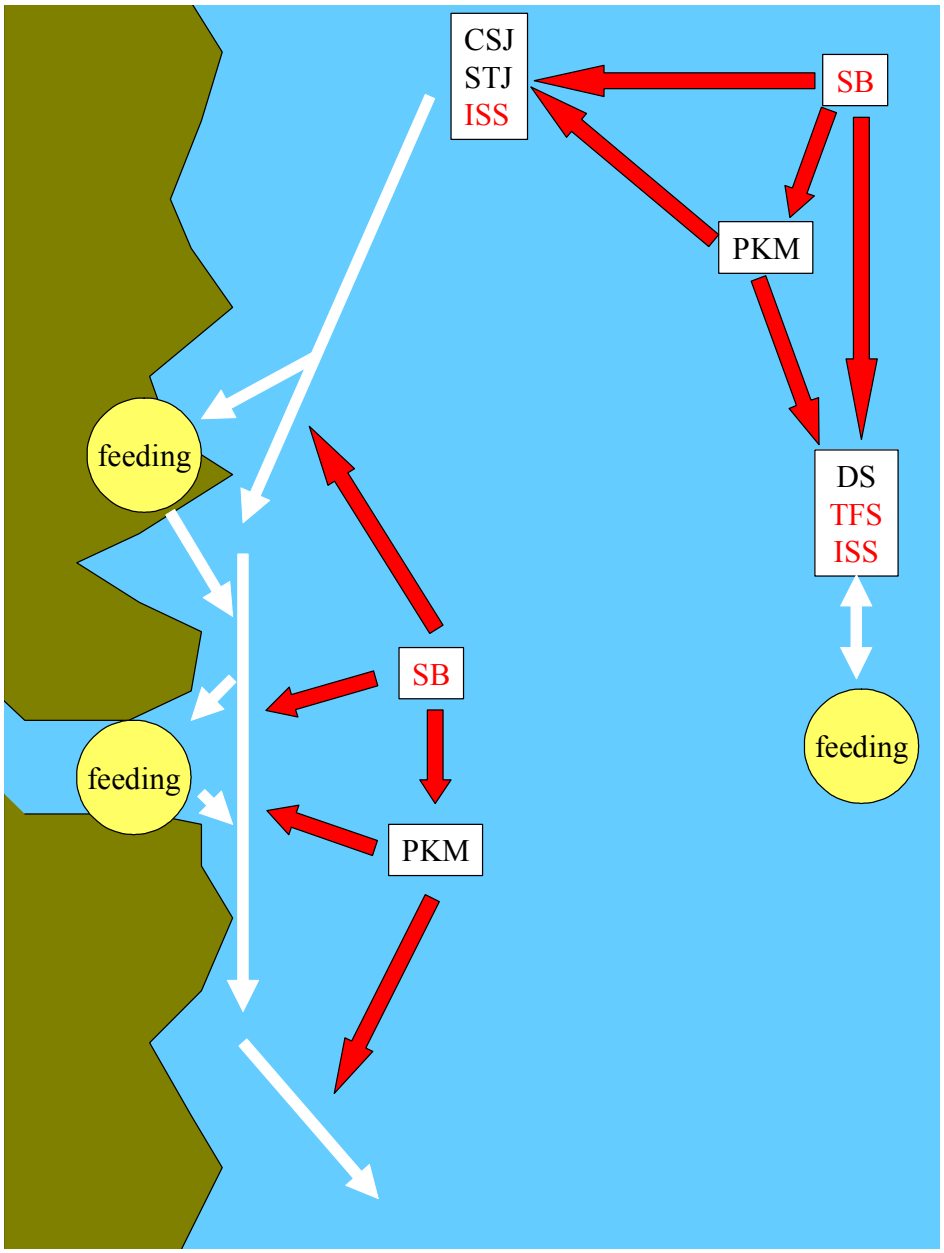

Figure 3 A conceptual model for fish habitat use in Delta freshwater tidal wetlands without submerged aquatic vegetation. Species codes in red indicate alien fishes. Red arrows indicate piscivory. White arrows indicate prey movements. Yellow "feeding" circles represent feeding activities of prey fishes. Blue indicates open water. Olive green indicates emergent vegetation. Species codes: CSJ–juvenile chinook salmon; DS–delta smelt; ISS–inland silverside; PKM–adult Sacramento pikeminnow; SB–adult striped bass; STJ–juvenile splittail; TFS–threadfin shad.

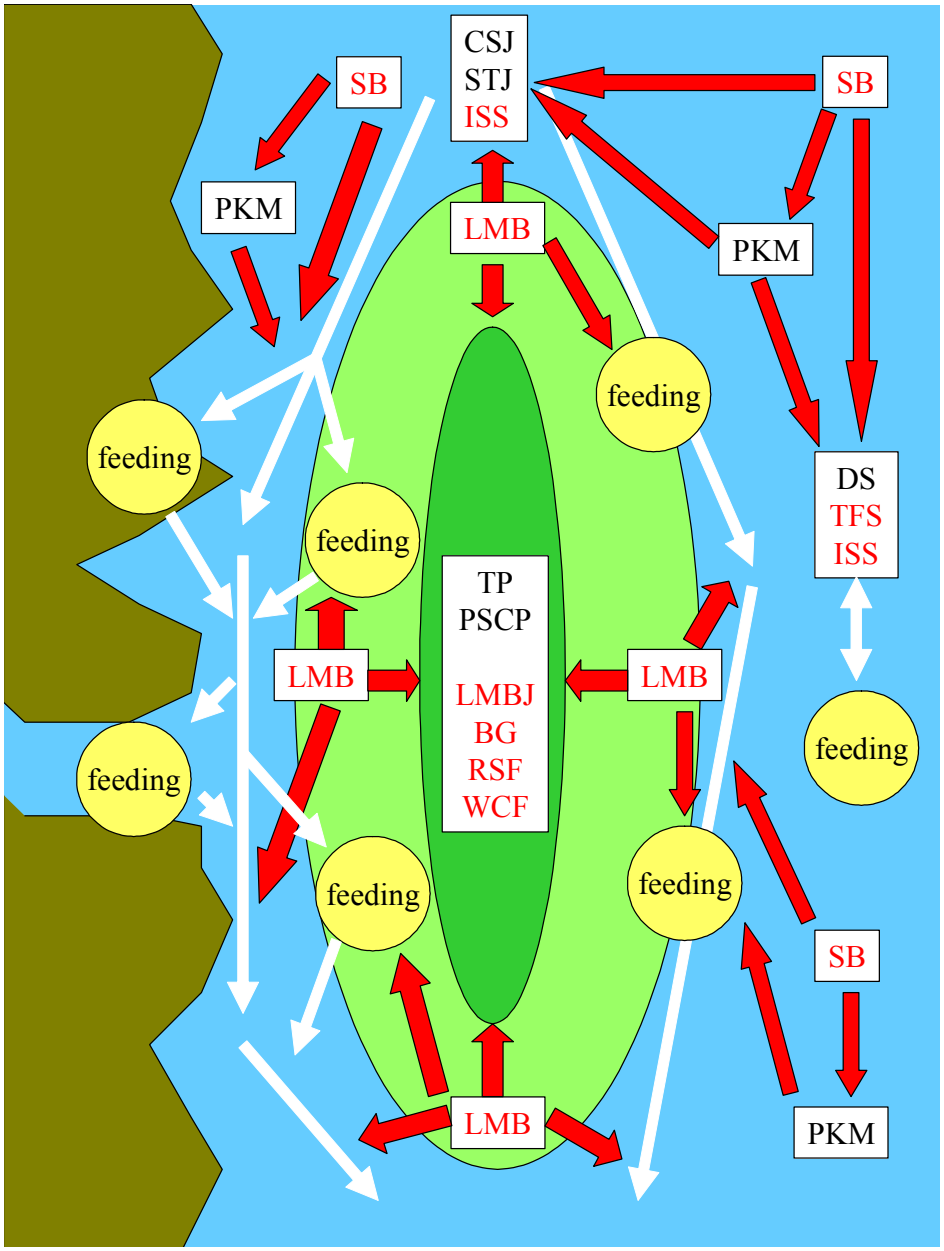

Figure 4 A conceptual model for fish habitat use in Delta freshwater tidal wetlands with submerged aquatic vegetation. Species codes in red indicate alien fishes. Red arrows indicate piscivory. White arrows indicate prey movements. Yellow "feeding" circles represent feeding activities of prey fishes. Blue indicates open water. Olive green indicates emergent vegetation. The light green oval represents low-density submerged aquatic vegetation and the dark green oval represents dense submerged aquatic vegetation. Species codes: BG–bluegill; CSJ–juvenile chinook salmon; DS–delta smelt; ISS–inland silverside; LMB–adult largemouth bass; LMBJ–juvenile largemouth bass; PKM–adult Sacramento pikeminnow; PSCP–prickly sculpin; RSF–redear sunfish; SB–adult striped bass; STJ–juvenile splittail; TFS–threadfin shad; TP–tule perch; WCF–white catfish.

In the absence of dense submerged aquatic vegetation (see Figure 3), fishes capable of exploiting marsh plains and tidal channels for feeding or predator avoidance move in and out of these habitats with the tides. Of the native species, juvenile chinook salmon and splittail probably benefit most from these habitat types. The primary food sources likely to be exploited by fishes in these situations are chironomid larvae, pupae, and adults. Other invertebrates abundant within these habitats will also be exploited. Feeding may also take place in nearshore open water subtidal habitats or in larger permanently wetted channels. It is noteworthy that under present conditions, the benefits of unvegetated tidal habitats for native species may be largely seasonal because the species exploiting them are migratory or transient in many portions of the Delta.

Delta smelt and threadfin shad are primarily offshore species and feed on microcrustaceans, including cladocerans and copepods. The presence of delta smelt in Delta freshwater tidal wetlands is largely seasonal. Young delta smelt move through the Delta in the spring as they move out into Suisun Bay. Mature delta smelt may be found in these habitats during the winter as they slowly move upstream in preparation for spawning. Resident inland silversides show no particular habitat or feeding affinity and exploit a wide range of available habitats and food sources.

The primary threats to small fishes in this simple model are larger roving predators including Sacramento pikeminnow and striped bass. These piscivores are able to feed on both the nearshore and offshore species. These predators may also feed on each other; however, it seems likely that striped bass are better able to feed on Sacramento pikeminnow than the converse. Striped bass grow larger and have morphological adaptations (spines) that make them difficult prey for a similar-sized Sacramento pikeminnow. In reality, the situation is almost certainly more complex because of the presence of other nonpiscine piscivores such as wading birds, which can affect habitat selection of fishes (Knieb 1982).

Clearly, these nearshore and offshore habitats are not truly separate, and there are ecological connections between them. As marsh plain and tidal channels drain with the tide, the fishes using those habitats move into the nearshore and perhaps the offshore areas. The offshore species may move inshore. Similarly, tidal action may move primary production (phytoplankton) and secondary production (microcrustaceans) from the intertidal and nearshore into offshore areas.

This relatively simple conceptual model (Figure 3) reflects many of the expectations for the benefits derived from Delta tidal wetland restoration and establishment of tidal wetlands along migration corridors. However, as noted earlier, *Egeria* often colonizes nearshore subtidal areas and could reduce many of the benefits expected from restoration activities. This occurs because dense beds of *Egeria* support a distinctive ecological community (Figure 4). The interior of the dense beds provide habitat for tule perch, prickly sculpin, alien centrarchids, and alien ictalurids. These species subsist largely on food resources associated with *Egeria*, such as insect larvae (e.g., zygopterans) and

amphipods (e.g., *Hyalella azteca*). These invertebrates are presumably exploiting epiphytic algae or other invertebrates on *Egeria* or decomposing plant material. The fishes and relationships in the simpler conceptual model (Figure 4) are still present; however, the *Egeria* beds add an element of structural complexity that may impede movements of both the nearshore and offshore fishes. For many fishes, the reduction in mobility might be offset by increased feeding success within or on the edges of the *Egeria* beds; however, this edge habitat is where piscivorous adult largemouth bass feed.

In this more complex conceptual model (Figure 4), the benefits of tidal wetland restoration are less clear. *Egeria* appears to provide good habitat for the native tule perch and prickly sculpin, but populations of these species are not perceived as requiring special protection. Juvenile chinook salmon and splittail may have their movements into and out of tidal wetlands restricted to some degree, but *Egeria* might produce similar or more abundant food resources. The presence of piscivorous largemouth bass might result in high mortality of fishes attempting to exploit the *Egeria* habitat, however; chinook salmon and splittail are most abundant when water temperatures are relatively low and largemouth bass metabolic rates and feeding rates are also low. It is also unclear how fish survival in areas with *Egeria* compares with fish survival in areas without *Egeria*.

Suisun Marsh Tidal Wetlands

Studies of relations between brackish-water tidal marshes and fish communities are basically limited to the Suisun Marsh study conducted by the University of California at Davis (UCD) (Moyle and others 1986; Meng and others 1994; Meng and Matern 2001; Matern and others 2002), although some additional data is available (Herrgesell and others 1981). The UCD Suisun Marsh study began in January 1979 and continues. The focus of sampling is monthly otter trawling at 17 sites (4 additional sites added in 1994 for a total of 21, Matern and others 1995), most of which are located in shallow distributary channels (dead-end sloughs). Emergent tules and reeds generally line these sloughs. Seining is also done when conditions permit, and larval fish sampling was conducted for several years, starting in 1994 (Meng and Matern 2001).

In recent years, salinities in Suisun Marsh have ranged from 0‰ to 16‰. The highest values occur during the early fall of dry years, and the lowest values occur during high river outflows in the spring (Meng and others 1994; Matern and others 2002). Average annual salinities generally exceeded 2‰ through the middle 1990s, except for high outflow years in 1982, 1983, and 1995. Salinity in Suisun Marsh can be controlled somewhat (since 1988) during much of the year through operation of a salinity control gate in Montezuma Slough near its confluence with the Sacramento River (see Figure 2).

Patterns in Distribution and Abundance

The Suisun Marsh study is particularly interesting because an understanding of the fish communities of the marsh has continued to evolve as more data are acquired and

analyzed. During the first 54 months of the study, a total of 42 species were collected, but only 22 of the species were native to California (Moyle and others 1986). Only 21 species were captured on a regular basis. Of these 21, 14 were classified as residents, 4 as winter seasonals, and 3 as spring-summer seasonals (seasonals = transients + migrants). Of the 14 resident species, the native species splittail, tule perch, and Sacramento sucker constituted a group that was most abundant in the shallow dead-end sloughs. Chotkowski (1999) considered 11 species common in shallow waters of the marsh (Table 1). A strong seasonal component in species abundances was related to the effects of freshwater inflows and resulting physical conditions. Moyle and others (1986) documented a decline in species abundances and species diversity over the course of the study that was hypothesized to be the result of gradual declines in strong year classes of some species that dominated the early part of the study. Also, the prevalence of freshwater conditions later in the study favored only a subset of the species using the marsh.

Moyle and others (1986) provided several important caveats to their work. First, they noted that trawling underrepresented a number of species that were commonly caught during seining of the few beaches available, particularly inland silverside, chinook salmon, Sacramento pikeminnow, western mosquitofish, and rainwater killifish. Second, they noted that the patterns they observed might not hold over time as the marsh continued to change in response to natural and human factors. For example, Herrgesell and others (1981) noted that the drought of 1976-1977 resulted in dramatic declines in resident freshwater fishes such as the alien white catfish and black crappie, presumably because of stressful salinities resulting from low freshwater outflows.

Continued sampling revealed changes in the marsh fish community (Meng and others 1994; Matern and others 2002). The trend of decreasing fish abundances and species diversity continued. The group of native fishes originally associated with dead-end sloughs was no longer identifiable as a distinct group on the basis of statistical techniques similar to Moyle and others (1986). The only species not showing overall declines in abundance were the alien yellowfin goby and shimofuri goby (*Tridentiger bifasciatus*), which fluctuated widely in abundance from year to year.

Factors Affecting Distribution and Abundance

Matern and others (2002) suggested that the presence of a species in the marsh is dependent on the ability of the species to withstand the natural fluctuations in environmental conditions that are typical of estuarine environments (Moyle and Cech 2000). The distribution and abundance of a species is dependent on several interacting factors including the timing of reproduction of resident species, recent reproductive success, and habitat differences among sloughs. The lack of community structure was attributed to interactions between the natural fluctuations of the estuary, the overall decline in fish abundance through time, and the frequent and successful invasions of the system by alien fishes and invertebrates. Species with the same general responses to environmental conditions included: (1) shimofuri goby, yellowfin goby, and striped bass adults and juveniles, which are associated with warm water temperature and high salinity;

(2) delta smelt and threadfin shad, which are associated with cool water temperature; (3) threespine stickleback and Pacific staghorn sculpin, which are associated with high variation in inflow; and (4) Sacramento sucker, splittail, tule perch, carp (*Cyprinus carpio*), and starry flounder, which have no strong response to seasonal changes in the environment.

Reproductive success of marsh species can depend on a number of factors. For example, the wet year of 1995 resulted in high recruitment of young-of-year splittail to the marsh as it did elsewhere in the estuary (Sommer and others 1997; Meng and Matern 2001). Larval sampling (February to June) has documented abundant larvae of a variety of species (Matern and others 1995, 1996, 1997, 1998, 1999), presumably resulting from spawning in the marsh or transport of larvae into the marsh. However, larval abundance appears to depend on species-specific responses to environmental conditions, particularly temperature and salinity, which are both related to flow (Meng and Matern 2001). The larvae of the alien species shimofuri goby, inland silverside, striped bass, and threadfin shad are associated with warm water temperatures and lower outflow that characterize late-season conditions. The larvae of the native species prickly sculpin, Sacramento sucker, threespine stickleback, longfin smelt (*Spirinchus thaleichthys*), and splittail are associated with cool water temperatures and high outflow conditions that characterize early season conditions. In 1994, a dry year, larvae of marine species were more numerous than in 1995 and 1996, which were wet years (Matern and others 1995, 1996, 1997, 1998, 1999). Delta smelt and longfin smelt larvae were more common in 1995 and 1996 than in 1994 (Matern and others 1995, 1996, 1997, 1998, 1999). Larvae of several freshwater fishes, including alien white crappie (*Pomoxis annularis*), were more numerous in 1996 than in the other years (Matern and others 1995, 1996, 1997, 1998, 1999). As found for rivers and Delta, native species appear to be most successful when hydrology and associated environmental measures most closely mimic natural “pre-development” conditions (Meng and Matern 2001).

Meng and others (1994) found that native fishes were more abundant in smaller sloughs and that seasonal species were more abundant in larger sloughs. Matern and others (2002) found differences in the physical and chemical characteristics of large and small sloughs and suggested that the differences in fish distributions between large and small sloughs reflected responses to those characteristics. Low species diversity and low abundance of fishes were noted in one small slough that receives outflow from a wastewater treatment plant (Matern and others 1997, 1998, 2002). The small slough with the highest diversity and abundance of fishes is located within one of the few remaining areas of undiked tidal wetlands in Suisun Marsh (Suisun Marsh Ecological Workgroup 2001). These observations suggest a response to water quality, habitat diversity, or both. Wetlands managed for waterfowl, the dominant Suisun Marsh land use, discharge water into the natural channels at times, which might have effects on fishes and ecological processes. For example, threespine stickleback are often captured in large numbers when managed wetlands are drained, suggesting they reproduce in the ponds and enter the marsh with the drainage water.

Trophic Processes

Studies of ecological processes and food web structure in Suisun Marsh have been limited, and such studies are lacking for the brackish-water tidal wetlands bordering Suisun and Grizzly bays. Food habits studies during the early part of the UCD Suisun Marsh program indicated seasonal use of the mysid shrimp, *Neomysis mercedis*, by many fishes (Herbold 1987). Since those studies, the abundance of *Neomysis* has declined dramatically, and an alien mysid shrimp, *Acanthomysis bowmani*, has increased in abundance but has not reached levels of abundance similar to *Neomysis*. More recent analyses of food habits indicate little consumption of mysid shrimp, except by juvenile striped bass (Feyrer 1999). Splittail, starry flounder, prickly sculpin, and yellowfin goby no longer consume *Neomysis*. Despite these changes in diet, there were no observable changes in stomach fullness or condition of individual fish. It is unknown if the changes in the food web are a causal factor of declining diversity and abundance of fishes in Suisun Marsh.

Management of Suisun Marsh

Because the salinity control gate gives managers the ability to influence the salinity of Suisun Marsh waters (both mean value and variability), the Suisun Marsh Ecological Workgroup was formed in 1995 to consider the potential and real effects of gate operations on beneficial uses of Suisun Marsh and to make recommendations about future operations (Suisun Marsh Ecological Workgroup 2001). The final recommendations of the various topic subgroups formed within the workgroup differed widely. These topic subgroups included aquatic habitat, brackish marsh vegetation, wildlife, and waterfowl (including managed wetlands). It is unclear how the different recommendations will be resolved and what the subsequent effects, positive or negative, on fishes will be.

Summary

The major driving force determining the relative abundances of fish species in Suisun Marsh appears to be reproductive success inside and outside of the marsh. The species assemblage at any particular time appears to be governed by young-of-year spawned within the marsh in areas where the spawning requirements of adults are met (yellowfin goby, shimofuri goby, and occasionally splittail), young-of-year recruiting to the marsh from upstream (e.g., striped bass, Sacramento sucker, splittail), young-of-year recruiting to the marsh from downstream (e.g,. starry flounder, Pacific staghorn sculpin), and young-of-year passing through the marsh during downstream migrations (e.g., chinook salmon, Pacific lamprey [*Lampetra tridentata*]), and adults passing through the marsh to spawn in upstream areas (e.g., longfin smelt, chinook salmon). Recent reproductive success carries over in the form of juvenile and adult fish, but because young-of-year fish dominate catches, this factor is of secondary importance in explaining the existing data. Gear biases may be limiting our understanding of the relationships between fish populations and habitats in Suisun Marsh. Trawling captured a much different group of fishes than seining.

As for freshwater tidal wetlands, population sizes of native and alien fishes are unknown, as are the effects of their populations on one another. The continued trend of depressed species diversity and abundances within Suisun Marsh suggest that some fundamental change in key ecological processes has taken place that is now limiting fish production and occurrence in brackish-water tidal wetlands. Matern and others (2002) suggested that the highly unpredictable pattern of species abundances will continue in the marsh until invasions of alien species halt and estuarine processes return to some semblance of their historic range of variability. Finally, we do not know how applicable the Suisun Marsh model is to tidal wetlands fringing Suisun and Grizzly bays.

Conceptual Model for Suisun Marsh Tidal Wetlands

The conceptual model for Suisun Marsh (Figure 5) is based almost exclusively on Matern and others (2002). In this model, the distribution of fishes in the marsh represents an interaction of spawning success in upstream and downstream areas and within the marsh. During wet years, freshwater riverine influences are more pronounced. Native freshwater spawners and alien striped bass have higher spawning success during wet years resulting in higher recruitment into the marsh. Similarly, successful reproduction of some native freshwater spawners can occur in smaller tributaries to the marsh during wet years. Because net freshwater outflow from the marsh and the Delta is higher during wet years, the probability of saltwater species spawning in the marsh, or of the transport of their larvae into the marsh, is low.

During dry years, the situation is reversed. Native freshwater spawners and striped bass reproduce poorly in both the Sacramento River and the smaller tributaries to the marsh. Net freshwater flow through the marsh is reduced, and the probability of saltwater species spawning in parts of the marsh, or of the transport of their larvae into the marsh, is higher.

In both types of years, spawning success and larval transport mechanisms provide a starting point. Seasonal changes in environmental conditions, such as salinity and temperature, influence the distribution and relative survival of resident species throughout the rest of the year. Similarly, these environmental influences likely influence the length of time that migratory and transient species spend in the marsh. Although not explicitly included in the conceptual model, operation of the salinity control gate could conceivably have important effects on fish distributions because of changes in hydrodynamics or alteration of mean values or variability of salinity.

San Francisco Bay Tidal Wetlands

Beach seining conducted as part of the CDFG Bay Study (Baxter and others 1999), represents the most geographically extensive sampling of shallow near-shore saltwater habitat in the Bay-Delta system. Accessible beaches at 27 stations distributed throughout San Francisco Bay and as far upstream as Sherman Island in the western Delta (see

Figure 2) were sampled on a monthly basis from 1980 to 1986. This study did not target tidal wetlands, but, similar to the USFWS beach seining survey in the Delta, shallow nearshore habitats adjacent to wetlands were sampled. In addition, a variety of smaller-scale studies have focused on existing or restored tidal wetlands around San Francisco Bay. Eighteen fishes were commonly captured in these studies (Table 1) with many others captured less frequently.

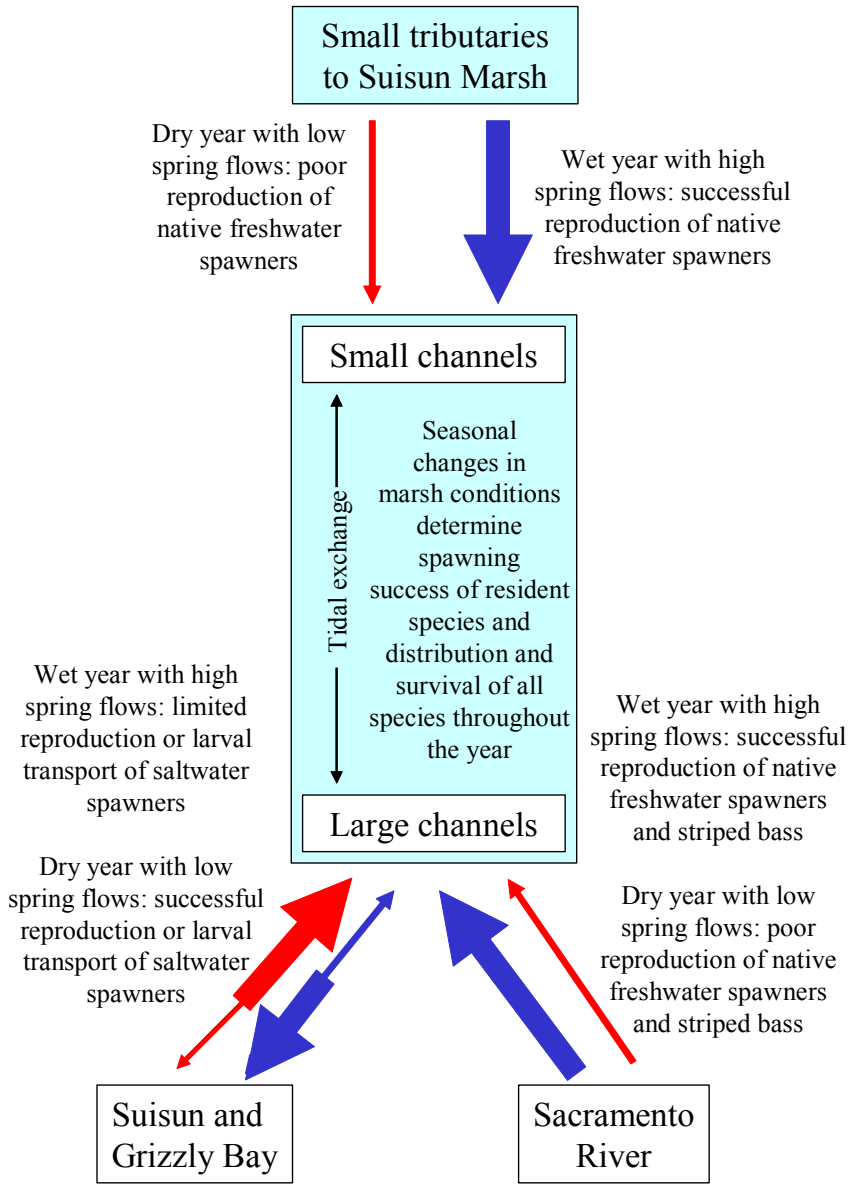

Figure 5 A conceptual model for sources of environmental variability that may be important to the fish community of Suisun Marsh. Blue arrows represent wet-year processes and red arrows represent dry-year processes. Unidirectional arrows represent riverine influence and bi-directional arrows represent tidal influence.

Patterns in Distribution and Abundance

Three native species—topsmelt (*Atherinops affinis*), northern anchovy (*Engraulis mordax*), and jacksmelt (*Atherinopsis californiensis*)—dominated the Bay seining study results (summarized by Chotkowski 1999) and contributed 59.3% of the fishes captured. Pacific staghorn sculpin, arrow goby (*Clevelandia ios*), striped bass, yellowfin goby, shiner surfperch (*Cymatogaster aggregata*), and dwarf surfperch (*Micrometrus minimus*) were the next most abundant species and contributed 30% of the catch. Of the latter species, only striped bass and yellowfin goby are alien. In total, 63 species were captured, of which 36 were marine species native to the northeastern Pacific Ocean; and only nine of the species captured were alien to the system (11.8% of the individuals).

On a regional basis, common species (>5% of the catch) in the South Bay included Pacific herring (*Clupea pallasii*), northern anchovy, topsmelt, jacksmelt, and arrow goby, and 96% of the fishes caught were native (Hieb, personal communication, see "Notes"). In Central Bay, the same species, except for arrow goby, were common and the percentage of native fishes was high (95%). The percentage of native fishes was lower in San Pablo Bay (80%) mainly because the alien yellowfin goby was common. Other common species were the same as Central Bay, except for the addition of Pacific staghorn sculpin. There was a major shift toward alien species in Suisun Bay and Carquinez Strait. Common natives included topsmelt and jacksmelt, but alien striped bass (46%) and inland silverside (7%) dominated the catch, which was 41% native and 59% alien. Alien fishes dominated the two sites in the western Delta (95%). All of the common species were alien including threadfin shad (8%), inland silverside (67%), and striped bass (19%). These data indicate that the freshwater Delta is dominated by alien fishes and San Francisco Bay by native marine fishes, whereas Suisun Bay acts as a transition zone with a mix of marine, freshwater, and estuarine fishes.

Topsmelt, arrow goby, yellowfin goby, and Pacific staghorn sculpin dominated a South Bay marsh restoration site (Woods 1984). Topsmelt appeared to use the site for spawning and juvenile rearing. Pacific staghorn sculpin were present only as juveniles. Other common fishes appeared to be resident, including arrow goby, threespine stickleback, yellowfin goby, and longjaw mudsucker (*Gillichthys mirabilis*). Juveniles of northern anchovy and starry flounder (*Platichthys stellatus*) were also captured in low numbers. Unfortunately, the study was conducted during the initial post-construction phase, before marsh vegetation was well established.

Twenty-five species were captured and shiner perch and topsmelt dominated catches in a South Bay tidal creek (Wild 1969). Threespine stickleback, rainwater killifish, arrow goby, cheekspot goby (*Ilypnus gilberti*), and bay goby (*Lepidogobius lepidus*) were also resident. Transient species including Pacific herring, threadfin shad, northern anchovy, longfin smelt, yellowfin goby, and staghorn sculpin used the creek as a spawning and rearing area.

Three tidal creeks and nearby mudflats in North Bay were dominated by staghorn sculpin, bay goby, and English sole (*Parophrys vetulus*) in the early spring with large numbers of shiner perch, northern anchovy, and arrow goby appearing in the late spring (CH2M Hill Inc. 1982). Differences in abundance were attributed to spawning activity. Northern anchovy, striped bass, and shiner perch dominated the catches during the summer and early fall. Patterns of abundance were similar in tidal marshes associated with the creeks. Topsmelt, Pacific staghorn sculpin, and threespine stickleback dominated catches in the winter and spring. Topsmelt, striped bass, and northern anchovy were dominant during the summer and early fall with topsmelt and yellowfin goby dominating catches during the remaining months. The absence of topsmelt from the tidal channel and mudflat catches was attributed to gear bias; otter trawling is unlikely to capture surface-oriented species such as topsmelt.

Beach seining and trawling in San Pablo Bay restored wetlands (USACE 1996, 1997) in the spring of 1996 indicated dominance of Pacific staghorn sculpin, inland silverside, threespine stickleback, and Pacific herring. Small numbers of chinook salmon and steelhead rainbow trout were also captured. Results in spring 1997 were similar except for the absence of longjaw mudsucker in 1997.

A long-term trawl study in the Bay has documented severe declines in surfperch populations, including shiner perch and dwarf surfperch (DeLeón 1999), the two surfperches most commonly associated with saltwater tidal marsh and channels. It is unknown if similar declines have occurred in tidal marsh habitat because there are no comparative data for the same sites before and after the declines in the trawl catch.

Spatial Variability in Distribution and Abundance

In general, resident native fishes dominate the 1st and 2nd order channels of the marsh plain of San Francisco Bay tidal marshes. Transient fishes, including many alien species, become more significant in the larger channels and open water (DeLeón and others, personal communication, see “Notes”; Hieb and DeLeón 2000). Several alien fishes appear to be habitat generalists. In lower Petaluma River marshes, alien yellowfin goby was common in all habitats sampled. Longjaw mudsucker and threespine stickleback dominated the 1st and 2nd order channels, but alien yellowfin goby was the third most abundant species. These three fishes, plus the splittail and prickly sculpin, were most commonly collected from emergent vegetation. A restored marsh, which was returned to tidal action in 1994, was dominated by splittail, alien yellowfin goby, and Pacific staghorn sculpin. In another San Pablo Bay marsh, the aliens inland silverside, rainwater killifish, and shimofuri goby were common in all habitats sampled. Prickly sculpin and threespine stickleback and the alien shimofuri goby dominated the 1st and 2nd order channels. In emergent vegetation, the aliens shimofuri goby, yellowfin goby, and inland silverside, were most common along with prickly sculpin and splittail. In all areas, striped bass, American shad, and splittail were most common in the larger channels and rivers. None of the fishes that were considered wetland residents (longjaw mudsucker, threespine stickleback, rainwater killifish, western mosquitofish) were ever

captured in the deeper channels. Some fishes that commonly occurred in the wetland habitats were captured in deeper waters, including yellowfin goby, prickly sculpin, Pacific staghorn sculpin, and inland silverside. Splittail were only collected in 1995 and 1998 (high outflow years), suggesting that splittail may successfully reproduce or rear in these habitats only occasionally.

Many of the differences in species composition among the existing studies are probably related to salinity regime. San Pablo Bay is heavily influenced by outflow from the Delta and the Petaluma and Napa rivers resulting in brackish-water to freshwater conditions in some years. Most other wetlands around the Bay are less influenced by fresh water. It is unfortunate that virtually no studies of wetlands in the estuary have addressed ecological processes in saltwater tidal marshes, and while some studies examined benthic macroinvertebrates, none have looked at fish food habits.

Conceptual Model for San Francisco Bay Tidal Wetlands

Because of the lack of data on processes, the conceptual model consists simply of distributional data (Figure 6) with more data for the marshes in the northern San Francisco Bay. Some fishes are more likely to be found in particular habitat types, but there is considerable overlap. Many fishes appear to move onto the marsh plain and into the lower order intertidal channels during tidal inundation, presumably to feed. Most of these fishes probably return to subtidal habitats during low tide although some may remain in isolated pools. The studies in southern San Francisco Bay have not documented differences in habitat use among fishes; however, there do seem to be differences in species composition between northern and southern San Francisco Bay.

Evaluation of Question: Will Tidal Wetland Restoration Enhance Populations of Native Fishes?

There have been few data collected that are useful in evaluation of the question, making any conclusion highly uncertain. On a qualitative basis, it seems likely that some native fishes would benefit from restoration of tidal wetlands, but not necessarily all fishes and not necessarily to a significant degree in terms of population size. There is evidence that native fishes use restored tidal wetlands, but it is unclear whether this represents increased production or redistribution of fish that would have survived and reproduced elsewhere. This is a common problem for habitat restoration and enhancement efforts and is still controversial in a variety of areas (e.g., artificial reefs, Bortone 1998). Benefits seem most likely for resident fishes such as tule perch, prickly sculpin, topsmelt and others (Table 1). Benefits are most difficult to assess for migrant and transient species because it is difficult to establish the period of residence for captured individuals, and these species tend to be captured in low numbers with the methods being used. These species also tend to be the special status native species including delta smelt, splittail, and the anadromous salmonids. For similar reasons it is difficult to assess the concept of migration corridors. The migratory and transient species expected to benefit from the creation of tidal wetlands

along migratory pathways are only present for a short time, making it difficult to assign benefit; however, that does not mean the potential benefits are not large. Finally, it is difficult to predict the outcome of restoration of large tracts of wetlands that resemble historical habitats with marsh plains and channel networks, because there are no such areas remaining in the Delta on which to base predictions.

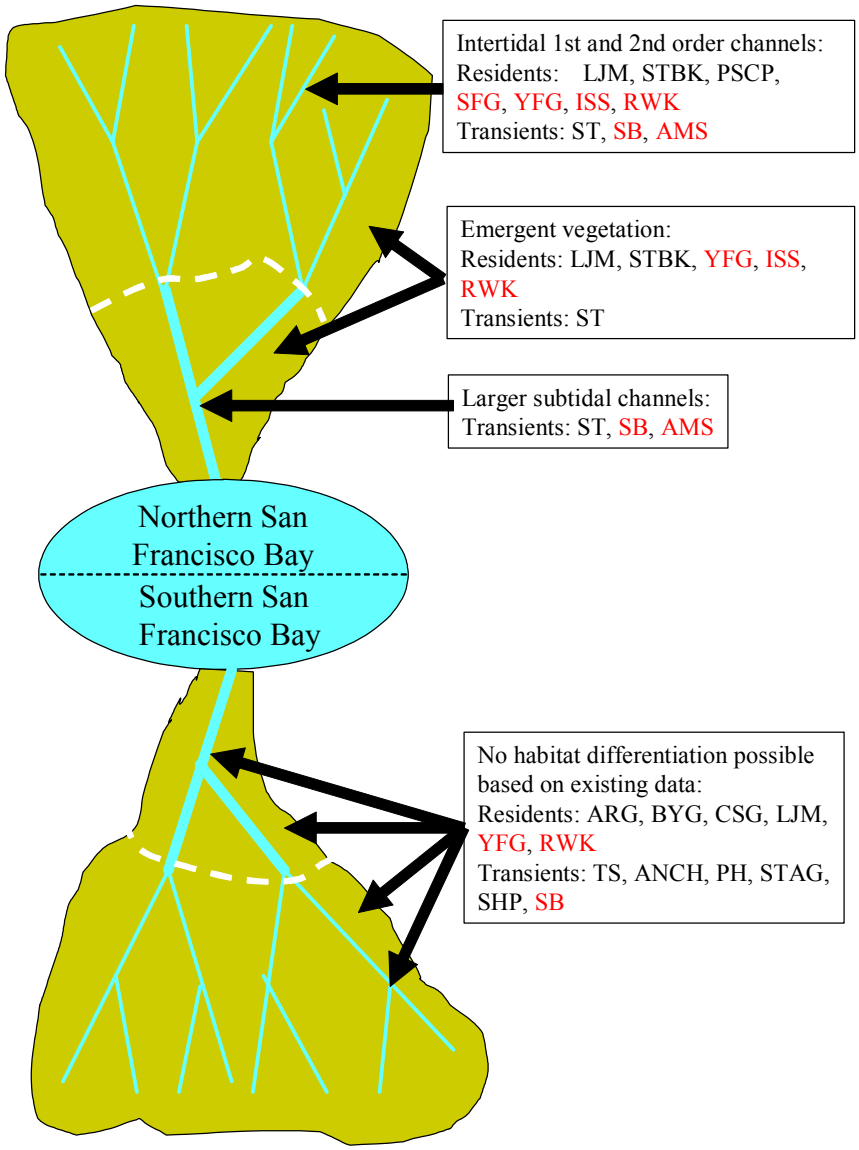

Figure 6 A conceptual model for fish habitat use in San Francisco Bay tidal wetlands. Species codes in red indicate alien species. Species codes: AMS–American shad; ANCH–northern anchovy; ARG–arrow goby; BYG–bay goby; CSG–cheekspot goby; ISS–inland silverside; LJM–longjaw mudsucker; PH–Pacific herring; PSCP–prickly sculpin; RWK–rainwater killifish; SB–striped bass; SFG–shimofuri goby; SHP–shiner perch; ST–splittail; STAG–Pacific staghorn sculpin; STBK–threespine stickleback; TS–topsmelt; YFG–yellowfin goby.

Major Uncertainties

For Delta tidal wetlands, the major uncertainty is the net benefit of restored tidal wetlands to native fishes in general and fishes of special concern in particular. This problem has three parts. First, large areas of existing or restored tidal wetlands with the physical characteristics desired for restored wetlands (extensive marsh plain and channel networks) do not exist, so cannot be studied to determine fishes' habitat needs to aid in predicting the outcome of restoration. Second, it seems likely that *Egeria densa* will invade subtidal areas in or adjacent to restoration projects. *Egeria densa* supports a unique assemblage of native and alien fishes that may not represent the desired outcome of restoration efforts. Finally, if *Egeria densa* does invade restoration projects or subtidal areas adjacent to the outlets of channel networks, there appears to be a high probability of predation on native fishes by resident alien fishes, primarily largemouth bass, but also other centrarchids and ictalurids. However, direct evidence for the importance of predation effects is quite limited, consisting of anecdotal information and inferences that are based on life history information available from other studies. The presumed predatory interaction is mediated by the distribution and abundance of the alien aquatic macrophyte, *Egeria densa*. Thus, the "predator problem" may, in many respects, be an "*Egeria* problem." These three primary uncertainties can be broken down into the following questions:

- How have gear biases affected perceptions of distributions and interactions of fishes? Sampling methods have varied from study to study and tend to be most efficient at capturing small juvenile fishes in particular habitat types, not including habitats expected in freshwater tidal wetlands, such as tules or small channels.

- Which fishes, alien or native, prey on native fishes, and is such predation limited to specific life stages (or size-classes) of prey? If predation on early life stages of prey is compensated by increased growth and survival of older, larger individuals in tidal wetlands, then the increased early mortality might be less important to the population.

- How large are the predator populations in different geographic areas and habitat types? In particular, does the presence of dense stands of *Egeria densa* in subtidal nearshore habitat facilitate predation on native species? This uncertainty could be important in determining both the locations where tidal wetland restoration could have the most benefit and the design and management of restoration projects.

- What environmental factors influence rates of predation? Such factors might include seasonal temperature regime, salinity regime, turbidity, flow conditions, type and density of vegetation, and habitat type. These considerations will be important in assessing the effect of predation on specific fishes. For example, chinook salmon are present in the Delta when water temperatures are low. Metabolic demands of predators would be lowest during this time, resulting in relatively low predation rates.

- How can restored tidal wetlands be designed to minimize invasion by *Egeria densa* if the presence of *Egeria densa* is found to be detrimental to restoration of desired fishes?

- How can the location of restored tidal wetlands be optimized to benefit migratory fishes or facilitate use of such restored habitats by resident native fishes?

For the Suisun Marsh, the major uncertainty is the same as for the Delta. It is unclear if restoration of tidal wetlands with an extensive marsh plain and a well-developed channel network will increase populations of native fishes and other desirable species. The situation is simpler than in the Delta because *Egeria densa* has not invaded Suisun Marsh. There is uncertainty about the factors causing the decline in species diversity and abundance that has occurred from 1979 to the present during a period with a relatively constant area of tidal wetlands. There is a need to characterize the tidal wetlands fringing Suisun and Grizzly bays to determine how applicable the Suisun Marsh model is to other brackish-water tidal wetlands and how the benefits of tidal wetland restoration around those bays would compare with the benefits in Suisun Marsh. These uncertainties can be summarized:

- How have gear biases affected perceptions of species distributions and interactions? Sampling methods have varied from study to study and tend to be most efficient at capturing small juvenile fishes in particular habitat types, not including habitats expected in freshwater tidal wetlands, such as tules or small channels.

- Will native fish species benefit from tidal wetland restoration in Suisun Marsh?

- What factors account for the decline in species diversity and abundance in Suisun Marsh?

- Do effluent or drainage water have negative effects on the ecosystem? If so, a list of management practices to minimize the effects is needed.

- What environmental factors have prevented invasion of submerged aquatic vegetation? This information could be important with regard to tidal wetland restoration in the Delta.

- Are the tidal wetlands bordering Suisun and Grizzly bays similar or different, compared with Suisun Marsh?

For San Pablo Bay tidal wetlands, the major uncertainty is more of a management issue. How important are Bay tidal wetlands to restoration of native fishes of concern in the estuary as a whole? Existing data suggest that these wetlands are not a major habitat for fishes of concern in the Bay-Delta. This uncertainty has two parts:

- To what extent can restoration of tidal wetlands in San Francisco Bay in general, and San Pablo Bay in particular, contribute to increased populations of native fishes of concern?

- How have gear biases affected perceptions of species distributions and interactions?

Addressing Uncertainties

One uncertainty common to all types of tidal wetlands sampling discussed above is the effect of gear bias. Although this uncertainty may seem somewhat trivial compared with the others, resolving this uncertainty is critical to obtaining valid data to resolve other uncertainties; thus, gear bias is discussed first. Biases in methodology are acknowledged in most studies; however, this does not make it less difficult to compare or combine results from different studies. Clearly, not all methods work equally well in all settings; however, it is clear that long-term use of a standard protocol has important benefits as demonstrated by the UCD Suisun Marsh study (Moyle and others 1986; Meng and others 1994; Matern and others 2002). Some standardization of methods and protocols is needed to obtain maximum benefit from information collected as part of any habitat specific, project specific, or regional monitoring effort; however, it is often difficult to obtain consensus among researchers regarding such standardization (Bonar and Hubert 2002). In the San Francisco Estuary, such protocols may have to be specific to habitat types or geographic areas. Bonar and Hubert (2002) suggest that standardized protocols should have the following characteristics if they are to be widely applied.

- Protocols supported by higher-level authorities (CALFED agencies in this case).

- Input to the selection processes from a wide variety of sources.

- Methods that are simple.

- Benefits of standard methods emphasized to the users.

- Procedures that are field tested.

- Procedures that are cost effective.

- Methods designed to minimize variation in catchability and catch.

- Procedures developed for determining needed sample sizes.

- Methods that are reviewed before implementation.

- Training developed in the use of the protocols.

The purpose of the San Francisco Estuary protocols would be to provide long-term standardized data sets that apply across many projects and areas within particular regions. Nevertheless, additional study designs, techniques, and gears to address specific questions of interest should not be discouraged. For example, a standardized sampling program often employs a fairly long sampling interval (e.g., monthly or yearly); however, much useful information can be obtained by sampling across spatial and temporal scales that have more meaning within the life histories of the organisms being studied, such as daily and tidal time scales (Kimmerer and others 1998; Bennett and others 2002). Such intensive studies could even be incorporated in a regional monitoring plan. Protocol development should also include the consideration of the performance measures to be used. Many biologists tend to focus on numbers of organisms as performance measures, but, especially for migrant and transient species, other performance measures such as growth rates or feeding success may be more appropriate.

The other uncertainties for Delta freshwater tidal wetlands are difficult to address under existing conditions because the questions revolve around the desirability of restoring large areas of tidal wetland with extensive tidal plain and well developed channel network, a type of habitat that does not exist at present. Thus, the habitat must be created and then the ecological effects monitored. This can only be accomplished as a large-scale adaptive management experiment because development of channel networks requires a minimum size of about 100 hectares or more. The experiment is particularly complex because it needs to test two very basic concepts at the same time. The first is the assumption that freshwater tidal wetlands with the desired structural components (marsh plain, channel network) can be constructed and will remain viable over time. The second is the assumption that the restored freshwater tidal wetland will provide benefit to desired fishes. The adaptive management experiment should have the following characteristics:

- The restoration sites chosen for the experiment should be fairly large, on the order of a hundred hectares per treatment as a minimum. Treatments could include different design methods (e.g., intensive versus minimal use of heavy equipment for sculpting desired habitat features) or designs that might minimize invasion of *Egeria densa* (e.g., maximizing intertidal habitat and minimizing subtidal habitat). Large size would also ensure that intense sampling events do not disturb large proportions of the available habitat area or the fish populations present.

- Multiple experimental sites would be desirable. For example, it would be desirable to have a site in proximity to a riverine source of sediment and a site in the western Delta where tidal influences predominate. Sediment processes may have important implications for the sustainability of projects over time, and might also have influences on the dynamics of fish use depending on the specific location.

- Standard monitoring protocols should be adopted and additional intensive studies undertaken, as determined by the research team in charge of the experiment.

- Measures beyond simple fish counts and length measurements should be considered for the monitoring program. Measures of fish condition such as weight, reproductive condition, presence of external anomalies (e.g., lesions or tumors), and growth should be considered. Monitoring of other organisms such as invertebrates may also be desirable.

- Short-term, smaller-scale field and laboratory studies should be encouraged both within and outside the adaptive management experiment site, especially those studies intended to elucidate processes taking place within the experiment (e.g., trophic dynamics).

- Experiments should be coordinated to the extent possible with any regional monitoring effort and other ongoing programs.

- Participants in the experiments should be prepared to modify the experiment if monitoring and assessment lead to changes in the conceptual model that suggest the experiment is unlikely to achieve its goals. Also, what is learned in the experiment should provide the basis for the conceptual model used in new restoration projects.

- A national panel of experts in tidal marsh restoration should review all aspects of the adaptive management experiment.

Conducting adaptive management experiments in a timely manner is critically important to addressing uncertainties. The design and implementation of adaptive management experiments will require top-level institutional support for the following reasons:

- The various monitoring programs and studies likely constitute a major increase in the capture of species protected by federal and state Endangered Species Acts. This is unavoidable as these are the species of major concern. Personnel from regulatory agencies should be included in all design teams to help balance increased capture of protected fishes against knowledge acquired.

- Design and implementation of adaptive management experiments will likely be slow, making it difficult to acquire information in a time frame that will satisfy the need to achieve short-term objectives.

The key uncertainties in Suisun Marsh and other brackish water marshes fringing the Suisun and Grizzly bays are basically similar to those in the Delta with regard to the benefits of tidal wetland restoration. As in the Delta, addressing the uncertainties will require large-scale adaptive management experiments. In addition, species diversity and abundance is declining in Suisun Marsh, but there are no well-articulated hypotheses about the processes responsible. Matern and others (2002) imply that restoration of more natural hydrologic and salinity regimes might favor native species with the caveat that new

invasive species could obscure any benefit. Opportunities seem somewhat limited at present but include:

- Designing a large tidal restoration experiment in Suisun Marsh similar to that proposed for the Delta.
- Designing salinity manipulation adaptive management experiments to take advantage of salinity control gate operations in Suisun Marsh at various times of the year.
- Determining the importance of the small tributary systems to Suisun Marsh fishes and whether restoration efforts in those systems would increase populations of desired species.
- Determining if discharges from managed wetlands have significant effects on fishes.
- Determining if tidal marshes fringing Suisun and Grizzly bays are important to native fishes.

There are no major technical constraints associated with most of the proposed work. However, salinity manipulations would be controversial because they would affect other beneficial uses in Suisun Marsh (Suisun Marsh Ecological Workgroup 2001).

The key uncertainty regarding San Francisco Bay tidal wetlands is the benefit to native fishes of restoring such wetlands compared with the benefits of tidal wetland restoration elsewhere in the Estuary. A number of habitat restoration efforts are currently underway. Additional information obtained from monitoring and assessment of these projects may help establish the importance of Bay tidal wetlands to special status species.

Conclusion

There is a general recognition that the declines in native fishes have been associated with many changes in the Estuary, including the loss of tidal wetlands (Bennett and Moyle 1996). The data are presently inadequate to assess the benefits of restoration of tidal wetlands to populations of native fishes. One reason for this uncertainty is that there are no extant wetlands of the size and with the attributes desired; thus, data cannot be gathered to help make predictions. Another reason for uncertainty is that gear biases may be affecting perceptions of habitat choices by fishes. In particular, techniques for sampling within vegetated habitats have not been widely applied in the Estuary. Another important consideration may be the numerous invasions of the system by alien plants and animals. In the Delta, the presence of *Egeria densa* is particularly important because dense beds of this alien submerged macrophyte support a distinctive assemblage of native and alien fishes. In particular, largemouth bass associated with the edges of the macrophyte beds may prey upon native species at a greater rate than the native and alien predators present

in open water. The best way to resolve some of these uncertainties is through large-scale adaptive management experiments. Even if these experiments are unsuccessful at increasing native fish populations, it seems likely that the increased extent of tidal wetlands will have beneficial effects for other parts the ecosystem, such as native mammals, reptiles, amphibians, birds, and plants.

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