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Plant Communities

Plants of Shallow Subtidal Habitat and Tidal Flats (with an emphasis on eelgrass)

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Introduction

There are about 200,000 acres of shallow subtidal habitat and tidal flats in San Francisco Bay, San Pablo Bay, and Suisun Bay. Of this area, approximately 171,000 acres are subtidal habitat and about 29,000 acres are tidal flats. While relatively simple in terms of species diversity, the plant communities that occur in these areas are important components of the estuarine ecosystem.

Although this paper describes the plant communities of shallow subtidal habitat and tidal flats, it focuses on the eelgrass (*Zostera marina*) community. For more detailed information on the other plant communities (primarily microalgae and macroalgae) that occur in the shallow subtidal areas and on tidal flats of the San Francisco Bay Estuary, please refer to Silva (1979), Nichols and Pamatmat (1988), Meiorin et al. (1991), and Herbold et al. (1992).

Environmental Setting

Shallow subtidal areas and tidal flats are defined by their elevation in relation to tidal height. The shallow subtidal range includes the areas between mean lower low water (MLLW) and the approximate bathymetric contour 18 feet below MLLW. Tidal flats generally occur between the mean tide level (MTL), or the lower elevation limit of *Spartina* (cordgrass) flats, to about 2.5 feet below MLLW. Tidal flat composition can include various combinations of clay, silt, sand, shell fragments, and organic debris. Daily tidal cycles submerge and expose tidal flat surfaces twice every 24.8 hours. During each tidal cycle, tidal flats are also exposed to fluctuating wave action, current velocities, and nutrient supply. Where tidal marshes still exist, incoming tides flood into the upper marsh areas. As these tidal waters recede, organic materials are transported downslope to tidal flats where they become food sources for millions of detritus-feeding invertebrates.

The environmental conditions of shallow subtidal areas and tidal flats are stongly influenced by suspended sediments. In general, the San Francisco Bay Estuary has high concentrations of suspended sediments (Hanson and Walton 1988). This suspended particulate matter is comprised of 70 - 97% non-organic sediment made up of silty clay; the remaining content is comprised of living and other organic matter (Conomos and Peterson 1977). Suspended sediment concentrations are influenced by wind speed, substrate, particle size, wave action, current velocity, tidal action, water depth and seasonal runoff (Cyrus and Blaber 1987). Human activities such as type of land use (Kemp et al. 1983), channel dredging (LaSalle 1988, Hanson and Walton 1988), construction and use of marinas and ferry terminals, and propeller wash (Walker et al. 1989, Thom and Shreffler 1995) can also affect water clarity.

Total suspended solids (TSS) in Suisun and San Pablo bays average between 50 mg/l in the summer to 200 mg/l in the winter (Nichols and Pamatmat 1988). In North Bay and Central Bay, tides can have a significant influence on sediment resuspension, particularly during spring tides and during the ebbs preceding lower low water when the current speeds are highest. Central Bay - characterized by cold, saline, and relatively clear ocean water - has the lowest TSS concentrations, at 10 to 60 mg/l. South San Francisco Bay has slightly higher TSS concentrations than Central Bay (O'Connor 1991).

Salinity levels vary depending on season, weather, amount of diverted fresh water, and location in the Bay. In general, salinity levels within the water column and within tidal flats increase along a gradient from the Delta to the Golden Gate. For example, the salinity in Suisun Bay averages about seven parts per thousand (ppt), and in Central Bay it averages about 30 ppt (Fox et al. 1991). During dry years, South Bay averages salinity levels up to 35 ppt.

Intertidal and Subtidal Plant Communities

The shallow subtidal areas and tidal flats of the San Francisco Bay Estuary support relatively few plant communities. These communities include diatoms and other microalgae, macroalgae, and eelgrass.

Microalgae form the basis for the estuarine food web. These algae, consisting of diatoms and blue-green algae, often form dense patches on tidal flats, creating a brown hue to the substrate surface during low tide. Microalgae and settled phytoplankton represent a readily available food source for creatures, such as worms and clams, within the mudflats (Nichols and Pamatmat 1988). Shorebirds and waterfowl then consume these creatures.

Macroalgae (seaweeds) are also found throughout the Estuary, particularly in the more saline areas. Few macroalgae can make the necessary adjustments in internal water and mineral content to survive at low salinity levels. The exceptions include *Gracilaria sjoestedtii*, *Enteromorpha* spp. and the closely related *Ulva* spp. *G. sjoestedtii* is usually found from the mid-intertidal to the shallow subtidal zone attached to rocks partially buried in coarse sand. It also grows attached to small bits of clam and oyster shell in muddy portions of the Bay. In such situations, the plants and associated substrata are easily moved by currents and wave action. *Enteromorpha* and *Ulva* form bright green patches and can occur in great abundance throughout the intertidal zone, often growing on any available hard substrate. *Enteromorpha* can be found occupying higher tidal zones where shade is available. It is especially prevalent on boat hulls, buoys, docks, and woodwork. *Ulva* occupies the lower tidal zones, completing its life cycle in a few weeks and varying its distribution over a short time period. These kinds of macroalgae often undergo seasonal cycles of abundance, becoming common in the warmer months and virtually disappearing in colder months. Maximum abundance occurs in late summer and early fall (Jones and Stokes Associates, Inc. 1981). Many species of *Ulva* are often common in heavily polluted areas because they can use ammonia as a nitrogen source and are generally tolerant of organic and metal pollution (Dawson and Foster 1982). In the absence of eelgrass, *Ulva* can provide a preferred habitat for several invertebrate species (Sogard and Able 1991).


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Uprooted *Zostera marina* from intertidal zone off of Alameda shroreline. Leaves may be 1.5–12 mm wide and up to 15 meters in length.

Eelgrass (*Zostera marina*) is currently the only seagrass found in San Francisco Bay. Belying its common name, it is not a grass but is a flowering plant that has adapted to living submerged in the shallow waters of protected bays and estuaries in temperate regions of the world (Den Hartog 1970, Phillips and Menez 1988). *Z. marina* reproduces both sexually through pollination of seeds, and asexually through a rhizome meristem that extends through the sediments (Setchell 1929). Where abundant, *Z. marina’s* dense, matted root and rhizome system functions to stabilize the soft bottom. Its leaves slow currents and dampen wave action, causing sediment and organic material to accumulate. *Z. marina* is found in intertidal areas, becoming exposed during the lower spring tides; it also occurs in subtidal areas at depths less than one to two meters below MLW (Kitting 1994).

Historic and Modern Distribution (of Eelgrass)

Information on historic distribution of *Zostera marina* in the San Francisco Bay Estuary is very limited. San Francisco Bay may have supported extensive *Z. marina* meadows in the past. (Setchell 1929, Wyllie-Echeverria and Rutten 1989). Low light availability within the water column has been found to limit the development of extensive eelgrass meadows and may be the principal cause of eelgrass decline in San Francisco Bay (Alpine and Cloern 1988, Zimmerman et al. 1991).

In 1989, Wyllie-Echeverria and Rutten published the first survey on the distribution of *Zostera marina* in San Francisco Bay (including San Pablo Bay) and mapped a total of 316 acres (**Table 1.1**). As **Table 1.2** and **Figure 1.1** show, the per area abundance of eelgrass within San Francisco Bay is much less than that of Humboldt Bay or Tomales Bay, two other northern California estuaries.

The 1989 Wyllie-Echeverria and Rutten survey described the *Zostera marina* populations as “patchy” and some as “stressed.” Since that time a few of these beds have increased in size, and new patches have been sited (Kitting 1993 and pers. comm.).

Table 1.1 Acreage of Individual Eelgrass Beds in San Francisco/San Pablo Bay in 1989

Location	Acres
San Pablo Bay	124
Point Orient	3
Naval Supply Depot	12
Point Molate Beach	26
Toll Plaza, East	0.5
Toll Plaza, West	0.5
Point Richmond, North	7
Point Richmond, South	4
Richmond Breakwater, North	18
Richmond Breakwater, South	7
Emeryville	13
Alameda	55
Bay Farm, North	2
Bay Farm, South	4
Coyote Point	1
Richardson Bay	13
Angel Island	3
Belvedere Cove	5
Point Tiburon	1
Keil Cove	10
Paradise Cove, North	4
Paradise Cove, South	3
TOTAL ACRES	**316**

Table from NMFS SW Region. Wyllie-Echeverria and Rutten 1989 Administrative Report SWE-89-05

Associated Fauna Including Rare and Sensitive Species

Tidal flats include a living system of diatoms, microalgae, and protozoa that are fed upon by suspension or surface deposit feeding invertebrates. The bottom invertebrates are in turn fed upon by larger consumers such as fish, shrimp, and crabs. During low tide, these primary and secondary consumers are exploited by millions of migratory shorebirds. The extensive intertidal mudflats of San Francisco Bay are considered a key migratory staging and refueling area for over-wintering shorebirds of the Pacific Flyway (Harvey et al. 1992).

Macroalgae and eelgrass provide food, shelter, and spawning grounds for many Bay fish and invertebrates. The major subtidal spawning areas for *Clupea harengus* (Pacific herring), recently the most valuable fishery in California, are Richardson Bay and the large shallow area between Richmond and Oakland. In these areas, spawning occurs predominantly on *Gracilaria* ssp. and small patches of *Zostera marina* (Spratt 1981). When available, *C. harengus* preferentially uses *Z. marina* habitats for spawning (Taylor 1964, Spratt 1981).

Zostera marina beds support a variety of organisms, more than that of non-vegetated areas (van Montfrans et al. 1984, Kitting 1993, Hanson 1997). *Z. marina* roots and leaves provide habitat for many plants and animals. For example, the long blade-like shoots provide shelter and serve as a nursery ground for many fish species. Small plants (epiphytes) and animals (epizoites) attach to the leaves, motile animals find cover between the leaves, and burrowing animals live among the roots. Epiphytes are an important part of the eelgrass community, contributing up to 22% of the total primary productivity (Jones 1968, Marshal 1970, Penhale 1977). They, in turn, provide food for resident invertebrate grazers (Kitting et al. 1984). Within the rich organic sediment, anaerobic processes of microorganisms regenerate and recycle nutrients and carbon (Kenworthy et al. 1982).

Because *Zostera marina* contains noxious sulfated phenolic compounds that can inhibit bacterial degradation and animal grazing, few animals consume it (Tenore 1977, Harrison and Chan 1980, McMillan et al. 1980). Notable exceptions include several species of waterfowl such as *Anas americana* (wigeon), *Anas strepera* (gadwall), *Anas acuta* (pintail), *Branta canadensis* (Canada goose), and *Branta nigricans* (black brant) (Phillips 1984). *Z. marina* has been an obligate food for black brant along its flyway (Einarsen 1965). Black brant populations are in great decline along the Pacific Flyway, possibly due to this species' dependence on dwindling eelgrass resources (Einarsen 1965).

Some bird species also forage on the fauna associated with *Zostera marina*. An example is the *Sterna albifrons browni* (California least tern) that was listed as an endangered species in 1970. Least terns are known to forage on juvenile and small fishes (Magenheim and Rubissow 1993) that inhabit *Z. marina* beds, particu-

Table 1.2 Comparison of Three Northern California Estuaries Relative to Size of Estuary and Total Acres of Eelgrass (*Zostera marina)*

Location	(km^2)	Extent of Eelgrass (Bottom coverage, acres)	Reference
Humbolt Bay	62.4	3,053	Phillips 1984
Tomales Bay	30.0	965	Spratt 1985
San Francisco Bay	1,140.0	316	Wyllie-Echeverria 1990

Table from NMFS SW Region. Wyllie-Echeverria (1990)

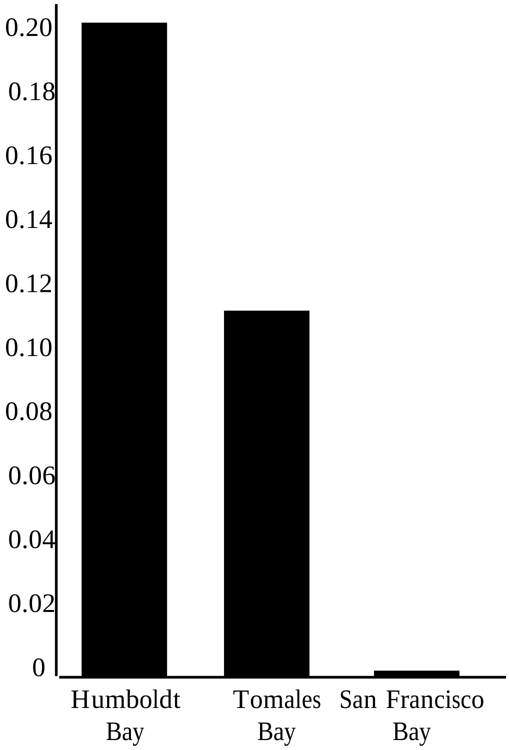

Figure 1.1 Comparison of Percent Eelgrass Coverage in Three West Coast Estuaries (Based on Wyllie-Echeverria (1990))

larly at a major nesting site near the Oakland International Airport and the Alameda Naval Air Station (Collins and Feeney 1983-6, Feeney 1988 and 1989, Harvey et al. 1992).

Invertebrates such as juvenile *Cancer magister* (Dungeness crab) appear to grow up most successfully in the nursery-like habitat that *Zostera marina* provides, particularly in the northern reaches of the Bay. The isopod, *Synidotea laticauda* is periodically found in high numbers (up to 200/m^2) among *Z. marina* beds in Central San Francisco Bay (Hanson 1998). They are an important food item for economically valuable sport fishes such as young striped bass, starry flounder, steelhead trout, king salmon, white sturgeon, plus other fishes in San Francisco Bay (Morris et al. 1980)

The transport of *Zostera marina* fragments acts as a vector for animal dispersal (Highsmith 1985, Worcester 1994). Kitting (1993) found several fish species and a variety of invertebrates usually associated with *Z. marina* on dead blades found at depths greater than four meters below MLW.

Conservation Issues

Exotic Plants - There is some potential for two exotic *Zostera* species to invade San Francisco Bay. The Asian seagrass, *Zostera japonica*, introduced to British Columbia, Washington, and Oregon has not yet been reported in San Francisco Bay. *Z. japonica* has a different life history, morphology, and preferred habitat than *Z. marina* (Harrison and Bigley 1982). Culture experiments determined that *Z. japonica* is not likely to displace existing *Z. marina* beds (Harrison 1982). This may not be the case in San Francisco Bay. *Z. japonica* favors the intertidal zones, the areas where *Z. marina* has been limited to in San Francisco Bay. Thus far, *Z.japonica* occupies only a small fraction of its potential habitat in North America, threatening significant changes in the ecology of the intertidal sediments as this seagrass spreads (Harrison and Bigley 1982).

Zostera asiatica is found from Tomales Bay in the north, to Santa Monica Bay in the south. Phillips and Wyllie-Echeverria (1990) published the first record of this species in the Eastern Pacific. It is a wide bladed *Zostera* that occurs sub-tidally from five meters below MLLW to 17 meters below MLLW. *Z. asiatica* has not yet been identified in San Francisco Bay. This is probably due to its deeper water distribution where photosynthetic processes could be limited in San Francisco Bay.

Factors Limiting Eelgrass Distribution - Under suitable conditions, *Zostera marina* can form dense, continuous, and extensive carpets as seen in Tomales and Humboldt bays. Light, temperature, salinity, tidal range and water motion all affect growth and productivity of *Z. marina* (Thayer et al. 1984, Fonseca et al. 1985, Fonseca and Kenworthy 1987). The amount of time it is exposed to air during low tides determines the upper limits of *Z. marina,* and the amount of available light determines the lower limits (Backman and Barilotti 1976; Dennison and Alberte 1982, 1985, 1986; Bulthuis 1983; Bulthuis and Woelkerling 1983; Wetzel and Penhale 1983; Lewis et al. 1985; Josselyn et al. 1986; Duarte 1991). The primary factor responsible for a worldwide decline in *Z. marina* and other submerged aquatic vegetation is reduced light availability (Giesen et al. 1990, Dennison et al. 1993).

In San Francisco Bay, *Zostera marina* requires somewhere between three and five hours of H_{sat} (length of irradiance-saturated photosynthesis) each day (Zimmerman et al. 1991). In areas with favorable light conditions, *Z. marina* plants have adequate carbon reserves to withstand at least 30 days of light limitation (Zimmerman et al. 1991); however, due to frequent and persistent periods of high turbidity, it is unlikely that plants at the deeper edge of eelgrass meadows in San Francisco Bay can accumulate large carbon reserves (Zimmerman et al. 1991). Average turbidity of the Bay and, more critically, brief periods of high turbidity limit *Z. marina* distribution in deeper water and limit establishment of seedlings and vegetative propagules (Zimmerman et al. 1991). If daily, monthly, and seasonal H_{sat} requirements are not met, long-term survival of the plants may be limited (Zimmerman et al. 1991). Any activities that increase turbidity within Bay waters, whether natural or

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Zostera marina plants, discernable as dark blotches in the foreground, near Belvedere Cove, Marin County.

anthropogenic, have detrimental effects on existing eelgrass populations and associated food webs.

Current Restoration Success - The technology for successfully establishing seagrass beds has been unreliable (Phillips 1974, 1980; Lewis 1987), although, in 1989 Zimmerman et al. (1995) successfully transplanted *Zostera marina* at two locations in San Francisco Bay. According to Fonseca et al. (1988), waning interest in *Z. marina* restoration was due to a net loss of habitat through seagrass mitigation projects. Planting projects have often failed as a result of poor selection of planting sites or plant material and incorrect use of planting methods. Factors that limited success include a general lack of knowledge of physiological requirements and unknown local environmental factors controlling *Z. marina* growth (Lewis 1987, Merkel 1990). For example, in 1984, an eelgrass transplant was initiated in San Francisco Bay. Limited transplant success was attributed to a lack of data on local eelgrass autecology coupled with nearby dredging operations and diminished water quality (Fredette et al. 1988).

Conclusions and Recommendations

There has been considerable interest in protecting and expanding existing *Zostera marina* beds in San Francisco and San Pablo bays (Fredette et al. 1988). Since the 1989 survey, sitings have indicated a marked change in the distribution and abundance of this species. Better conserving this species in the Estuary will require more frequent monitoring of individual populations.

It also is imperative to protect the current eelgrass beds from further decline. Because of the inherent difficulties in establishing eelgrass, plantings conducted in exchange for permitted losses (mitigation projects) could result in a greater loss of habitat and should not be allowed. The current *Zostera marina* populations may be the last remnants in San Francisco Bay and are extremely vulnerable to local extinction (Kitting and Wyllie-Echeverria 1991); therefore, plantings should be used to enhance current beds or to create new beds.

There are several actions that should be undertaken when designing potential restoration or enhancement projects:

1. Conduct a thorough survey to assess physical conditions of the site. Collect and evaluate environmental data and/or pilot test the planting at a particular site before commitment of a full restoration project. The success of any seagrass revegetation effort, including long-term plant growth, is strictly dependent upon a physical environment suitable for initial establishment (Zimmerman et al. 1991).
2. Carefully evaluate light availability before proceeding with any major transplant effort. Water column turbidity is sufficiently high throughout much of the Central Bay, limiting the euphotic zone (depth where irradiance falls to 1% of surface irradiance) to less than 1 m (Alpine and Cloern 1988).
3. Use stocks for planting from a site with conditions as similar as possible to the planting site. There should be similar or equal water depths, salinity, temperature, tidal currents, wave exposure, and sediment composition (Fonseca 1994). Until we learn more about the genetic structure of this species, matching of phenotypes among restoration and donor sites remains the best guide for stock selection.
4. Limit planting to areas with small tidal ranges rather than high tidal ranges to provide greater light availability (Koch and Beer 1996), thus increasing survival success.
5. Plant in areas where parameters for deeper vertical distribution are available make the bed less vulnerable to adverse conditions (such as storm events or desiccation) due to availability of energy from the neighboring deeper shoots (Tomasko and Dawes 1989).
6. Plant in late spring and summer. Periods of high *Z. marina* growth and production coincide with warmer temperatures and greater light availability (Ewanchuk and Williams 1996).

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Tidal Marsh Plants of the San Francisco Estuary

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Introduction

The general ecology San Francisco Bay has been reviewed by Josselyn (1983), who included a brief treatment of its tidal marsh plant community composition and structure. Macdonald (1977, 1988) reviewed the vegetation of California salt marshes, including San Francisco Bay, with emphasis on sedimentation, drainage, topography, salinity, flooding, community structure, and summaries of autecology of selected dominant species. Newcombe and Mason (1972) made descriptive accounts of the Suisun Marsh area vegetation. Atwater et al. (1979) summarized and interpreted the relationships between tidal marsh vegetation of the San Francisco Estuary and its landforms and geomorphic processes. Wells and Goman (1994) reviewed and expanded the quaternary history of the San Francisco Estuary. The purpose of this plant community profile is to supplement previous reviews, and provide additional information on historic changes in the composition, distribution, and abundance of tidal marsh plants of the Estuary.

Environmental Setting

Prehistoric Tidal Marsh Development - Tidal marshes of the modern San Francisco Estuary formed around 10,000 years ago during the Holocene submergence when the rate of sea-level rise slowed sufficiently for tidal marsh sediments to accrete near sea-level (Atwater et al. 1979). Prior to that time, during the Pleistocene epoch, the site of the modern Estuary consisted of broad stream valleys far above glacial low sea level. Pleistocene tidal marsh plant communities were probably associated with either stream mouths or backbarrier lagoons at the edge of an emergent broad coastal plain, now submerged and eroded or buried offshore from the modern Golden Gate. Tidal marsh plant species probably migrated upstream in valleys and embayments as sea level rose. Ancestral Pleistocene populations of tidal marsh plant species in today's estuaries may not have been as discontinuously distributed as they are today: coastal plain shorelines (e.g., East Coast of North America) often provide widespread tidal inlets and tidal marsh (Davies 1980). Holocene fragmentation of salt marshes from more extensive or continuous Pleistocene coastal plain salt marsh distributions may account for historic disjunct, relict populations of species in San Francisco Bay which are now found only in south-central or southern California tidal marshes (e.g., *Solidago confinis* (southern goldenrod), *Suaeda californica* (California sea-blite)).

Tidal marshes of the Estuary fluctuated in vegetation composition during the Holocene epoch, apparently in relation to changes in long-term climate. This is indicated by stratified deposits of fossil pollen and plant fragments which indicate periods of accumulation of plants associated with near-freshwater marsh conditions with species associated the more saline (brackish) conditions (Wells and Goman 1994). These findings are consistent with independent evidence on climate changes during the last 6,000 years which show prolonged periods of drought and high rainfall compared with historic conditions (Ingram et al. 1996, Peterson et al. 1989). The tidal marshes in San Francisco Bay were also not static prior to European influence. Some marsh shoreline configurations indicate long-term scarp retreat across marshes with large sinuous tidal creeks and growth of berms and sand spits (Atwater et al. 1979). Areas of rapid marsh growth in some parts of south San Francisco Bay,

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Tidal Marsh along Petaluma River shows complex channels and natural salt pans.

outside the influence of Sierran gold mining and prior to extensive diking, were evident in maps of the Bay prepared in the 1870s (U.S. Coast Survey maps).

Marsh Sediments and Plants - Depositional environments of tidal marshes in the San Francisco Estuary are variable and are significant for the distribution of uncommon plant species. In most of the San Francisco Estuary, the sediments of the middle-marsh marsh plain consists of bay mud (fine silt and clay) with significant percentage of organic matter in mature marshes. Local coarse sediment deposits, often beach ridges (marsh berms, or marsh-beach ecotones) composed of sand, shell fragments, organic debris, or mixtures, create physically mobile (periodically eroded and redeposited), well-drained high marsh habitats with affinity for some common high marsh species (e.g., *Grindelia stricta* var. *angustifolia*, gumplant) and probably also species now locally extinct or rare, such as *Suaeda californica, Atriplex californica* (California saltbush), and *Castilleja ambigua* (salt marsh owl's clover or Johny-nip). Marsh berms are associated with relatively high wave energy environments in the Estuary, located near coarse sediment sources such as eroding bluffs, submerged fossil sand and shell deposits, stream mouths, and eroding marsh edges. Such features were commonly represented on U.S. Coast Survey maps of the mid-1800s, but persist today in very few localities of the Estuary (e.g., Point Pinole, Redwood City area, San Leandro area, and northern San Francisco peninsula). Similar coarse-sediment features probably occurred as natural levees of upstream reaches of large tidal sloughs with significant coarse sediment loads, as is observed today in Morro Bay. Alluvial fans also create gradually sloping ecotones with uplands, with variably textured sediments and freshwater runoff and seeps. Few small alluvial fans exist at tidal marsh edges of the Estuary today (e.g., Point Pinole, Whittell Marsh), but were historically abundant in parts of the Estuary, supporting diverse ecotonal plant communities (Cooper 1926). Analogous alluvial fan-tidal marsh ecotones occur in maritime salt marshes of Point Reyes and Tomales Bay areas, where they support distinctive local plant assemblages, including uncommon to rare species.

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Regionall rare salt marsh owl's clover, or Johnny-nip (*Castilleja ambigua* ssp. *ambigua*). (Tidal marsh, Whittell Marsh, Point Pinole)

Comparison With Other Estuaries - The tidal marshes of the San Francisco Estuary are the most extensive on the central coast of California, and their plant communities are distinct from other central coast tidal marshes in many respects. Most other large central coast tidal marshes are associated with shallow embayments with large open tidal inlets (e.g., Tomales Bay, Drakes Estero and Bolinas Lagoon in Marin County; Bodega Bay in Sonoma County; Elkhorn Slough in Monterey County; Morro Bay in San Luis Obispo County) which impose strong marine influence on the character of their sediments, salinities, and vegetation. Central coast tidal marshes tend to be isolated and few because of the steep modern shoreline with few valleys or wave-sheltered bays. These tidal marshes have extensive sandy substrates, relatively small, local inputs of fine sediment and freshwater discharges and brackish (mesohaline) conditions, and are inundated by water approaching marine salinity (34 ppt) during most of the growing season. Some tidal marshes associated with stream mouths have relatively more freshwater influence and brackish marsh vegetation (e.g., pre-historic Elkhorn Slough and Salinas River, Monterey County; Russian River estuary, Sonoma County), but in association with seasonal reduction in tidal influence because of partial or complete closure of coastal inlets at river mouths (dammed by sand beach ridges during periods of relatively low river discharge). In contrast, the tidal marsh plant communities of the San Francisco Bay Estuary developed under conditions of abundant and predominantly fine sediment (bay mud, clayey silts and silty clays with high nutrient-holding capacity), relatively large tidal range, and extensive brackish marshes associated with relatively large freshwater discharges, distributed over broad, fluctuating salinity gradients (Atwater et al. 1979)

Historically, salt pans (unvegetated, seasonally inundated depressions or flats within the tidal marsh) and local salt ponds (perennial deposits of crystalline salt in hypersaline ponds) were well-developed in San Francisco Bay tidal marshes (U.S. Coast Survey T-charts, 1850s), supporting distinctive vegetation (widgeongrass, *Ruppia maritima*, in some pans) or microalgal floras (in salt ponds). Pans are relatively infrequent in other central coast tidal marshes compared with the historic conditions of the San Francisco Estuary, and natural salt ponds were not known to occur in other central coast tidal marshes. Today, edges of high marsh pans are associated with at least two regionally rare species (*Cordylanthus maritimus* ssp. *palustris* and *Castilleja ambigua* ssp. *ambigua*), and may have been associated with many others in the past (e.g., *Lepidium latipes, L. oxycarpum*; **Table 1.3**)

Tidal Marsh Plant Communities

The distribution of tidal marsh plants is strongly (but not exclusively) influenced by tidal elevation and salin-

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Pickleweed (*Salicornia virginica*), a dominant within the salt marsh middle marsh zone, shown enshrouded by parasitic dodder (*Cuscuta salina*).

ity (Hinde 1954, Atwater and Hedel 1976). Following Peinado et al. (1994), three elevation "zones" of the tidal marsh can be objectively distinguished (and are visually conspicuous): (1) the low marsh zone, occurs from approximately mean sea level to mean high water; (2) the middle marsh zone, occurs from approximately mean high water to mean higher high water; and (3) the high marsh zone (colloquially also called the "upland transition" or "peripheral halophyte" zone; "upper salt marsh zone" of Peinado et al. 1994), occurs near and above mean higher high water up to several meters above extreme high water line (Peinado et al. 1994). The typical species composition of these zones is described below for tidal salt marsh and tidal brackish marsh. Unlike beach, dune, and bluff communities (Barbour and Johnson 1977, Barbour et al. 1973), there is no empirical evidence of salt marsh zonation attributable to salt spray; estuaries and embayments are relatively low-energy wave environments (Davies 1980, Carter 1988). Other potentially significant influencing factors have not yet been well studied.

There are significant floristic differences between the tidal marshes of San Francisco Estuary and other central coast tidal marsh systems. These include:

1. The dominance of *Spartina foliosa* (Pacific cordgrass), either absent today or historically absent from most or all other central coast tidal marshes (Macdonald 1977);
2. The presence of rare species of disjunct distribution, such as *Suaeda californica* (native only to Morro Bay and San Francisco Bay); and
3. The presence of local endemic species such as soft bird's-beak (*Cordylanthus mollis* ssp. *mollis*) and Suisun thistle (*Cirsium hydrophilum* var. *hydrophilum*).

Conversely, some uncommon tidal marsh species which have either declined severely or become extirpated in the San Francisco Estuary still occur in local abundance in some maritime salt marshes of the region (e.g., *Atriplex californica*, *Castilleja ambigua*, *Puccinellia nutkanensis*). Few species associated with high marsh zones of maritime salt marshes in the region were historically absent from the San Francisco Estuary (e.g., *Astragalus pycnostachyus* var. *pycnostachyus* (coastal marsh milk-vetch), *Castilleja ambigua* ssp. *humboldtiensis* (Humboldt Bay owl's clover), *Leymus* x *vancouveriensis* (Vancouver's ryegrass), and *Grindelia stricta* var. *stricta* (gumplant)).

Differences exist also between the structure of vegetation found in predominantly marine-influenced salt marshes of the central coast and tidal marshes of the San Francisco Estuary. Although the middle marsh zone of San Francisco Bay salt marshes has been described as supporting "prostrate" growth forms of pickleweed (Macdonald 1977), the middle marsh plains of sandy or sandy peat salt marshes of Bolinas Lagoon (Allison 1992), Point Reyes, Tomales Bay, and Morro Bay often support very thin, low (< 10 cm) turf-like vegetation mosaics with extremely short, sparse, or prostrate pickleweed as a relatively minor component, or at most co-dominant with species such as *Triglochin concinna* (slender sea arrow-grass; uncommon to rare in San Francisco Estuary). These salt marsh turfs often support high plant species diversity compared with San Francisco Bay salt marsh plains, which tend to be dominated by pickleweed, which often grows in dense stands (usually over 20 cm thick; up to 50-60 cm in some fringing marshes of San Pablo Bay). Low, turf-like middle marsh vegetation is very uncommon in San Francisco Bay, both in brackish and salt marshes.

Salt Marsh Plants and Their Associations - Salt marsh here refers to tidal marsh plant associations that approximate the species composition typical of near-marine salinity during the growing season (34 ppt). Few if any salt marshes in the San Francisco Estuary are ac-

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Soft bird's-beak (*Cordylanthus mollis* ssp. *mollis*). The hairy bracts of the flowering stems are jeweled with salt-encrusted glands. (Brackish tidal marsh, Southhampton Marsh, Benecia) tually regularly exposed to near-marine salinity, but in the upper estuarine salinity range (roughly 20 ppt and above), they are effectively salt marsh in vegetation character. The salt marsh plant community is typical of San Francisco Bay and the outer marshes of most of San Pablo Bay.

The low salt marsh zone in San Francisco Bay is usually dominated by a single species, *Spartina foliosa* (Pacific cordgrass), but is increasingly becoming dominated by the invasive introduced Atlantic species, *Spartina alterniflora* and its highly variable hybrids and novel "ecotypes" (Callaway and Josselyn 1992; Daehler and Strong 1994, 1997; Daehler et al. 1999). *S. foliosa* stands occur as uniform fringes along tidal creek banks or as broad uniform plains on prograding marshes at the edges of broad tidal mudflats. They extend from approximately mean high water to mean sea level (Hinde 1954, Atwater et al. 1979). On gentle elevation gradients, they intergrade with middle marsh plains in mixed stands of *Salicornia virginica* (pickleweed), as at Dumbarton-Mowry marsh and eastern San Pablo Bay fringe marshes. They may also occur as abrupt zones at the edge between tidal mudflats and wave-cut peat scarps. Pioneer colonies of Pacific and smooth cordgrasses on mudflats are abundant in some years, particularly in years of high or late rainfall. They apparently establish by seedlings and regenerated rhizome fragments, but the relative proportion of these of propagule types is unknown. Pioneer colonies of *S. alterniflora* were observed on open mudflats of the San Lorenzo Creek delta in 1991, and are visible in aerial photographs of the Alameda Creek area around 1980. Seedlings and pioneer colonies of *S. foliosa* were common on high mudflats of San Pablo Bay and its tributaries in the late 1990s. The taller *S. alterniflora* appears to be able to spread clonally below mean sea level, but long-term comparisons of colonial spread between native and introduced cordgrasses have not yet been conducted. The only other species of the low marsh is *Salicornia europaea* (annual pickleweed), which occasionally occurs in the upper edge of the zone, often in accreting high mudflats in transition between low and middle marsh zones.


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Annual pickleweed (*Salicornia europaea*)- Occasionally found in conspicuous colonies on higher mudflats between upper cordgrass and lower pickleweed zones, it more commonly grows as a short, dense single plant. It turns brilliant crimson in fall, in contrast with the dominant dull green-brown *Salicornia virginica*.


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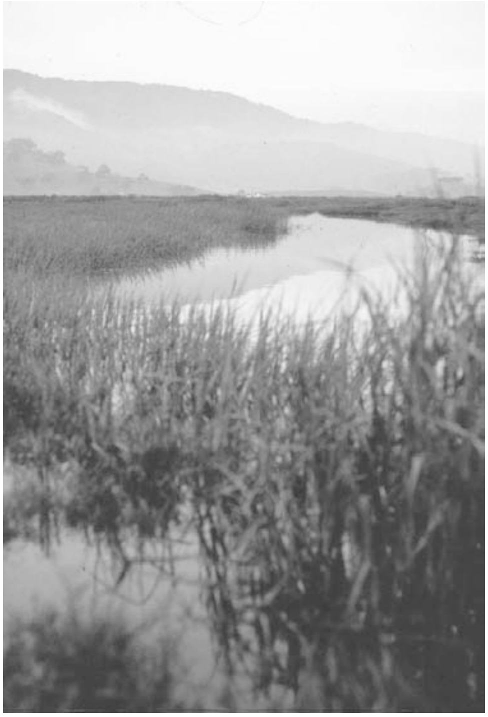
Locally rare Point Reyes bird's-beak (*Cordylanthus maritimus ssp. palustris*), is abundant in salt marshes of Tomales Bay, Bolinas Lagoon, and Limantour Estero. (Salt marsh, Marin City shoreline)

The middle salt marsh zone composes the extensive salt marsh plains of San Francisco Bay (Hinde 1954, Atwater et al. 1979). Younger marshes tend to be characterized by low-diversity vegetation dominated by *Salicornia virginica* (Cuneo 1987), but some older marsh remnants (e.g., Greenbrae and Heerdt Marsh; upper Newark slough marsh) may comprise complex and annually variable mosaics of *S. virginica*, *Distichlis spicata* (saltgrass), *Cuscuta salina* (salt marsh dodder), *Jaumea carnosa* (fleshy jaumea), *Frankenia salina* (alkali-heath) and *Atriplex triangularis* (spearscale or fat-hen). Species diversity in the middle salt marsh is not necessarily correlated with marsh age: old marshes at China Camp and Whittell Marsh (Point Pinole) also support relatively low-diversity vegetation dominated by *S. virginica*. The parasitic *Cuscuta salina* (dodder) can become conspicuously co-dominant or even dominant in the middle marsh zone by mid-summer in some marshes in some years, turning the middle marsh into an orange and green mosaic visible at great distances (Dumbarton-Mowry marsh, San Pablo Bay fringe marshes). Colonization and species recovery dynamics associated with dodder-induced dieback of marsh vegetation have not been investigated.

Relatively uncommon species of the middle marsh zone of San Francisco Bay include *Triglochin maritima* (sea arrow-grass), *Limonium californicum* (sea-lavender), and *Polygonum prolificum* and *P. patulum* (non-native knotweeds). Reports of the rare Point Reyes endemic *Polygonum marinense* (Marin knotweed) in San Francisco Bay require taxonomic verification. Species which seldom occur in the middle salt marsh zone of San Francisco Bay include *Cordylanthus maritimus* ssp. *palustris* (Pt. Reyes bird's-beak; Richardson Bay, Heerdt Marsh), *Puccinelia nutkaensis* (Pacific alkali grass; Ravenswood fringe marshes and Newark), *Plantago maritima* (sea-plantain) and *Triglochin concinna* (slender arrow-grass). These latter species are locally abundant in maritime salt marshes of Marin County. Invasive exotic species of the middle salt marsh include *Spartina densiflora* (Chilean cordgrass; Richardson Bay and Point Pinole), *Spartina patens* (saltmeadow cordgrass; near Burlingame and in brackish middle marsh at Southhampton Bay) and *Cotula coronopifolia* (brass buttons; early introduction, widespread but never persistent as a dominant in tidal marsh). The invasive exotic *Salsola soda* (Mediterranean saltwort) also is spreading from high salt marsh to the middle marsh zone (Dumbarton-Mowry marsh).

<u>High or upper salt marsh</u> may occur as topographic highs within the marsh plain (e.g., channel bank levees, wave-deposited ridges or mounds) or along the upland or alluvial edges of the marsh. This zone today commonly includes natives such as *Grindelia stricta* var. *angustifolia* (frequently a dominant in this zone), *Distichlis spicata*, erect-ascending phenotypes of *Salicornia virginica*, *Cuscuta salina*, *Frankenia salina*, *Limonium californicum* (sea-lavender), and *Atriplex triangularis* (spearscale, fat-hen). Where the upper marsh intergrades with low-lying alluvial soils and high groundwater (a condition today very rare in San Francisco Bay), the high marsh zone is dominated by dense stands of *Leymus triticoides* or *L.* x *multiflorus* (creeping wildrye), or *Juncus lesueurii* (salt rush, wire rush), as still occurs commonly in maritime salt marshes of the region.


Josh Collins

Tiidal salt marsh low marsh zone dominated by Pacific cordgrass *(Spartina foliosa).*

Cooper (1926) described a broad high salt marsh zone along the Palo Alto shoreline dominated by *Distichlis spicata* and *Grindelia stricta* var. *angustifolia* (an association still evident in reduced extent today), and a high salt marsh - alluvial transition zone which no longer exists. Cooper's reconstructed high salt marsh ecotone community was dominated by native composites—*Hemizonia pungens* ssp. *maritima, H. congesta* (tarweeds), *Helianthus bolanderi* (Bolander's sunflower), *Aster subulatus* (as "*A. exilis*"; slim or salt marsh aster), *Aster chilensis* (Chilean aster; possibly also including the rare *A. lentus),* *Baccharis douglasii* (salt marsh baccharis), *Euthamia occidentalis* (western goldenrod), and *Iva axillaris* (poverty weed). Of these, *I. axillaris*, *A. chilensis*, *H. pungens*, *B. douglasii*, and *E. occidentalis* still occur in high tidal brackish marsh of San Pablo Bay and Suisun Marsh. It therefore appears likely that historic upper edges of some salt marshes were at least locally brackish or subsaline rather than hypersaline in character, influenced by surface and subsurface freshwater discharges. This is also indicated by Cooper's description of water table-dependent, salt-intolerant tall (to 9 m) thickets of willow, cottonwood, box-elder, ash, blackberry, ninebark, and California rose at the high marsh edge (*Salix lasiolepis*, *Populus trichocarpa*, *Acer negundo*, *Fraxinus oregona*, *Rubus ursinus*, *Physocarpus capitatus*, *Rosa californica*). Cooper (1926) interpreted this community from isolated remnants of what he assumed was undisturbed vegetation, but the disturbance history of the South Bay marsh edge at the time of his observations, and older reports he collected, is uncertain.

The high salt marsh zone also historically included many other native species, which are now uncommon, rare, or extirpated in San Francisco Bay (**Table 1.3**). Most of these still persist at other California salt marsh localities. Most high salt marsh zones in San Francisco Bay today occur on artificial slopes and substrates at the upper marsh edge, and include many non-native species that sometimes dominate the zone. Common non-native plants of the high salt marsh zone include *Lepidium latifolium* (broadleaf peppercress, perennial peppergrass), *Bassia hyssopifolia* (bassia), *Salsola soda* (saltwort), *Beta vulgaris* (wild beet), *Mesembryanthemum nodiflorum (annual iceplant)*, *Carpobrotus edulis* and its hybrids (iceplant), *Atriplex semibaccata* (Australian saltbush), *Bromus diandrus* (ripgut brome), *Hainardia cylindrica* and *Parapholis incurva* (sicklegrasses), and *Polypogon monspeliensis* (rabbit's-foot grass).

Brackish Marsh Plants and Their Associations - Brackish tidal marshes prevail over northern San Pablo Bay (slough systems of the Petaluma River, Tolay Creek, Sonoma Creek, and Napa River), the Suisun Marsh area, and the Contra Costa marshes (North Bay marshes).

They also occur in transition with San Francisco Bay salt marshes where significant freshwater discharges occur (e.g., fringing marshes of Mud Slough, Coyote Creek, Artesian Slough, Alviso Slough, and Guadalupe Slough). The distinction between "salt marsh" and "brackish marsh" is a recent convention in descriptions of San Francisco Bay Area tidal marshes: brackish marshes were indiscriminately described as "salt marshes" by early California botanists, making it difficult to separate distinct elements of "salt" and "brackish" marsh associations. The description and demarcation of brackish marsh plant communities is essentially a matter of convenience and convention: there is no precise, stable salinity threshold at which tidal marshes are known to switch from one "type" to another (Adam 1990). Instead, brackish marsh vegetation in the San Francisco Estuary is typically a dynamic continuum between salt marshes of San Francisco Bay and freshwater tidal marshes of its major tributary rivers, fluctuating with variable influence of rainfall and freshwater discharges which alter marsh salinity and vegetation gradients geographically and over time. Associated changes in local tidal elevations (related to freshwater discharges) may also possibly interact with salinity variations in altering the character of brackish marsh vegetation. Changes in brackish marsh vegetation between dry and wet years at the same location may be dramatic: cover can change from that typical of San Francisco Bay salt marsh (dominant pickleweed) to that typical of Suisun Marsh (mosaic of rushes, bulrushes, alkali-bulrush, cattails, saltgrass, and many broad-leaved herbaceous species) in very few years. The causes of these dramatic changes in brackish tidal marsh vegetation are presumably related to plant interactions (competition, facilitation, and parasitism) which are influenced by seasonal and annual variation in salinity and drainage (Pearcy and Ustin 1984), but are poorly understood beyond descriptive observation.

The most extensive tidal brackish marshes occur in the Petaluma Marsh, but relatively large relict tidal brackish marshes also occur along the Napa River (Fagan Slough marsh) and in the Hill Slough/Rush Ranch area in Suisun Marsh. Relatively young but large and well-developed brackish marshes also occur bayward of dikes constructed after the 1870s, particularly in the Napa-Sonoma marsh complex and Suisun Marsh, including marsh islands of Suisun Bay. The Contra Costa marshes are predominantly intermediate between fully tidal marsh and diked (reduced tidal range) brackish marshes. The extensive wave-influenced, prograded pickleweed-dominated marsh plain and low natural marsh levee along northern San Pablo Bay are transitional between salt marsh and brackish marsh, exhibiting increases in brackish-associated species (particularly *Scirpus maritimus* at the east end of the Bay) in series of wet years.

Plant species richness and diversity markedly increase in brackish marshes of the San Francisco Estuary compared with salt marsh. Grewell (1993 *et seq.*) compiled extensive vascular plant species lists of the Suisun Marsh (including uplands of dikes and artificial uplands), and presented the only comprehensive and contemporary synthesis of Suisun Marsh plant ecology and its history (Grewell et al. 1999). Mason (Newcombe and Mason 1972) described plant community composition of brackish tidal marshes extending into the Sacramento-San Joaquin Delta.

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Sea-milkwort (*Glaux maritima*) is found in tidal marshes on the northern Pacific Coast, and on the Arctic, American, and European Atlantic coasts. (Tidal marsh, Rush Ranch, Suisun Marsh)

The <u>low brackish marsh zone</u> differs from the corresponding zone in the San Francisco Estuary salt marshes in several respects: it supports multiple dominant species in variable mixtures or monospecific stands; it extends to the low end of intertidal zone, and it regularly develops tall, dense vegetation. In San Pablo Bay and western Suisun Marsh, alkali-bulrush (predominantly *Scirpus maritimus* around San Francisco and San Pablo bays and western Suisun Marsh, but also including *S. robustus*, a taxon formerly misapplied to *S. maritimus* in floras of the region) occurs in the upper portion of the low marsh, often dominant in the saline end of the brackish marsh gradient. The tallest graminoid species, tules and cattails, dominate where freshwater influence is relatively strong; these include *Typha angustifolia*, *T. latifolia*, *T. dominguensis* and hybrids; *Scirpus californicus* (California tule), *S. acutus* (hardstem tule) and hybrids. These graminoid species can also establish within poorly drained portions of the middle marsh plain.

The <u>middle brackish marsh zone</u> was historically dominated by *Distichlis spicata* (saltgrass), as it commonly is today (Newcombe and Mason 1972). Other native species of the high marsh which occur in variable abundance (common to co-dominant) include *Salicornia virginica*, *Atriplex triangularis*, the *Juncus balticus-lesueurii* complex, *Jaumea carnosa*, *Frankenia salina* and *Cuscuta salina*. Locally common natives include *Limonium californicum* (sea-lavender), *Glaux maritima* (sea-milkwort), and *Scirpus koilolepis cernuus* and *S. cernuus* (clubrush; also in high brackish marsh), *Eleocharis macrostachya* (creeping spikerush), *Helenium bigelovii* (Bigelow's sneezeweed), and *Deschampsia cespitosa* ssp. *holciformis* (tufted hairgrass; especially eastern Suisun Marsh). Infrequent to rare species of this zone include *Lilaeopsis masonii* and *L. occidentalis* (Mason's and western lilaeopsis; on exposed eroding channel bank edges as far west as Tolay Creek), *Triglochin maritima* (locally common), *T. concinna*, *T. striata*, *Sium suave* (water parsnip), *Oenanthe sarmentosa* (ditch-carrot), *Cicuta maculata* ssp. *bolanderi* (water hemlock), *Eleocharis parvula* (slender spikerush), *Pluchea odorata* (salt marsh fleabane), and *Lythrum californicum* (California loosestrife; eastern Suisun Marsh and Delta). In wet years, depressions in the middle marsh plain support increased abundance of *Scirpus americanus* (Olney's bulrush) or *S. maritimus* (alkali-bulrush; western Suisun and San Pablo Bay) and *Phragmites australis* (common reed; eastern Suisun Marsh, also in the low-middle marsh zone). The dominant non-native species of the middle brackish marsh is again *Lepidium latifolium*, which rapidly forms dense monotypic clonal populations, spreading into the marsh plain. Other exotic species which have established in the brackish middle marsh zone include *Apium graveolens* (wild celery, widespread and abundant in Suisun Marsh), *Lythrum hyssopifolium* (annual loosestrife), *Cotula coronopifolia* (brass-buttons) and *Chenopodium chenopodioides* (fleshy goosefoot; Napa-Sonoma marshes).

The high brackish marsh zone is today typically altered by artificial dikes and invasive plants (particularly *Lepidium latifolium* (perennial or broadleaf peppercress), *Conium maculatum* (poison hemlock), *Foeniculum vulgare* (fennel), and Mediterranean grasses. However, many native remnants of the brackish high marsh community have regenerated on old, stable, relatively undisturbed levees, or have persisted locally along undiked tidal marsh edges. They include *Achillea millefolium* (yarrow), *Baccharis douglasii* (salt marsh baccharis), *B. pilularis* (coyote-brush), *Leymus triticoides* and *L.* x *multiflorus* (creeping wildrye), *Scrophularia californica* (California bee-plant), *Rubus ursinus* (blackberry, in the upland ecotone) *Rosa californica* (California rose, also in the upland ecotone), *Iva axillaris* (poverty-weed), *Atriplex triangularis* (fat-hen or spearscale), *Grindelia stricta* var. *angustifolia* (and intermediates with *G. camporum*), *Calystegia sepium* ssp. *limnophila* (morning-glory), *Cressa truxillensis* (alkali-weed), *Frankenia salina* (alkali-heath), *Lathyrus jepsonii* var. *californicus* (California tule pea), *Juncus balticus - lesueurii* complex (salt or wire rush), *Juncus mexicanus* (Mexican rush), *J. bufonius* (toad rush), *Ambrosia psilostachya* (western ragweed), *Euthamia occidentalis* (western goldenrod), *Epilobium brachycarpum, E. ciliatum* (willow-herbs), *Polygonum* spp. (smartweeds, knotweeds), *Triglochin maritima* (sea arrow-grass) and *Eryngium articulatum* (coyote-thistle). Uncommon to rare species such as *Lathyrus jepsonii* var. *jepsonii* (Delta tule pea), *Aster lentus* (Suisun aster), *A. subulatus* var. *ligulatus* (slim aster), *Plantago elongata* (dwarf plaintain), *Rumex occidentalis* (western dock), *Eleocharis parvula* (spikerush), and endangered *Cordylanthus mollis* ssp. *mollis* (soft bird's beak) and *Cirsium hydrophilum* var. *hydrophilum* (Suisun thistle) typically occur locally in the lower end of well-drained high marsh gradient, often on slight topographic relief above the marsh plain. *Salicornia virginica* (common pickleweed) and occasionally *S. subterminalis* (Parish's glasswort) can also be abundant elements of high brackish marsh near Suisun. The composition of high brackish marsh vegetation appears to vary with slope, drainage, and local surface or subsurface freshwater influence, but no studies have yet analyzed vegetation patterns or related environmental factors in brackish marshes of the region.

Invasive non-native species (weeds of mesic and wetland habitats with slight salt tolerance) of the high brackish marsh zone are numerous, particularly in years of high rainfall, but the most aggressive and successful is again *Lepidium latifolium*. *Lotus corniculatus* (bird's-foot trefoil) and *Lolium multiflorum* (ryegrass) are other exotics which are locally abundant along portions of the upper brackish marsh edge some years. *Elytrigia pontica* ssp. *pontica* (tall wheatgrass, currently local around Alameda Creek and Mare Island), *Rumex crispus* and *R. pulcher* (curly and fiddle docks), *Asparagus officinalis* (locally abundant near Napa-Sonoma marshes) have also naturalized along brackish marsh edges, but are seldom invasive.

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Ditch-carrot (*Oenanthe sarmentosa*), a common freshwater marsh plant, also occurs in fresher phases of brackish tidal marshes. (Southhampton Marsh, Benicia)

Tidal Marsh Pans and Vegetation - Poorly drained flats, depressions, and barrier-impounded areas of tidal marsh lacking emergent vascular vegetation, called pans (alternatively spelled "pannes"), range from nearly planar unvegetated marsh areas subject to shallow periodic ponding, to steep-sided or cliff-edged shallow ponds which are persistently inundated (Pestrong 1965, Pethick 1974, Atwater et al. 1979). Pans have various modes of origin and development, which have not been completely clarified (Adam 1990, Carter 1988, Pethick 1974, Chapman 1960). In San Francisco Bay Area marshes, pan variation includes nearly circular ponds between drainage channels (Pestrong 1965), historic long ponds parallel with impounding bayfront marsh berms (Atwater et al. 1979), shore-parallel pans historically present along portions of the back edge (upland or lowland margin) of tidal marsh (depicted in 1880s U.S. Coast Survey Maps), and natural historic salt ponds impounded by low estuarine ridges (Atwater et al. 1979). Some sloped to planar pans in the high marsh (bare flats, rarely submerged) may be related to wrack deposition and smothering, or local substrate conditions. Little is known of the ecology of pan types that are no longer represented in the altered modern Estuary.

Many pans are reported to become seasonally hypersaline (Pestrong 1965) or even salt-crystallizing (Atwater et al. 1979; see also salt pond profile, this volume) and lack vascular plants, but some pans along the landward edge of the tidal marsh develop marginal vegetation typical of brackish or fresh marshes (e.g., China Camp). Ponded pans within the marsh plain have been described as "unvegetated" (Pestrong 1965), but they often support a dense submerged mixed vascular and non-vascular vegetation variously composed of widgeongrass (*Ruppia maritima*) and membranous green algae (particularly *Enteromorpha* and *Ulva* spp.). According to Mason (Newcomb and Mason 1972), brackish ponds in Suisun Marsh also support *Zannichellia palustris* and *Potamogeton pectinatus*, submerged species typical of freshwater ponds. The halophilic microflora of salt ponds is discussed in the salt pond profile(this volume). Shallow, relatively planar and ephemeral pans in San Pablo Bay are either periodically or marginally colonized by pickleweed, which dies back during years of frequent flooding or high rainfall. The steep-sided edges of well-defined, nearly circular old pans sometimes develop small natural levees of locally improved drainage, and sometimes support certain species at frequencies more typical of high marsh vegetation. In the high marsh, on gently sloping alluvial fans, "dry pans" (small playa-like flats with very short flooding periods and superficial salt films) also develop, often on relatively coarse (sandy, silty, or even gravel-silt mixtures) sediments. These features are very rare today because of diking, but fine examples persist at Point Pinole (Whittell Marsh). Here, as at similar pans on alluvial fans at tidal marsh edges in maritime Marin County, the pan-marsh edges are associated with local abundance of the regionally rare salt marsh owl's clover (*Castilleja ambigua* ssp. *ambigua*; salt-tolerant ecotypes). Salt marsh bird's-beak (*Cordylanthus maritimus* ssp. *palustris*) also exhibits a pan-margin local distribution pattern in western San Pablo Bay (e.g., JEPS83457). Analogous artificial features (gently sloping, formerly disturbed silty to sandy high marsh fills with residual vegetation gaps) elsewhere in the Estuary have also become colonized with rare plants such as *Cordylanthus mollis* (Hill Slough near Lawler Ranch; B. Grewell, pers. obs.) and *Cordylanthus maritimus* (near Marin City). Natural and artificial high marsh pans of this type, associated with alluvial or deltaic deposition


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High marsh pan in Whittell Marsh (Point Pinole, Contra Costa County), fringed with salt-marsh owl's clover (*Castilleja ambigua*). Whittell Marsh is the last known tidal marsh locality of this species in the San Francisco Estuary.

Regionally rare smooth goldfields (*Lasthenia glabrata*). (Whittell Marsh, Point Pinole, Contra Costa County)

or erosion, have not been identified in the regional literature on salt marsh ecology, and require study.

The number of species from former alkali-subsaline vernal pools around San Francisco Bay which were historically reported from local salt marshes as well (see diked wetlands profile, this volume) suggests that ecologically equivalent habitat occurred in both ecosystems. Although there are very few intact remnants of the elongate pans which occurred along tidal marsh edges (represented clearly in historic U.S. Coast Survey maps of the 1850s), it is possible that some of these seasonally ponded depressions in the upper marsh ecotone were partial ecological equivalents of subsaline vernal pools. Strong historic evidence for this conclusion is found in Jepson's (1911) range and habitat descriptions for the typical vernal pool species, *Downingia pulchella*, which he described as "abundant and of rank growth in the salt marshes near Alvarado" [now Union City]. Other species indicative of vernal pools and similar seasonally ponded/desiccated alkaline/subsaline environments, such as *Lasthenia conjugens* (JEPS25099), *L. platycarpha* (DS695549, Greene 1894) and *L. glabrata* (CAS897444, DS73122, DS286573) have been collected from the edges of San Francisco Bay.

Although pans are often presumed to be generally hypersaline, some appear to have occurred historically in alluvial lowlands with probable groundwater or surface discharges that could maintain brackish conditions in pans along tidal marsh edges. A number of characteristic freshwater marsh species were reported by Jepson (1911) and others from historic salt marsh habitat (e.g., *Agrostis exarata*, *Carex aquatilis*, *C. densa*, *Lycopus asper*), suggesting that freshwater sub-habitats occurred marginally along tidal salt marshes. Unpublished historic writings of southeastern San Francisco Bay marsh borders by 19th century botanist Joseph Burtt-Davy, archived at the Jepson Herbarium, University of California, describe extensive colorful wildflower meadows with species typical of vernal pools and wet grassland (R. Grossinger, pers. comm. 1999). Examples of brackish and even freshwater vegetation at edges of salt marsh with pans near zones of groundwater discharge can be observed today at China Camp (Marin County) and Point Pinole (Contra Costa County), and in maritime Marin County tidal marshes. Diked seasonal wetlands in historic tidal marsh (this volume) may also approximate this type of lost habitat, since numerous seasonal wetland species of vernal pools and alkali basins have colonized diked Baylands.

Uncommon, Rare, Declining, and Extirpated Plant Species

There is a widespread impression, even among ecologists familiar with the San Francisco Estuary, that native plant species richness of tidal marshes (particularly salt marsh) is relatively low, and that rare species in the Estuary are principally wildlife taxa, not plants. This impression is due in part to reviews of species richness in tidal marshes based solely on modern surveys: for example, Atwater et al. (1979) reported only 15 vascular plant species for San Francisco Bay, based on modern reports. Josselyn (1983) discussed only a small representation of the San Francisco Estuary flora, and did not address either its historic or modern species richness. In addition, very few plants native to the San Francisco Estuary are federally listed as endangered or threatened, and only two of these (soft bird's-beak, *Cordylanthus mollis* ssp. *mollis*, and Suisun thistle, *Cirsium hydrophilum* var. *hydrophilum*) currently inhabit this Estuary. The modern lack of attention to rare plants in the Estuary is probably due to unfamiliarity with plant species which were known only to early botanists, but are either now entirely extinct (or even extirpated) in the Estuary. Plant species that were historically recorded in the tidal marshes of the Estuary, or along its edges (high marsh), but have become uncommon, rare, regionally extirpated, or extinct, are summarized in **Table 1.3**. Most of these species were known from tidal marsh edges, transitional habitats of high ecological diversity. This is significant, because original remnants of this ecotone are almost completely eliminated from the Estuary, and their modern counterparts are mostly weedy, disturbed habitats like dikes.

Extinct species of the Estuary include California sea-blite, *Suaeda californica*, a federally endangered shrubby true halophyte (salt-tolerant plant) which today inhabits relatively well-drained marshy beach ridges along relatively high-energy shorelines with coarse sediment in Morro Bay. According to Jepson (1911) and Greene (1894), it was never abundant in San Francisco Bay even in the late 19th century. The distribution of its sandy marsh habitats was unfortunately in areas of the greatest urbanization: San Francisco, Oakland, Alameda, and San Leandro were its core populations, although it was also collected in Palo Alto (where shell hash beaches today occur) and at the former San Pablo Landing (Richmond, where local sand beaches still persist). The species today is restricted to sandy salt marsh edges of Morro Bay, San Luis Obispo County, and also exists in cultivation. It was last collected in San Francisco Bay in 1958 in San Leandro (JEPS25020) More recent local reports are based on misidentification of the similar species, *S. moquinii*, in diked Baylands.

Many other salt marsh species that have affinity for high sandy salt marsh were also reported from San Francisco Bay, but are now extinct or rare in the Bay (Jepson 1911, Greene 1894). They include California saltbush (*Atriplex californica*), still found in Tomales Bay and Point Reyes sandy salt marshes, but extinct in the Bay, and *Plantago maritima*, common in sandy maritime salt marshes, uncommon to rare in the Bay. The sea-pink (*Armeria maritima*) a showy pink spring wildflower which still occurs locally along sandy edges of Point Reyes salt marshes, was cited by Jepson (1911) to range within San Francisco Bay. (This may possibly have been along former sandy beaches, sandy salt marsh, or stabilized former bayside dunes. There are no historic herbarium specimens from San Francisco Bay salt marshes to corroborate Jepson's report, however.) Other rare species, such as *Cordylanthus maritimus* ssp. *palustris* and *Castilleja ambigua* ssp. *ambigua*, are less uncommon in sandy maritime salt marshes, but are rare in San Francisco Bay. The decline or demise of these species in the Bay is very likely a result of the near-complete elimination of its sandy estuarine barrier beaches.

Two other species which are probably extinct in San Francisco Bay, but occur elsewhere, include two members of the Aster family: southern goldenrod (*Solidago confinis*) and *Pyrrocoma racemosa (=Haplopappus racemosa)*. Southern goldenrod was formerly reported as rare only by Henry Bolander in 1863 (Jepson 1911), when it was misidentified as seaside goldenrod (*S. sempervirens*). In California tidal marshes today, *S. confinis* is known only locally from the high brackish marsh zone of southern Morro Bay. *P. racemosa* was formerly reported from the edges of salt marshes and saline soils at Cooley's Landing and near Alviso (Thomas 1961), but has not been reported from salt marsh edges in recent decades. Another species, Adobe sanicle (*Sanicula maritima*), was found locally in lowlands adjacent to salt marshes at Alameda (Behr 1888, Greene 1894, Jepson 1911) and in San Francisco (Brandegee 1892). It is now extinct in the Bay Area, and is very rare elsewhere (known from fewer than 10 sites in Monterey and San Luis Obispo Counties today; Skinner and Pavlick 1994).


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Federally listed as endangered, California sea-blite (*Suaeda Californica*) is extinct in San Francisco Bay. (Morro Bay)

Two popcornflower species (genus *Plagiobothrys*, well represented in vernal pools) that were found in saline soils near the edge of the Estuary are now presumed to be extinct (although it is possible that buried dormant seed may persist somewhere in diked Baylands, awaiting resurrection). They include Petaluma popcornflower (*Plagiobothrys mollis* var. *vestitus*), which was probably distributed in alkaline or subsaline seasonally wet depressions (vernal pools) in grasslands and lowlands adjacent to tidal marsh in the Petaluma Valley, and Hairless popcornflower (*P. glaber*), a species of seasonally wet alkaline/subsaline soils of tidal marshes of the south San Francisco Bay (reported by Jepson (1911) from Alvarado [now Union City]), as well as some interior valleys. Almost nothing is known of the ecology of these species because of their early historic extinction.

Other species that are known to occur in subsaline to alkaline vernal pools, and which historically occurred in salt marshes (presumably along lowland edges), include several species of goldfields (*Lasthenia* spp.). Fleshy goldfields, *Lasthenia platycarpha* (presumed extinct in the Estuary) was known from salt marshes near Vallejo (Greene 1894), and smooth goldfields (*L. glabrata* ssp. *glabrata*) was reported from edges of salt marshes (Thomas 1961, Jepson 1911, Greene 1894). *L. glabrata* was recently confirmed to occur naturally at Whittell Marsh, Point Pinole, and a population of undetermined origin occured briefly in 1998 on a hydroseeded levee at the Sonoma Baylands tidal marsh restoration project's pilot unit. Behr (1888) listed *L. glabberima* as a species occurring "near salt marshes," but is not otherwise reported from tidal marshes in the region. The federally endangered vernal pool goldfields species, Contra Costa goldfields (*L. conjugens*) was reported by Jepson (1911) from "subsaline soils" near Antioch and Newark, and was recently discovered in subsaline vernal pools in Fremont near the diked edge of the at the Warm Springs Unit of the National Wildlife Refuge in Fremont and adjacent derelict fields. *L. conjugens* was also observed along high tidal marsh edges of Hill Slough in the early 1990s. Another well-known vernal pool species, the showy *Down-*

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The southern-most population of Point Reyes bird's-beak (*Cordylanthus maritimus* ssp. *palustris*), in a small marsh on the Marin City shoreline.

ingia pulchella (producing spring masses of blue, white, and yellow flowers resembling lobelias) was described by Jepson (1911) to occur abundantly in South Bay salt marshes. It still occurs in the subsaline vernal pools adjacent to tidal marsh at the Warm Springs Unit of the Refuge in Fremont, and in diked agricultural Baylands (former tidal marsh) near Fairfield. The rare annual milkvetch (locoweed), *Astragalus tener* var. *tener*, was formerly collected from "saline areas along San Francisco Bay" as far south as Mayfield (Mountain View area; Thomas 1961). Once found in alkali vernal pools, it was collected in the Bay Area in 1959 (Skinner and Pavlick 1994) and was recently rediscovered near the historic Bay edge in Fremont (G. Holstein, pers. comm. 1999).

Two hemiparasitic annual snapdragon family herbs are extinct in the salt marshes of south San Francisco Bay, but occur elsewhere in the Estuary or region. The Point Reyes bird's-beak (*Cordylanthus maritimus* ssp. *palustris*), a close relative of the endangered salt marsh bird's beak of Southern California (*C. m.* ssp. *maritimus*), was formerly found almost throughout San Francisco Bay. It is now restricted to very few populations in the Central Bay, with small remnant populations probably persisting in Petaluma Marsh and near Gallinas Creek, Marin County. The remaining San Francisco Bay populations of Marin County are typically showier (usually more conspicuous, rosy purple flowers and purplish herbage) than most of the core populations of Point Reyes, which typically have gray-green foliage and white-and-maroon flowers. Another annual Snapdragon family herb, Johnny-nip or salt marsh owl's clover (*Castilleja ambigua* ssp. *ambigua*) was formerly found in the salt marshes of San Francisco Bay (Berkeley, Oakland, Alameda, Bay Farm Island, Burlingame), but is nearly extinct there now. The only salt marsh population of this colorful annual herb in the San Francisco Estuary is from Point Pinole, which supports a form with purple-tinged foliage, bracts, and flowers (atypical of the subspecies *ambigua*, but typical of ssp. *insalutata* of Monterey County). Salt-tolerant locally adapted populations of this subspecies also occur at Rodeo Lagoon and Bolinas Lagoon, but are otherwise rare in central coast tidal marshes (very local in Limantour estero and Tomales Bay). A related salt marsh endemic subspecies, *C. a.* ssp. *humboldtiensis*, occurs only in Humboldt Bay and Tomales Bay. Non-halophyte populations of *C. a.* ssp. *ambigua* occur somewhat more widely in coastal grasslands, headlands, and bluffs.

Still surviving but rare within its historic range in brackish tidal marshes from Petaluma Marsh to Antioch is another annual Snapdragon family herb, soft bird's-beak (*Cordylanthus mollis* ssp. *mollis*). This white-yellow flowered herb is covered with salt-encrusted secretory glands. It is listed as federally endangered, and is restricted mostly to the Suisun Marsh area, especially in old relict tidal brackish marsh. It formerly ranged as far west as Petaluma Marsh (Howell 1949). Like the other annual hemiparasitic salt marsh Snapdragon relatives, its numbers fluctuate tremendously from year to year (Rugyt 1994), sometimes disappearing for a year or more before regenerating from dormant seed banks.

Numerous other species, particularly grasses and sedge species, were cited by early California botanists as commonly occurring in salt marshes, but are scarce or absent today in the San Francisco Bay Area. By analogy with relatively intact tidal marshes of Point Reyes to the north and Elkhorn Slough to the south, it appears very likely that these "missing" salt marsh species occurred along upland or lowland (alluvial) margins of tidal marshes. Some, like *Agrostis exarata* (= *A. asperifolia*), *Juncus xiphioides*, *J. lesueurii*, and *J. effusus* var. *brunneus* were described as common in Bay Area salt marshes (Jepson 1911, Brewer et al. 1880, Howell 1949), although they occur only very locally in Bay Area tidal marshes today. Other grass species, like *Leymus triticoides* (including *L.* x *multiflorus*), are presumed to be former marsh edge dominants based on relict occurrences at intact lowland tidal marsh edges (e.g., Rush Ranch, Point Pinole) and colonizing behavior on levees which have not been maintained (Dutchman Slough and Mare Island, San Pablo Bay). The salt marsh grass *Puccinelia nutkaensis*, in contrast, occurred in periodically inundated middle salt marsh zones in the South Bay as well as on levees (Thomas 1961). It is rarely found in San Francisco Bay today, such as near Ravenswood, Palo Alto and Newark. Other grasslike plants, such as *Plantago elongata*, were reported as common in Bay Area tidal salt marshes (Brewer *et al* 1880, Greene 1894) but have become uncommon or rare here. Other grasslike plants of uncertain former abundance in tidal marshes, which are scarce or absent in Bay Area tidal marshes today, include *Carex aquatilis* var. *dives*, *C. densa*, and *C. praegracilis* (Thomas 1961, Jepson 1911); *C. praegracilis* occurs infrequently in tidal brackish marshes of the Suisun Marsh area. Sedges such as *Carex subbracteata*, and *C. obnupta* would also be expected to have occurred in former salt marsh edges, as they do in other estuaries of the Central Coast, especially northward.

Many broadleaved herbs were also more plentiful along tidal marsh edges, but have become localized or rare today. They include *Aster lentus* (Greene 1984, Jepson 1911), a species now generally rare in any estuarine habitat; Chilean aster (*Aster chilensis*) (Howell 1949, Thomas 1961), a common species of non-saline habitats which has nearly disappeared from salt marsh edges but persists occasionally in Suisun, Petaluma, and Napa-Sonoma marshes. Salt marsh baccharis (*Baccharis douglasii*) was formerly abundant in salt marshes (Jepson 1911) but is now uncommon to rare in brackish marshes, mostly in the North Bay (Best et al. 1996, Thomas 1961). Two species which were inferred by Cooper (1926) to be major elements of his reconstructed "willow-composite" community at South Bay salt marsh edges, slim aster (*Aster subulatus* var. *ligulatus*), and spikeweed (*Hemizonia pungens* var. *maritima*) are now scarce in tidal marshes, and occur mainly in the North Bay (Best et al. 1961; B. Grewell, pers. obs. 1997). Other spikeweeds, *H. parryi* sspp. *parryi* and *congdonii*, were locally common in the South Bay salt marshes (Munz 1959), but are generally rare today. Species that were formerly frequent in North Bay brackish and salt marshes (Greene 1894) include morning-glory (*Calystegia sepium* var. *limnophila*) and sea-milkwort (*Glaux maritima*), which are now uncommon to rare. Other herbs which have historically declined to a significant extent in frequency, distribution, and abundance in Bay Area tidal marshes and their edges include *Hutchinsia procumbens* (Greene 1894, Thomas 1961), tidy-tips, *Layia chrysanthemoides* (Howell 1949, Thomas 1961), native annual peppercress species *Lepidium dictyotum*, *L. latipes*, and *L. oxycarpum* (Thomas 1961, Munz 1959, Howell 1949, Greene 1894), salt marsh fleabane, *Pluchea odorata* (Jepson 1911), and butterweed, *Senecio hydrophilus* (Greene 1894, Jepson 1911).

Conservation Issues

Exotic Plants - There are many exotic plants that have become established within, or along the edges of, the San Francisco Estuary, but only a few are aggressive invaders that have become widespread and dominant, or threaten to do so (Grossinger et al. 1998). Of these, *Lepidium latifolium*, *Spartina alterniflora* (and hybrids), and *Salsola soda* have demonstrated ability for rapid, extensive invasion and development of monodominant stands in the San Francisco Estuary. *Spartina densiflora*, an exotic cordgrass from Chile with a bunchgrass growth habit, has become a dominant species in Humboldt Bay, and is expected to be able to achieve the same dominance if its spread is unchecked in San Francisco Bay. The taller stature of *S. alterniflora* enables it to endure high tides with relatively little submersion of its foliage, even when rooted below mean sea level. Turf-forming *S. patens* (salt meadow cordgrass) and dwarf strains of *S. alterniflora* (Daehler et al. 1999) present in the Bay may be latent invaders of salt marsh plains. The tendency for *S. alterniflora* pollen to swamp the pollen of the native *S. foliosa* and produce hybrids and introgressants threatens to genetically assimilate the native Pacific cordgrass over a significant portion of its geographic range (D. Ayers and D. Strong, pers. comm. 1999). The higher densities, larger plant size, and greater colonizing ability of *S. alterniflora* at lower tidal elevations also suggest that its spread may have significant geomorphic impacts on the Estuary, particularly on channel stability, sedimentation, and mudflat colonization, and their indirect effect on wildlife habitat (Grossinger et al. 1998).

Lepidium latifolium invasion is particularly a concern for the conservation and recovery of rare or endangered plant species of the San Francisco Estuary, most of which occur in the high marsh zone where *L. latifolium* is dominant. *L. latifolium* actively encroaches on populations of endangered *Cordylanthus mollis* ssp. *mollis* and *Cirsium hydrophilum* var. *hydrophilum* in Suisun Marsh (B. Grewell, pers. obs. 1998) and Southhampton Bay (P. Baye, pers. obs. 1998). The impact of exotic plant invasions in the high marsh zone is magnified by the truncation and degradation of this habitat by widespread diking, which compresses the high marsh zone into a relatively invariant, steep slope of disturbed Bay mud.

Tidal Marsh Restoration Design - Tidal marsh restoration in the San Francisco Estuary has convention-

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Invasive exotic *Lepidium latifolium* (background) looms over the endangered *Cordylanthus mollis* ssp. *mollis* at the high marsh edge. (brackish tidal marsh, Southampton Marsh, Benecia.)

ally been designed for wildlife species, treating plants only as habitat for wildlife species rather than as the subject of restoration aims. Restoration designs have generally afforded little or no consideration for soils or slopes of the high marsh zone, variations in sediment texture, surface or subsurface freshwater flows, and variation in incident wave energy that influence the microenvironmental variables which are significant for plant diversity. Highly managed estuarine wetlands (e.g., artificial salt ponds, extremely microtidal or non-tidal salt marshes) generally support an artificially low diversity of native tidal marsh plant species. Plans for rare tidal marsh plant reintroduction have only recently been proposed (e.g., Pier 98, Port of San Francisco; Crissy Field, Presidio/Golden Gate National Recreation Area), and none has yet been implemented. Of the rare plant refugia in relict tidal marshes of the Estuary (e.g., Hill Slough, Fagan Marsh, Rush Ranch, Peytonia Slough, and Whittell Marsh), none has site-specific rare plant management plans or programs, despite imminent threats by invasive species. There is no Estuary-wide program to survey and map rare plant species populations; plant inventories are biased towards species with special legal status, and are typically driven by environmental impact assessment for projects rather than regional conservation. Other surveys consist of voluntary and opportunistic reports. Conservation of plant diversity in the Estuary will require both active protection of remnant rare plant refugia, active management of conserved areas, systematic inventory of the Estuary's botanical resources, and large-scale, scientifically sound tidal marsh restoration and reintroduction projects.

Many natural resource agencies are cautious about restoration and reintroduction of rare plants, probably because this has conventionally been considered in a mitigation context (Berg 1996). Restrictive generalized policies on geographic specificity of reintroduction to documented historic localities, regardless of natural temporal and spatial scales of plant population dynamics and ecosystem processes, in some cases has narrowed opportunities for re-establishment of rare plants (White 1996). In situations where the range of rare plants is extremly reduced, historic collection data are sparse and vague (which is generally the case), and relatively few potential source populations for founders exist, an experimental approach may be most appropriate for reintroduction planning. Successful reintroduction will likely require much replication over years (variable climate conditions) and at many localities. Caution is appropriate, however, when the taxonomic interpretation or population variability is at issue when determining suitable populations for reintroduction.

Artificial Salinity Manipulation - In Suisun Marsh, salinity control gates on Montezuma Slough were installed to enforce standards for salinity based on the perceived needs of waterfowl marsh management in diked wetlands, aimed at maintaining low channel water salinity. The impacts of sustained low marsh salinity on the progression of exotic plant invasions and the natural dynamics of brackish tidal marsh vegetation (particularly rare and endangered species) were not considered in the design and operation of the salinity control gates, and no long-term monitoring of rare plant populations during gate operation was authorized. The reduction of periodic high salinity events during drought cycles, and

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Pioneer plants (1st year seedling) of native *Spartina foliosa* and *Salicornia virginica* colonize the well-consolidated upper mudflats bayward of the marsh edge at Mare Island, eastern San Pablo Bay. The erosional scour pools and drainages adjacent to the plants indicate the relatively hight wave energy estuarine environment in which they are able to establish, given stable microhabitats.

the subtle changes in tide elevations caused by gate operation, could potentially have significant adverse long-term impacts on rare plant persistence. Scientific investigations of the effects of gate operation on plant communities and rare plant populations of Suisun tidal marshes are urgently needed, as recommended by the Brackish Marsh Subcommittee of the Suisun Ecological Workshop (CWRCB 1999).

In the South Bay, perennial urban wastewater discharges in confined, diked tidal sloughs have caused conversion of salt marsh to brackish marsh (Harvey and Associates 1997). The Alviso and Milpitas area marshes were the sites of historic rare plant populations (**Table 1.3**) which could not be re-establish naturally or be re-introduced in marsh vegetation dominated by perennial pepperweed, bulrushes and tules which are stimulated by augmented and confined freshwater flows and elevated nutrient concentrations throughout the growing season.

Loss of Restorable Habitat - Economic pressure to convert diked Baylands to land uses that are incompatible with potential tidal marsh restoration over large contiguous tracts (particularly in connection with uplands and alluvial areas) remains high today. Developments in diked Baylands for extensive housing (Redwood Shores, San Mateo County), golf courses (Black Point, Marin County), business parks (old Fremont Airport, Alameda County) have proceeded into the 1990s, and other large scale land use conversions for dredged material disposal and rehandling (Napa salt crystallizers) have been considered. The largest tracts of undeveloped diked Baylands are in San Pablo Bay, where vineyard expansion threatens to encroach into restorable former tidal marsh sites. Single-purpose management of other diked wetland types at large scales (salt production, waterfowl production) also restricts opportunities for tidal marsh plant community restoration. Large-scale tidal marsh restoration near centers of relict tidal marsh plant populations (e.g., Cullinan Ranch, Hamilton Airfield, Redwood Landfill, and Skaggs Island) offer some hope for long-term recovery of tidal marsh plant species in decline.

Conclusions and Recommendations

The San Francisco Estuary tidal marshes are poorly understood in terms of modern and historic plant species composition, the dynamics of the vegetation, and the interaction between vegetation and geomorphic and hydrologic processes. Many plant species have become extirpated or nearly so with little or no attention from botanists or ecologists, and many more species have declined significantly. The Estuary's historic and modern flora is considerably richer than has been generally recognized. Further attrition of native plant diversity in the Estuary is likely because of the uncontrolled spread of invasive exotic plants, and insufficient planning, management, and restoration of the Estuary's plant community. Carefully designed tidal marsh restoration projects that promote native plant species diversity and recovery are needed to conserve the Estuary's flora. Recommendations for the conservation of the Estuary's plant communities are presented in the Baylands Ecosystem Habitat Goals Report (Goals Project 1999, Appendix A).

Peter Baye

An example of marsh progradation - Seedling plants of *Salicornia virginica* and *Spartina foliosa* are frequently comingled without clear zonation, as in these exceptionally firm upper mudflats in eastern San Pablo Bay. (Mare Island, north of the jetty)

Table 1.3 Historic Changes in the Distribution and Abundance of Selected Native Vascular Plant Species Occurring in Tidal Marshes of the San Francisco Estuary

Taxon	Historic References	Contemporary Distribution
Agrostis exarata Trin. [*A. asperifolia* Trin.]	**Jepson 1911**: Common in the San Francisco Bay region in salt marshes and other wet places: Berkeley… San Francisco; Martinez.”	Not currently reported from tidal marsh ecotone in San Francisco Bay Estuary, but common and widespread in non-tidal moist habitats [Hickman et al. 1993].
Armeria maritima (Miller) Willd. ssp. ***californica*** (Boiss.) Pors. [*Armeria vulgaris* Willd.] [*Statice armeria* L.]	**Greene 1894**: “ Along sandy beaches in wet ground…” **Jepson 1911**: “ common on the sandy beaches or fields near the sea… or about San Francisco Bay.”	Apparently extirpated in San Francisco Bay Estuary; otherwise restricted to maritime coastal salt marshes, dunes, bluffs.
Aster chilensis Nees.	**Cooper 1926**: [presumed species of reconstructed “ willow-composite” community at salt marsh edges, Palo Alto vicinity] **Howell 1949**: [Marin Co.] Common and widespread from salt marshes and coastal swales to low valleys…” **Thomas 1961**: “… edges of salt marshes…”	Few current reports known from edges of San Francisco Bay or San Pablo Bay tidal marshes; local in Suisun Marsh edges. Presumed rare from tidal marshes.
Aster lentus E. Greene [*A. chilensis* Nees. var. *lentus* Jepson] [*A. chilensis* var. *sonomensis* (E. Greene) Jepson]	**Greene 1894**: [*A.c.* var. *lentus*] “ Plentiful along tidal streams in the western part of the Suisun Marsh…” [*A. c.* var. *sonomensis*]“ In open plains of the Sonoma Valley, in low subsaline ground.” **Jepson 1911**: [*A.c.* var. *lentus*]“ very common and conspicuous in the Suisun Marshes.” [*A. c.* var. *sonomensis*] “ subsaline lands: Petaluma, Napa” **Munz 1959**: [*A.c.* var. *sonomensis*]: Coastal Salt Marsh; saline ground around San Francisco Bay. Sonoma, Napa…”	Rare; restricted primarily to Suisun Marsh. Some herbarium collections known from San Francisco Estuary prior to 1960 (Berkeley, Alviso, Napa). Recent status uncertain in San Pablo Bay area tidal marshes.
Aster subulatus Michaux var. ***ligulatus*** Shinn. [*Aster exilis* Ell.] [*Aster divaricatus* Nutt.]	**Behr 1888**: [*A. divaricatus*] “ Salt marshes.” **Greene 1894**: “ Borders of Suisun Marshes and elsewhere on subsaline land” **Jepson 1911**: “ Saline soil, not common… .Alvarado.” **Cooper 1926**: [presumed species of reconstructed “ willow-composite” community at salt marsh edges, Palo Alto vicinity] **Thomas 1961**: “ Salt marshes along San Francisco Bay and occasionally elsewhere. San Francisco, Palo Alto, Alviso…”	No current reports known from edges of San Francisco Bay . Uncommon to rare in San Pablo Bay and Suisun tidal marshes.
Astragalus tener Gray var. ***tener***	**Jepson 1911**: “ Alkaline fields, mostly in moist places.” **Thomas 1961**: Known locally only from saline areas along San Francisco Bay. San Francisco and Mayfield.”	Recently rediscovered near historic Bay edge in Fremont, Alameda County. Known in region from alkali vernal pools, Solano County.

Table 1.3 (continued) Historic Changes in the Distribution and Abundance of Selected Native Vascular Plant Species Occurring in Tidal Marshes of the San Francisco Estuary

Taxon	Historic References	Contemporary Distribution
Atriplex californica Moq.	**Greene 1894**: "… along the edges of salt marshes, from near San Francisco and Alameda, southward." **Jepson 1911**: "Sandy beaches along the ocean and about San Francisco Bay."	Extirpated in San Francisco Bay Estuary margins. Small relict populations occur on bluffs of Golden Gate in San Francisco. Maritime salt marsh populations occur at Limantour Estero and Tomales Bay (Marin Co.).
Baccharis douglasii DC.	**Jepson 1911**: "… abundant in the salt marshes about San Francisco Bay." **Thomas 1961**: [SW San Francisco Bay] "… occasionally along the edges of salt marshes… Alviso…" **Best** et al. **1996**: "Uncommon. Damp thickets, salt marshes."	Now uncommon to rare in alluvial high marsh and upland ecotone, San Pablo Bay area and and Suisun Marsh; one colony occurs along salt pond edge at a seep in Coyote Hills, Alameda Co., possibly rare elsewhere in San Francisco Bay.
Carex aquatilis Wahlenb. var. ***dives*** (Holm) [*C. sitchensis* Prescott]	**Brewer** et al. **1880:** "In salt marshes, about San Francisco Bay (*Bolander*)…" **Jepson 1911**: "Salt-marshes about San Francisco Bay and northward along the coast". **Munz 1959**: "Rare, swampy places, usually near the coast…"	No current reports known from edges of San Francisco Bay or San Pablo Bay tidal marshes. Presumed rare or extirpated from tidal marshes.
Carex densa Bailey [*C. brogniartii* Kunth. var. *densa* Bailey]	**Jepson 1911**: [*C. b.* var. *densa*] "Salt marshes near San Francisco…"	No current reports known from edges of San Francisco Bay or San Pablo Bay tidal marshes. Presumed rare or extirpated from tidal marshes.
Carex praegracilis W. Boott [*Carex Douglasii* var. *brunnea* Olney] [*C. usta* Bailey]	**Thomas 1961**: " Boggy areas along the edges of salt marshes; San Francisco, Woodside, Mayfield…"	Rare in Suisun area tidal marshes, west to Southampton Bay. Common in alkaline, moist places in California floristic province.
Castilleja ambigua Hook and Arn. [*Orthocarpus castillejoides* Benth.]	**Behr 1888**: "Marsh near Tamalpais." **Greene 1894**: "Common along the borders of salt marshes." **Jepson 1911**: "Marshy ground near the coast. Alameda; W. Berkeley; Napa Valley; Sonoma Co." **Howell 1949**: "low ground along the upper reaches of the salt marshes, occasional:..Mount Tamalpais; Greenbrae Marshes; Hamilton Field…"	Currently reported only from Point Pinole salt marsh and pan edges; other historic records at Greenbrae, Tamalpais (Mill Valley), Hamilton Field, Burlingame, Oakland. Halophytic populations rarely occur in brackish marsh and salt marsh at Rodeo Lagoon, Tomales Bay, Drakes Estero, Limantour Estero (maritime Marin Co. marshes)
Centaurium trichanthum (Griseb.) Robinson [*Erythrea trichantha* (Griseb.)]	**Howell 1949**: "in typical form… known in Marin only from low ground bordering the salt marsh near Burdell Station". **Munz 1959**: "Moist often saline places… edge of Coastal Salt Marsh… San Mateo Co. to Siskyo Co."	No current reports known from edges of estuarine tidal marshes. Similar species *C. muehlenbergii* occurs in subsaline diked wetlands, Napa-Sonoma marsh, and tidal marsh edge at China Camp.

Table 1.3 (continued) Historic Changes in the Distribution and Abundance of Selected Native Vascular Plant Species Occurring in Tidal Marshes of the San Francisco Estuary

Taxon	Historic References	Contemporary Distribution
Calystegia sepium (L.) R.Br. ssp. ***limnophila*** (E. Greene) Brummit [*Convolvulus sepium* L.]	**Greene 1894**: " Plentiful in brackish marshes toward the mouth of the Napa River and about Suisun Bay; its roots within reach of tide water; its stems twining upon rushes and sedges. **Munz 1959**: " Occasional in swampy saline places; Coastal Salt Marsh; Marin, Solano and Contra Costa Cos."	Occasional in Suisun Marsh area west to Southhampton Bay; rare in San Pablo Bay edges.
Cicuta maculata L. var. ***bolanderi*** (S. Watson) Mulligan [*Cicuta bolanderi* Watson]	**Jepson 1911**: " Suisun marshes, abundant and conspicuous." **Munz 1959:** " Salt marshes, Marin to Solano and Contra Costa cos."	Uncommon to rare in Suisun Marsh; not currently reported elsewhere in the Estuary.
Cirsium hydrophilum (E. Greene) Jepson var. ***hydrophilum*** [*Carduus hydrophilus* Greene]	**Jepson 1911**: " Suisun marshes" **Munz 1959**: " Brackish marshes about Suisun Bay" .	Extremely rare (federally endangered) in Suisun Marsh.
Cordylanthus maritimus Benth. ssp. ***palustris*** (Behr) Chuang and Heckard [*Cordylanthus maritimus* Nutt.] [*Adenostegia maritima* (Nutt.) Greene]	**Brewer** et al. **1880**: " Sandy salt-marshes along the coast, from San Francisco Bay to San Diego." **Behr 1888**: " Salt marshes, San Francisco." **Greene 1894**: " Sandy salt marshes from near San Francisco southward." **Jepson 1911**: 'Salt marshes near the coast from San Francisco Bay south…" **Howell 1949**: " *Salicornia* flats in salt marshes along the bay..:.Almonte, Greenbrae…" **Thomas 1961**: " Salt marshes along the borders of San Francisco Bay; San Francisco, Redwood City, Palo Alto, and near Alviso."	Currently reported only from Richardson Bay, Greenbrae, and Petaluma marsh (Marin Co.). Recently reported from Gallinas Creek area marsh. Extirpated in central and southern San Francisco Bay. Major populations occur in maritime tidal salt marshes of Tomales Bay, Bolinas Lagoon, and Limantour Estero (Marin Co.). San Francisco Estuary populations have purplish foliage, and rosy, well-exerted inflated flowers.
Cordylanthus mollis Gray ssp. ***mollis***	**Brewer** et al. **1880.** " Salt-marshes of San Francisco Bay, at Mare Island and Vallejo, *C. Wright, E.L. Greene*." **Behr 1888**: " Salt marshes. Vallejo." **Greene 1894**: " Brackish marshes about Vallejo and Suisun." **Howell 1949**: [Marin Co.] "… San Rafael, acc. Ferris; Burdell Station, San Antonio Creek… ." **Best** et al. **1996**: [Sonoma Co.]: Rare, estuarine… Petaluma Marsh between San Antonio and Mudhen Slough… (1978)…"	Rare (federally endangered): local in tidal brackish marsh around Napa River, Carquinez Straits tidal marsh, Suisun Marsh area. Presumed extirpated in Petaluma River marshes. Putative San Francisco (city) record is erroneous interpretation of early San Francisco Bay Area collection acc. L. Heckard.
Downingia pulchella (Lindley) Torrey [*Bolelia pulchella* E. Greene]	**Jepson 1901**: "… Abundant and of rank growth in salt marshes near Alvarado [Union City]" . **Munz 1959**: "… Coastal Salt Marsh."	Extirpated in Union City. Occurs in alkaline/saline vernal pools at Warm Springs, Fremont, Alameda Co., and in some diked baylands near Fairfield, Solano Co.

Table 1.3 (continued) Historic Changes in the Distribution and Abundance of Selected Native Vascular Plant Species Occurring in Tidal Marshes of the San Francisco Estuary

Taxon	Historic References	Contemporary Distribution
Eleocharis parvula (Roemer and Shultes) Link	[not reported in early floras; Munz 1959 reported only from coastal salt marshes of San Luis Obispo and Humboldt Cos.]	Rare in brackish tidal marshes of San Pablo and Suisun Bay area. Local in diked baylands, lower Napa River.
Festuca rubra L.	[reported only from generalized habitats in early floras; halophytic populations not distinguished. Speculative likely component of historic sandy salt marsh edges of Central Bay.]	Not currently reported from San Francisco Bay estuarine tidal marsh edges; halophytic populations presumed extirpated. Halophytic populations occur along edges of maritime salt marsh and brackish marsh at Rodeo Lagoon, Limantour Estero, Tomales Bay (Marin Co).]
Glaux maritima L.	**Behr 1888**: “Salt marshes.” **Greene 1894**: “Frequent both along the seabord and in subsaline soils in the interior” **Jepson 1911**: “Marshy shores of … San Francisco and Suisun bays.” **Howell 1949**: [Marin Co.] “salt marshes… Burdell…” **Thomas 1961**: “… Palo Alto, but expected elsewhere in salt marshes” **Atwater** et al. **1979**: [recorded as present in San Pablo Bay] **Best** et al. **1996**: [Sonoma Co.] “Rare, salt marshes: Petaluma, *Davy* (1893 UC).”	Few recent reports known from San Francisco Bay or San Pablo Bay salt marshes; reported as infrequent in Petaluma Marsh; local in tidal marsh near mouth of Tolay Creek, Sonoma Co.; occasional to locally frequent in Suisun Marsh area and Fagan Slough (Napa River).
Heliotropium curassavicum L.	**Howell** et al. **1958**: “salt marsh near Visitacion Valley [southeastern San Francisco].”	No current reports known from San Francisco Bay. Recently reported from Suisun Marsh area.
Hemizonia pungens (Hook and Arn.) Torrey and A. Gray ssp. ***maritima*** (E. Greene) [*Centromadia maritima* Greene]	**Greene 1894**: “Borders of salt marshes about San Francisco Bay.” **Cooper 1926**: [dominant species of reconstructed “willow-composite” community at salt marsh edges, Palo Alto vicinity.]	Local, infrequent species along tidal marsh edge around the San Francisco Estuary.
Hemizonia parryi E. Greene ssp. ***parryi***, ssp. ***congdonii*** (Robinson and Greenman) Keck	**Munz 1959**: [ssp. *congdonii*] “Locally common… s. end of San Francisco Bay, mostly Alameda Co.” [ssp. *parryi*] “Coastal Salt Marsh… to N. San Mateo Co…” [not reported from salt marsh in Jepson 1901, Greene 1894)	No current reports known from San Francisco Bay Estuary tidal marsh edges. Rare.
Hutchinsia procumbens (L.) Desv. [*Bursa divaricata* (O. Ktze) Nutt.] [*Capsella divaricata* Walp.] [*Capsella procumbens* Fries.] [*Capsella elliptica* C.A. Mey.] [*Lepidium procumbens* L.] [*Hutchinsia californica*, *H. desertorum* A. Davids]	**Greene 1894**: “Borders of salt marshes.” **Jepson 1911**: Alkaline soil from Vallejo (acc. Bot. Cal.), Alameda…” **Thomas 1961**: Known locally from saline areas along San Francisco Bay; Palo Alto and Mayfield.”	No current reports known from San Francisco Bay Estuary tidal marsh edges. Occurs in high marsh ecotone of central CA coast salt marsh, and in other alkaline or subsaline habitats in California floristic province.

Table 1.3 (continued) Historic Changes in the Distribution and Abundance of Selected Native Vascular Plant Species Occurring in Tidal Marshes of the San Francisco Estuary

Taxon	Historic References	Contemporary Distribution
Juncus effusus L. var. ***brunneus*** Engelm.	**Brewer** et al. **1880:** "… common in the salt-marshes about San Francisco Bay…" **Brandegee 1892**: " Salt marshes about the bay shore." **Jepson 1911**: " Common in marshy ground: Monterey to San Francisco and Bolinas Bays and northward." **Howell 1949**: " Swamps and swales generally near the ocean… Tiburon; Sausalito…" **Thomas 1961**: " Usually along or near the coast… Palo Alto, near Alviso…"	Rare, local at edges of salt marsh and brackish marsh ecotones in San Pablo Bay (China Camp). No known reports from San Francisco Bay tidal marshes.
Juncus lesueurii Boland.	**Brandegee 1892**: " Salt marshes at Visitacion Bay. South San Francisco." **Howell 1949**. " Common along the upper reaches of salt marshes… Tiburon; Tamalpais Valley… . In Marin County,… [*J. balticus*] is not readily distinguished from *J. Leseurii*…]"	Apparently associated with sandy salt marsh edges of maritime coast. Intermediates with *J. balticus* not uncommon in San Francisco Bay Area tidal marshes; difficult to separate. Rare in south San Francisco Bay tidal marshes; one colony in seep at salt pond edge, Coyote Hills.
Juncus xiphioides E. Meyer	**Jepson 1901**: " A common species of salt marshes… Berkeley; Belmont… Suisun Marshes…" **Thomas 1961**: " Occasional in sloughs … Palo Alto, nr. Alviso…"	Not recently reported; presumed rare or possibly extirpated in most tidal salt marshes of San Francisco Estuary.
Lasthenia glaberrima D.C.	**Behr 1888**: " Near salt marshes."	No other reports, historic or current, are known from San Francisco Bay estuarine marshes.
Lasthenia conjugens E. Greene [*Baeria fremontii* (Torr.) A. Gray in part]	**Greene 1894**: " Subsaline soil near Antioch…" **Jepson 1911**: " Subsaline fields in the Bay region; Antioch; Newark, etc."	Occurs in alkaline/saline vernal pools bordering salt pond 22 in Fremont, Alameda Co., and in diked baylands at upper end of Hill Slough (Potrero Hills), Solano Co. Historic localities near Mt. Eden along bay shore and near Newark. Rare; federally endangered.
Lasthenia platycarpha (A. Gray) E. Greene [*Baeria carnosa* E. Greene] [*B. platycarpha* A. Gray]	**Greene 1894**: " Border of salt marsh north of Vallejo: rare or local." **Jepson 1911**: " Salt marshes at Vallejo (Greene)."	Historic locality at Redwood City shoreline. Apparently extirpated from San Francisco Bay estuarine marshes. Occurs infrequently in alkaline vernal pools, Solano Co.
Lasthenia glabrata Lindley ssp. ***glabrata***	**Behr 1888**: " Common." **Greene 1894**: " Borders of salt marshes only; not common." **Jepson 1911**: " Borders of salt marshes." **Thomas 1961**: Edges of salt marshes along San Francisco Bay… Millbrae… Belmont, Redwood City, Mayfield."	Currently reported within San Francisco Bay Estuary only from Point Pinole (Whittell marsh) salt marsh and new seeded levee slope at Sonoma Baylands. Many historic salt marsh collections known from Burdell, Alvarado, Mt. Eden, Alameda, Mowry's Landing, Denverton. Maritime salt marsh population occurs in Limantour Estero, Marin Co.

Table 1.3 (continued) Historic Changes in the Distribution and Abundance of Selected Native Vascular Plant Species Occurring in Tidal Marshes of the San Francisco Estuary

Taxon	Historic References	Contemporary Distribution
Lasthenia minor (DC.) Ornd. [*Baeria minor* (DC.) Ferris [*Baeria uliginosa* Nutt.] [*Lasthenia uliginosa* (Nutt.) E. Greene]	**Brandegee 1891**: "About the borders of marshes, Islais Creek, Visitacion Valley, Presidio, South San Francisco."	Apparently extirpated from San Francisco Bay estuarine marshes.
Lathyrus jepsonii E. Greene var. ***jepsonii*** Jepson	**Greene 1894**: "Suisun marshes." **Jepson 1911**: "Suisun marshes."	Occasional to rare in Suisun Marsh. Also occurs locally in tidal brackish marshes along Napa River (Dutchman Slough). May be under-reported in drought years.
Layia chrysanthemoides (DC.) A. Gray [*Blepharipappus chrysanthemoides* Greene]	**Howell 1949**: "Locally common on flats bordering the salt marshes: Ignacio;… Chileno Valley." **Thomas 1961**: "occasionally in low alkaline soils of San FranciscoBay… Millbrae, Redwood City."	No current reports known from San Francisco Estuary tidal marsh edges.
Leymus triticoides (Buckley) Pilger [incl. *Leymus* X *multiflorus* (Gould) Barkworth and D.R. Dewey [*Elymus triticoides* Buckley]	[general grassland habitats reported historically. Presumed abundant or dominant species of historic tidal marsh edges.]	Occurs locally (abundant) at salt marsh edges at Newark, Alameda Co.; Rush Ranch, Solano Co; Petaluma Marsh, Marin Co.; China Camp, Marin Co.; Dutchman Slough, Solano Co.
Lepidium dictyotum A. Gray	**Greene 1894**: "Along the borders of marshes at Alameda."	No current reports known from San Francisco Bay tidal marsh edges. Presumed extirpated or rare in Estuary.
Lepidium latipes Hook.	**Greene 1894**: "in saline soil at Martinez, Alameda, etc." Jepson 1901: "… alkali flats… Martinez…"	No current reports known from San Francisco Bay tidal marsh edges. Reported rarely in diked baylands and tidal marsh edges, Solano Co. (Suisun Marsh area).
Lepidium oxycarpum Torrey and A. Gray	**Greene 1894**: "Borders of salt marshes at Vallejo… also in subsaline soils… near Alameda." **Howell 1949**: "A rare peppercress of alkaline valley floors and of saline flats adjacent to coastal salt marshes, in Marin Co. known only from low pastures bordering San Francisco Bay near Novato." **Munz 1959**: "V. Grassland and edge of Coastal Salt Marsh; largely about San Francisco Bay…" **Thomas 1961**: "Saline and alkaline flats along San Francisco Bay and Santa Clara Valley: Redwood City, Cooley's Landing, Palo Alto, Mayfield…"	No current reports known from San Francisco Bay tidal marsh edges. Rare, Suisun Marsh edges.
Lilaeopsis masonii Mathias and Constance [*Lilaeopsis lineata* (Michx.) Greene, in part	**Jepson 1911**: [as *L. lineata*, in part] "Salt marshes or brackish mud flats:… Port Costa to Antioch; Robert's Island".	Rare in tidal brackish tidal marshes, Napa Marsh, Suisun Marsh area, to Tolay Creek, San Pablo Bay. Uncommon in western Sacramento river delta fresh-brackish marshes.

Table 1.3 (continued) Historic Changes in the Distribution and Abundance of Selected Native Vascular Plant Species Occurring in Tidal Marshes of the San Francisco Estuary

Taxon	Historic References	Contemporary Distribution
Lycopus asper E. Greene [*Lycopus lucidus* Turcz.] [*L. lucidus* Benth. misapplied]	**Jepson 1911**: “Salt marshes: Suisun; Benicia; San Francisco.” **Hickman** et al. **1993**: Uncommon. Moist areas, marsehs, streambanks… Deltaic GV, SnFrB, GB; to w Can, Great Plains.	No current reports known from San Francisco tidal marsh edges; presumed rare or extirpated in Estuary there.
Plagiobothrys glaber (A. Gray) I.M. Johnston [*Allocarya salina* Jepson] [*Allocarya glabra* Macbr.]	**Jepson 1911**: “Alvarado [Union City], margin of salt marshes.” **Munz 1959**: “Coastal Salt Marsh; s. shore of San Francisco Bay…”	**Hickman 1993**: “PRESUMED EXTINCT. Wet, alkaline soils in valleys, coastal marshes… CCo, s SnFrB… Perhaps a var. of *P. stipitatus.”*
Plagiobothrys mollis (A. Gray) I.M. Johnston var. ***vestitus*** (E. Greene) I.M. Johnston [*Allocarya mollis* A. Gray var. *vestita* E. Greene [*A. vestita* E. Greene]	**Jepson 1911**: Petaluma, *Congdon, 1880*; not since collected.	**Hickman 1993**: “PRESUMED EXTINCT. Wet sites in grassland, possibly coastal marsh margins…”
Plagiobothrys stipitatus (E. Greene) var. ***stipitatus***	**Best** et al. **1996**: “salt marsh near Sears Point, Keck 1935”	Reported at Sonoma Baylands, high tide line, 1996. Otherwise no current reports known from San Francisco Estuary tidal marsh edges
Plantago elongata Pursh [*Plantago bigelovii* Gray]	**Brewer** et al. **1880:** “Salt-marshes, San Pablo Bay, at Benicia and Vallejo, *Bigelow, E.L. Greene*.” **Greene 1894**: “Borders of saline or brackish marshes; quite common about the Bay…” **Howell 1949**: [Marin Co.; not reported from estuarine stations] **Thomas 1961**: [SW San Francisco Bay] “… edges of salt marshes… Mayfield, Alviso…] **Best** et al. **1996**: [Sonoma Co.] “uncommon, salt marshes… Petaluma, *Congdon* (1880); 5 mi. n. of Sear’s Point, *Rubzoff* (1970).	Rarely reported from San Francisco Bay Area high tidal marshes (Suisun Marsh). No recent localities in tidal marsh edges confirmed.
Plantago maritima **L.** [*P. maritima* L. ssp. *juncoides* (Lamk.) Hulten, *P. juncoides* Lamk. var. *juncoides*]	**Greene 1894**: “… sandy salt marshes” **Jepson 1911**: “… West Berkeley…” **Howell 1949**: [Marin Co.] “occasional in salt marshes bordering the bay or ocean: Almonte…” **Thomas 1961**: “occasional in salt marshes and on coastal bluffs as far south as San Mateo County: San Francisco, Redwood City, and Mayfield.” **Best** et al. **1996**: *[Not reported from estuarine Sonoma Co. stations.]*	Infrequent to rare in San Francisco Bay tidal marshes, mostly Richardson Bay. Relatively common in maritime salt marshes, and occaisional in Suisun Marsh (Hill Slough).

Table 1.3 (continued) Historic Changes in the Distribution and Abundance of Selected Native Vascular Plant Species Occurring in Tidal Marshes of the San Francisco Estuary

Taxon	Historic References	Contemporary Distribution
Pluchea odorata (L.) Cass. [*P. camphorata* (L.) DC. and *P. purpurascens* (Sw.) DC. misapplied]	**Behr 1888:** Salt marshes. **Greene 1894**: “ Borders of brackish marshes about Suisun Bay, etc.” **Jepson 1911**: “ Common in the salt marshes about Suisun and San Francisco Bays…” **Howell 1949:** [Marin Co.; not cited] **Thomas 1961**: [SW San Francisco Bay; not cited]	No current reports known from San Francisco or San Pablo Bays; uncommon in Suisun marshes.
Puccinelia nutkaensis (J.S. Presl.) Fern. and Weath. [*P. grandis* Swallen]	**Thomas 1961**: “ levees and salt marsh along San Francisco Bay” .	Rare, local, south San Francisco Bay. No records of San Pablo Bay collections in Howell 1949, Best et al. 1996.
Pyrrocoma racemosa (Nutt.) Torrey and A. Gray var. ***racemosa*** [*Haplopappus racemosa* (Nutt.) Torr.; *P. elata* E. Greene]	**Greene 1894**: “ A somewhat rare plant of subsaline soils at Calistoga and near San Jose.” **Thomas 1961**: “ edges of salt marshes, saline soils, and occasionaly disturbed areas. Cooley’s Landing, Near Alviso, Agnews, and San Jose.”	No current reports known from San Francisco Bay high tidal marsh. Presumed extirpated in San Francisco Bay.
Rumex occidentalis S. Watson [*R. fenestratus* E. Greene]	**Greene 1894**: “ Frequent in marshy places.” **Jepson 1911**: “ Marshes bordering San Francisco Bay.” **Munz 1959**: “ Coastal, often brackish marshes, San Francisco Bay…” **Hickman** et al. **1993**: “ Uncommon. wet +/- salty places.”	Infrequent to rare in North Bay, Suisun Marsh area brackish tidal marshes.
Salicornia subterminalis Parish [*Arthrocnemum subterminale* (Parish) Standley]	[Not reported from estuarine stations in early floras.]	Local, rare in South Bay, south Fremont, Milpitas (in diked wetlands, former Fremont Airport), and at Hill Slough, Suisun Marsh.
Sanicula maritima Wats. *(S. maritima* Kellogg)	**Behr 1888**: “ Alameda marshes.” **Greene 1894**: “ In lowlands adjacent to salt marshes near Alameda, San Francisco, etc.” **Jepson 1911**: “ Local species of low and wet adobe lands in the vicinity of salt marshes bordering San Francisco Bay; near Alameda… and Potrero Hills, San Francisco, the only recorded localities.”	Extinct in San Francisco Bay; known from fewer than 10 stations in 1988, Monterey and San Luis Obispo Counties.
Senecio hydrophilus Nutt.	**Brewer** et al. **1880**: “… salt marsh at Vallejo *(Greene)*…” **Greene 1894**: “ Brackish marshes; formerly plentiful at West Berkeley, and on the lower Napa River; still abundant in the Suisun marshes.” **Jepson 1911**: Abundant in the Suisun Marshes and found in other marshes about San Francisco Bay”	Apparently extirpated in San Francisco, San Pablo Bay (incl. Petaluma R.); infrequent but locally common in Suisun Marsh area and Carquinez Strait tidal marshes; possibly Napa R..” **Hickman 1993**: “ Reduced from wetland development.”

Table 1.3 (continued) Historic Changes in the Distribution and Abundance of Selected Native Vascular Plant Species Occurring in Tidal Marshes of the San Francisco Estuary

Taxon	Historic References	Contemporary Distribution
Sium suave Walter [*Sium cicutaefolium* Gmel. var. *heterophyllum* Jepson]	**Jepson 1911**: "Suisun marshes; Stockton"	Rare in Suisun Marsh, primarily in wet years. Recently observed near Rush Ranch, Hill Slough, and Brown's Island.
Suaeda californica Wats.	**Brewer** et al. **1880:** "In salt-marshes on the coast, about San Francisco." **Behr 1888:** "Salt marshes on an island near Alameda." **Greene 1894**: "Vicinity of sand beaches about San Francisco Bay, but seldom seen." **Jepson 1911**: "Sandy beaches bordering San Francisco Bay, the known stations few: San Pablo Landing; Bay Farm Island." **Thomas 1961**: "Occasional in salt marshes along San Francisco Bay; San Francisco and Palo Alto."	Extinct in San Francisco Bay Estuary, probably since ca. 1950. Restricted to one large population at Morro Bay, where it occurs primarily along sandy high marsh edges. Planned for reintroduction. Misreported occurrences often due to confusion with *Suaeda calceoliformis*, *S. moquinii*, *Salsola soda*, and *Bassia hyssopifolia*.
Solidago confinis Nutt. [*S. sempervirens* L. misapplied] [*S. confinis* var. *luxurians* Jepson]	**Jepson 1911**: "Salt marshes, San Francisco Bay, *Bolander* [1863]. Rarely collected.	Apparently long extirpated in San Francisco Bay Area. Occurs in brackish tidal marsh edges of Morro bay, San Luis Obispo co.

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Plants and Environments of Diked Baylands

Peter R. Baye

Introduction

This report focuses on wetland areas within historic tidal marshes that have been isolated from tidal action by dikes (levees) and converted to non-tidal salt marsh, non-tidal brackish marsh, or subsaline to freshwater seasonal wetlands. These areas are referred to herein interchangebly as " diked wetlands" or " diked Baylands." Because instantaneous salinity (or even average annual salinity) of diked wetland soils does not consistently correspond with plant community composition, and varies over time, these salinity categories are intended to be broadly descriptive of plant associations rather than quantitative threshold values of soil salinity. Accordingly, the marsh types described are not discrete, but intergrade continuously and may vary over time at any site. Diked wetlands as treated below do not include artificial salt ponds (treated separately) or " muted tidal" managed marshes (marshes with reduced tidal range controlled by tidegates), and cover only wetlands with non-tidal hydrologic inputs (rainfall, groundwater, surface runoff, streamflow, engineered water control structures, or very infrequent overtopping of dikes by extreme tides).

Published and unpublished sources of useful, precise data and other information on the vegetation and flora of diked Baylands are very scarce. Most usually are limited to short-term observations and coarse descriptive accounts (such as lists of dominant species) at a particular time of year, or generalized accounts of resource management plans (e.g., Eicher 1988, Hudson 1980). Vegetation was usually described for wildlife habitat evaluation, rather than for floristic analysis or quantative plant community description. Relatively more detailed information about some individual diked Bayland sites is sometimes available for sites which are proposed for major development projects, and become the subject of detailed wetland delineations and field studies for environmental evaluations (e.g., Rugyt 1991, Kaufman and Harvey 1987). The level of detail in vegetation analysis of diked Baylands even for site-specific studies was still low until the mid 1980s when technical vegetation criteria for wetland jurisdictional delineations were promulgated (WES 1997). There are no long-term studies of changes in vegetation in diked Baylands. Some coarse information about vegetation change in diked wetlands is available through inspection of historic aerial photographs, particularly color infrared photos from the 1980s to the present. Based on recent information from some of the more intensively surveyed diked wetlands (e.g., Montezuma Wetlands, Solano County; Cullinan Ranch, Solano County; Renaissance Faire site, Marin County), it appears that the diversity and dynamics of diked wetland vegetation have been substantially underestimated in past assessments.

Historic information on the diking of San Francisco Bay tidal marshes is based on numerous sources, particularly U.S. Coast Survey maps (multiple series); historic accounts of salt pond levee development (Ver Planck 1958); and field observations of modern levee maintenance and repair methods and agricultural drain systems.

Environmental Setting

The physical origins of diked wetlands are similar throughout the San Francisco Estuary. Most of the tidal marshes were reclaimed for agricultural use in the late 19th century when the use of mechanical dredges became commercially available to landowners (after *ca*. 1870), although many dikes were constructed manually (Madrone Associates 1977). Tidal marshes were diked for reclamation either as pasture, hayfields, salt ponds, or (rarely) cropland. Reclamation involved construction of dikes (earthen levees made of locally excavated Bay mud) along the margins of marsh plains (middle marsh between approximately MWH and MHHW) where they bordered mudflats or major tidal creeks. The borrow ditches for dike construction were typically located inside of the dike, creating narrow canals about 20 ft from the foot of the dikes. Enclosure of tidal marshes by dikes, and resulting fluctuation between winter flooding and summer desiccation of saline basins, would have rapidly killed most standing tidal marsh vegetation. When levees were stabilized after several lifts (sequential layers of dewatered dredged Bay muds) tidegates were installed to enable the enclosed basins to drain on low tides. After stabilization, dikes typically stood about 3 (to 4) ft above the marsh plain (VerPlanck 1958).

Environmental Changes From Diking - Following the initial phase of dike construction, several changes occurred. Mature tidal marsh soils accumulated peaty organic matter under anaerobic conditions, which minimizes decomposition. Drained marsh soils high in peaty organic material underwent aerobic decomposition and dewatering, causing land elevations to subside. Dikes also caused compression of underlying plastic clayey silts and peats, and subsided (Madrone Associates et al. 1983). Differential subsidence of the marsh surface tended to exaggerate relict marsh topographic relief, causing natural levees (containing coarser silts) to stand out against isolated depressions where peat content was relatively great, and the effects of aerobic peat decomposition were greatest. Tidal creek topography typically persisted as depressional sinuous swales. Early-succession diked marsh plant communities, typically dominated by perennial pickleweed (*Salicornia virginica*; drier, more saline conditions) or alkali bulrush (*Scirpus maritimus*), bulrush (*Scirpus californicus*; less often *S. acutus*) or cattails (mostly *Typha angustifolia*; wetter brackish to subsaline ditches) tend to be best developed in relict swales and depressions. As salts were drained from the diked basins and lands were managed for agriculture, these pioneer diked salt marsh communities were reduced or eliminated (Madrone Associates et al. 1983, Harvey 1987).

Marsh Progradation and "Second Generation" Diked Wetlands - The strong reduction in tidal flows caused by diking all but the largest tidal creeks in the marsh system caused significant increases in sedimentation outside of diked marshes, causing rapid marsh progradation on sloping mudflats. In addition, slow migration of the pulse of hydraulic mining outwash from the Sacramento River contributed to marsh progradation in San Pablo and Suisun Bays (Doane 1999, Jaffe et al. 1998). In some areas (e.g., south of Novato Creek), marsh progradation was so extensive that a second phase of diking occurred in the newly accreted marshes. These progradational marshes are typically broad pickleweed-

Ruth Pratt

Agricultural areas within the diked historic Baylands can pond water and exhibit seasonal wetland plant associations. (North San Pablo Bay diked Baylands after a storm event) dominated plains with fringes of cordgrass, cordgrass/alkali bulrush mixtures, or erosional scarps in pickleweed peats. Like early-succession diked salt marsh, they support relatively low salt marsh species diversity, and low densities of narrow, sparsely branched shore-perpendicular tidal creeks. Because of the influence of wave deposition of sediment and coarse organic debris, the tidal elevations of these dike-fringing salt marshes is often above MHHW in some areas, particularly where incipient natural levees form at the edge of mudflats. These secondary prograded high marshes with little antecedent topography were readily converted to diked agricultural land, as in the Baylands of Novato (Hamilton, Bel Marin Keys).

Dike Disturbance Cycle and Vegetation - Subsidence of dikes themselves caused a need to maintain dike crest elevations by dredging borrow ditches to resupply material. This established a periodic disturbance regime to dike vegetation and adjacent ditches. In areas of high wave energy (long fetch distance, narrow mudflats), maintenance by topping dikes with dredged muds and repairing erosional slopes may occur in cycles as short as five years or less. Many bayfront dikes unsheltered by fringing marsh require armoring by placement of rock or concrete fragments. Well-protected dikes behind extensive salt marsh on firmer peats may have maintenance cycles longer than a decade or two. Repaired dike slopes provide bare mineral substrate which is gradually leached of salts and open to colonization by upland weeds.

The dike disturbance cycle has favored a ruderal flora along the upper slopes and crests of dikes (including many native and exotic halophytic weeds as well as glycophytes; e.g., mustard *(Hirschfeldia incana, Brassica* spp.), radish (*Raphanus sativus*), fennel (*Foeniculum vulgare*), plantain (*Plantago coronopus, P. major, P. lanceolata*), annual ice-plant (*Mesembryanthemum nodiflorum*; mostly South Bay), sea-fig (*Carpobrotus chilense*), hottentot fig (*Carpobrotus edulis* and hybrids with *C. chilense*), poison hemlock (*Conium maculatum*), Mediterranean brome species (*Bromus* spp.), wild barley (*Hordeum murinum* ssp. *gussonianum*,), ryegrass (*Lolium multiflorum, L. perenne*). Lower portions of disturbed outboard (bayward) dike slopes are typically more saline and wetter, and support brackish marsh or salt marsh species, often with an exaggerated proportion of weedy halophytes (e.g., spearscale, *Atriplex triangularis;* perennial peppercress, *Lepidium latifolium*, sicklegrasses *Parapholis incurva, Hainardia cylindrica;* bassia, *Bassia hyssopifolia*; saltwort, *Salsola soda;* wild beet, *Beta vulgaris*). Interior slopes of dikes which face salt ponds, and contiguous fringing nontidal saltmarsh, are either bare or vegetated with saltgrass (*Distichlis spicata), Salicornia virginica*, dodder *(Cuscuta salina)*, and alkali-heath *(Frankenia salina)*. Dikes with very infrequent maintenance tend to become dominated by dense stands of coyote brush *(Baccharis pilularis*; South Bay) or mixed coyote brush and bee-plant (*Scrophularia californica*; North Bay), often with sub-dominant mustard, poison-hemlock, and radish. High marsh halophytes (pickleweed, alkali-heath, gumplant, spearscale) tend to dominate the lower portion of the outboard dike slopes adjacent to salt marshes, although weedy species can persist for many years after a levee has been disturbed by maintenance and repair activities.

The ecological significance of the dike disturbance cycle for wetland plants is that it has provided corridors through tidal marshes and diked marshes for a weedy flora (both exotic halophytes and glycophytes) to disperse, and places weed seed sources along a topographically superior location for dispersal into adjacent diked and tidal wetlands. The rapid local spread of weedy halophytes on dredge spoils along recently maintained/repaired dikes (especially *Salsola soda, Lepidium latifolium, Mesembryanthemum nodiflorum*) can be observed throughout the Bay. Similar halophyte weed dispersal occurs along side-cast spoils in diked marshes where drainage ditches are created or maintained. Dike disturbance corridors may accelerate the spread of exotic halophyte population outposts into uninvaded wetland habitats. In particular, *Lepidium latifolium'*s invasion of brackish marshes appears to have tracked patterns of dike disturbance, invading first along dredge spoil at levee edges, subsequently spreading into diked and tidal wetlands.

Hydrologic Changes in Diked Wetlands - Patterns of soil waterlogging and inundation in diked conditions differ fundamentally from tidal marsh. They depend principally on the efficiency of artificial drainage, the permeability of substrate (related to soil clay content), and the amount and seasonal distribution of rainfall. The efficiency of the early drainage systems in diked marshes was based on the amount of ditching and the pattern of ditching in relation to subsided marsh topography. Because of the great extent of the areas diked, density of drainage ditches was relatively low. Ditches were mostly confined to the borders of farmed parcels, but sometimes

Josh Collins

Diked wetlands in Suisun are managed primarily for waterfowl production.

reached across extensive marsh depressions. The drains were originally driven by gravity, drawing drainage water downslope to one-way flapgates which discharged to adjacent tidal marshes at low tide. This original gravity-driven drainage system had limited efficiency. Topographic lows in the diked basins (swales of relict tidal creeks, relict marsh pans) remained poorly drained into the crop growing season, while relict creek levees and higher relict tidal marsh became better drained. Relictual tidal marsh patterns of wetland and upland are evident in black and white photographs of diked hayfields in the mid-20th century. Even with modern pump-driven drainage systems, persistent soil waterlogging and inundation in depressions occurs following rainstorms (Granholm 1986, Madrone Associates et al. 1983).

The proportions of poorly drained (waterlogged or inundated in spring) and well-drained (aerobic soils in spring) soils in diked Baylands vary with precipitation amounts and patterns. Years of normal or above normal rainfall, particularly those with large storms late in the precipitation season, cause expansion of wetland areas in diked conditions. These contract during years of below-normal precipitation, especially with a lack of spring storms. The proportions of effective wetland and upland also vary with drainage efficiency and the degree of subsidence.

Long-term Drainage of Diked Wetlands - As subsidence increased, wetland areas increased behind dikes, particularly in peaty soils. In the early 20th century, many diked farmlands failed because the costs of compensating for increased subsidence and dike degeneration at times exceeded the return on agricultural benefits. Many derelict agricultural parcels with degenerated dikes are evident in aerial photographs of San Pablo Bay in the 1940s. After abandonment of diked farmlands, partial levee and drain failures increased, causing reversion of agricultural lands to brackish or salt marsh conditions. For example, prior to conversion to salt ponds, many of the Napa Marsh area's derelict hayfields in the 1940s had partially reverted to wetland (Madrone Associates 1977).

Contemporary Drainage of Diked Wetlands - Today, subsidence of diked active agricultural lands has increased to the point at which it cannot be compensated by passive gravity drainage through flapgates alone; drainage sufficient for oat hay farming depends primarily on active pumping of water in ditches for discharge to the Bay. It is common for elevations in diked Baylands of San Pablo Bay to average as low as 0 - 1.0 ft N.G.V.D, and some average below -3.0 ft or more over extensive areas, as at Bel Marin Keys and Hamilton Field (USACE 1988). In south San Francisco Bay, which was affected by past subsidence due to long-term groundwater extraction, diked wetland elevations may be even lower (Moffett and Nichols and Phil Williams Associates 1988). These subsided diked marsh surfaces are often very close to the groundwater surface. Accordingly, the proportion of wetland and upland in contemporary conditions depends on the intensity of pumping and ditch maintenance. These conditions vary significantly among diked parcels under different ownership and management. Therefore, the mosaic of wetland and upland in diked agricultural lands is relatively variable and unpredictable among years and between parcels.

Variability of Artificial Hydrologic Conditions - The patchiness and instability of diked wetlands is evident, for example, in recent land-use changes in San Pablo Bay. Cullinan Ranch, actively drained and farmed oat hayfield until the early 1990s, supported a matrix of upland cropland and many seasonally wet depressions with wetland weeds. After cessation of pumping by the mid-1990s (a period of above average rainfall), the Ranch rapidly (within 2 years) and spontaneously converted to a seasonal freshwater marsh dominated by cattails and flats of *Eleocharis parvula* (Takekawa et al. 1999). Nearby, between Tolay Creek and the Petaluma River, adjacent hayfields with differing schedules of ditch maintenance changed from very similar extensive winter-ponded swale patterns to striking contrasts of ponded and drained fields. At another location near Sears Point, San Pablo Bay, cessation of pumping in relict hayfields caused conversion to seasonal wetlands dominated by annual plant species typical of vernal pool communities (many of which are present in the ephemeral weed floras of depressions within hayfields; *Downingia pulchella, Plagiobothrys bracteatus, Eryngium aristulatum, Callitriche* spp., *Eleocharis macrostachya*). Thus, the extent of diked wetlands and their character today are very much artifacts of drainage pump activity.

Similar artificial drainage controls wetland plant communities in the diked basins of the Suisun Marsh, which is managed mostly for waterfowl production. There, relatively low-salinity tidewaters are admitted to the basins selectively to sustain fresh-brackish perennial and seasonal marshes (Jones and Stokes 1976, Mall 1969, Meiorin et al. 1991). The proportion of ponded to vegetated marsh may be controlled by modifying managed hydroperiods, so that prolonged flooding causes dieback of vegetation in areas of relatively lower substrate elevation. The seasonal variations in tidewater salinity enable the timing of flooding to control substrate salinity, also. Managed marsh hydroperiods are usually designed to favor mixtures of shallow submerged mud, bulrushes (*Scirpus maritimus, S. americanus, S. pungens*), tules (*S. californica, S. acutus*), cattail (Typha spp.) and brass-buttons (*Cotula coronopifolia*), and some non-native annual grasses (*Echinochloa crus-gallii, Polypogon monspeliensis*). Also common in diked brackish marshes are baltic rush (*Juncus balticus*), saltgrass *(Distichlis spicata*) and pickleweed (*Salicornia virginica*). Other species have colonized these brackish managed wetlands, including goosefoot *(Chenopodium chenopodioides*), docks (*Rumex crispus, R.*

pulcher), purslane (*Sesuvium verrucosum*, a recent invader native to the Great Basin), celery, *(Apium graveolens)*, *Lepidium latifolium*, and *Conium maculatum*. Some diked brackish marsh communities are essentially artificial, in contrast with the incidental nature of wetland communities in diked Baylands which are either derelict or managed for hay production, pasture, or salt production.

Salinity in Diked Wetlands - The substrate salinity conditions in the diked, drained marshes were modified by leaching the silty clay Bay muds with precipitation, eliminating leached salts through drainage ditches and tidegates, and excluding tidal inundation by dikes. This caused rapid desalinization of the substrate, enabling glycophytes with relatively low salt tolerance (compared with the salt marsh flora), such as oats and agricultural weeds, to dominate the converted tidal marsh soils (Harvey 1987, Madrone Associates et al. 1983, Meiorin et al. 1991). The desalinized conditions of the substrate were maintained by drainage through ditches and tidegates. Subsidence caused (and continues to cause today) decreased efficiency of drainage, and therefore also decreased flushing of residual or reintroduced salts.

Diked wetlands which have been effectively desalinized for agricultural production do not remain so unless substantial maintenance efforts are applied to drainage and dikes. Diked wetlands become resalinized by partial failure of tidegates and levees (Madrone Associates et al. 1983). Leaking or ruptured tidegates allow influx of saline tidal waters in drainage ditches. Saline or brackish ditch water can recharge salts locally in groundwater, and move into the soil through evapotranspiration and capillary movement. In derelict cattail-lined ditches of abandoned diked hayfields, late summer ditch water salinity can reach 15 ppt, due to salt leaching and evaporation. In addition, seepage through dikes (particularly where Bay mud is silty) introduces salts locally. Overtopping (cresting) of dikes during storm surges floods reclaimed salt marsh soils with brackish or saline water. All these processes recharge soil salinity in diked wetlands. Overtopping typically occurs in winter, and is not a rare event, particularly in south San Francisco Bay (USACE 1988). If poor drainage conditions prevail following a substantial tidal flooding event in a diked basin, wetlands rapidly become recolonized by salt-tolerant vegetation. High salinity in diked Baylands is often maintained by episodic tidal flooding events which are not often observed. Residual salinity tends to decline very rapidly except where drainage is very poor.

Acidification of Diked Wetlands - Soil acidity affects plant growth primarily by altering the availability of soil nutrients, or liberating excessive amounts of otherwise low-solubility ions into the soil solution, creating toxicity problems for roots. Acid-related toxicity occurs only at very low pH (Reuss and Johnson 1986). Soil acidity is normally not highly variable in tidal salt marshes, which are buffered by cations of estuarine water and relatively stable reduction-oxidation conditions established by groundwater surface position in the marsh soil profile (Adam 1990). In diked conditions, extreme seasonal fluctuations in the soil saturation levels may occur, causing release of sulfides and free metals in marsh soils with high sulfur contents. Some depressions in diked wetlands develop very low pH (pH 4 and occasionally lower) and high concentrations of iron oxide precipitates (Madrone Associates et al. 1983, Madrone Associates 1977). These areas are often barren of vegetation, or develop sparse, low diversity vegetation. Less extreme but low pH in diked wetlands may inhibit plant production, but the abundant phytomass of many diked wetlands (e.g., rank growth of pickleweed, cattails, peppercress) suggests that the seasonal drainage and aeration of diked wetland soils commonly has a stronger overall effect on vegetation production than low pH. Extremely low redox potential and sulfite toxicity, which often accompany low pH, are highly significant inhibitors of plant growth (Russell 1973). Soil acidity is highly variable in diked wetlands and depends on local soil conditions and prevailing hydroperiods.

Disturbance in Diked Wetlands - The disturbance regimes of diked wetlands are influenced primarily by discing and flooding. Discing is performed for agriculture, suppression of weed biomass, and suppression of mosquito production. Episodes of discing have maintained a significant ruderal (weedy) element to the diked wetland flora of San Francisco Bay, creating large vegetation gaps suitable for invasion by non-native plants, particularly annuals. Extreme flooding events which are possible in non-tidal diked marshes also cause disturbances: deep, prolonged flooding causes mass dieback of most standing perennial vegetation. Following dieback events, similar or very dissimilar plant associations may establish.

Diked Bayland Plant Communities

The plant communities present in the diked Baylands can resemble those of local tidal salt marshes, tidal brackish marshes, non-tidal perennial freshwater marshes, or seasonally wet grasslands. Some also have characteristics similar to components of tidal marshes which are now regionally scarce or extirpated, such as high marsh pans and alluvial high marsh ecotones. Diked wetlands usually have lower native species richness than their analogous natural plant communities, and often a larger component of exotic plant species. The typical "weediness" of many diked wetlands is probably more a result of past land uses rather than an intrinsic susceptibility to invasion by exotic vegetation. Some diked wetlands are managed actively to maintain community dominance by marsh plant species favored by wildlife or game managers (Mall 1969). Most are either managed for purposes other than wildlife conservation (hayfields, grazed pasture, flood detention basins, salt evaporation ponds) or are derelict (i.e., pending conversion to urban development), but may still support significant marsh plant communities.

Plant community composition in diked wetlands is strongly influenced by the degree of residual soil salinity or salt recharge of soils, the efficacy of artificial drainage, and the relictual factors of land use history. These factors vary extremely in diked Baylands: some exhibit insignificant salinity, maximal drainage and disturbance in some intensively cropped oat hayfields in San Pablo Bay; others exhibit high salinity, poor drainage and little disturbance in diked pickleweed marshes in south San Francisco Bay. Other modifications persisting from past land uses which affect plant community composition include importation of soils or fill (e.g., former airport landing strips, derelict building pads), abandoned berms and ponds of gun clubs, residual effects of past fertilizer applications; industrial waste disposal, and soil contamination.

Relict Halophytic Vegetation - The majority of derelict diked wetlands in central and southern San Francisco Bay are dominated by species native to local tidal salt marshes and brackish marshes, such as *Distichlis spicata* and *Salicornia virginica* (BCDC and Harvey 1983, Madrone Associates et al. 1983). Salt-tolerant glycophyte species have very low physiological nutritional requirements for salt, and flourish in non-saline and subsaline soils (Waisel 1972). They often co-exist with species with little affinity for saline soil, such as *Polypogon monspeliensis* and *Lolium multiflorum* (Harvey 1987, Kaufman and Harvey 1987). *S. virginica* and *D. spicata* have a significant competitive advantage over salt-intolerant plant species when substrate salinities are in the range of halophytes (over 5 ppt soil salinity), and rapidly establish dominance during episodes of high salinity conditions. Some halophytes like *S. virginica* are efficient colonizers of bare wet mud even when salinity is low if seed rain intensity is high. Pioneer halophytes do not necessarily decline in abundance, however, when substrate salinities decline as a result of progressive leaching and drainage of salts. Many apparent diked "salt marshes" are composed of relict vegetation halophyte vegetation which persists in relatively low salinity conditions. This condition is indicated by the presence of a minor to subdominant component of species with relatively low salt-tolerance (e.g., ruderal composites, bedstraws, mustards), growing vigorously among halophytes without indications of salt stress (stunted growth, leaf tip burn, pale leaves) in diked "salt marshes." Examples are sometimes found in abandoned dredge disposal sites (Zentner and Zentner 1995, Huffman and Associates 1996). Some mixed halophyte-glycophyte associations may also occur where stratification of rooting zones occurs in distinct salinity horizons, caused by near-surface leaching of salts and accumulation in deeper portions of the soil profile.

Thus, apparent salt marsh vegetation in diked Baylands may indicate either current high salinity or former high salinity, and does not necessarily indicate sustained high residual salinity. It often represents inertia in plant community structure after relaxation of salinity stress. The term "non-tidal salt marsh" in the context of the San Francisco Bay Estuary should be interpreted narrowly in floristic rather than physiological terms, because dominance of halophytes in the unstable substrate salinity conditions in diked wetlands is an unreliable indicator of current substrate salinity. Some diked salt marshes are truly saline and tend to remain so because of chronically poor drainage or frequent partial dike failures. Others are in gradual succession to other vegetation types. Some diked salt marshes with low residual substrate salinity are subject to rapid conversion to other vegetation types following disturbances (e.g., discing or flooding).

Species Richness and Composition - The species richness and composition of diked marshes is highly variable among sites, and among different marsh types. High salinity and hypersalinity in diked marshes tend to promote low species diversity, selecting for a few tolerant species. Other extreme soil conditions, such as strong acid production and mass release of free iron (often associated with prolonged inundation followed by summer drought) minimize plant species diversity. Truly hypersaline seasonal wetlands in the Bay usually support only sparse *Salicornia virginica*, *Distichlis spicata*, and *Salsola soda*, with a minor component of *Frankenia salina*. Hypersaline seasonal wetlands are now scarce in the Bay Area, mostly scattered around South Bay salt ponds and adjacent lands. A few occur in the North Bay (e.g., parts of Gallinas Creek diked salt marshes, peripheral portions of the Napa salt ponds). Many former hypersaline diked wetlands have been altered by water management for mosquito abatement and wildlife habitat enhancement, and are now muted tidal marshes (e.g., New Chicago Marsh in Alviso, Oro Loma Marsh in Hayward).

Species diversity in nontidal diked brackish and salt marshes is generally much higher than in hypersaline basins, but this does not reflect relatively greater overall diversity of native plant species. Diked brackish to saline nontidal wetlands support a number of common native tidal brackish and salt marsh species (*Salicornia virginica*, *Distichlis spicata*, *Frankenia salina*, *Cuscuta salina*, *Atriplex triangularis*) and sometimes support relatively infrequent native species typical of the natural high tidal marsh and upland ecotone (*Iva axillaris*, *Leymus triticoides*, *Baccharis douglasii*). The native perennial grass *Leymus triticoides*, historically a dominant species of the upper transition zone of tidal salt and brackish marshes, is infrequently found in some diked brackish marshes, particularly where disturbance has been infrequent. A relatively rare historic component of subsaline tidal marsh ecotones, *Centaurium muehlenbergii* is found in diked subsaline wetlands at Cullinan Ranch. It is currently reported known from only one tidal marsh/upland ecotone (China Camp). The sedge *Scirpus maritimus*, a dominant native component of tidal brackish marshes, is often abundant or dominant in brackish to saline ditches or deep, wet depressions in diked marshes ((Madrone Associates et. al. 1983, Mall 1969).

Conversely, diked salt and brackish marshes generally fail to support some important species of corresponding tidal marsh communities; *Spartina foliosa* is excluded from nontidal conditions, and *Jaumea carnosa, Plantago maritima*, *Triglochin* spp. and *Limonium californicum* are absent or very infrequent in nontidal salt marsh; *Grindelia stricta* is generally less abundant in nontidal salt marsh than tidal marsh. Diked salt marshes typically lack rare tidal marsh species (e.g., *Cordylanthus* spp., *Castilleja ambigua, Lasthenia glabrata*, *Lilaeopsis masonii*, *Cirsium hydrophilum*, *Aster lentus*), and also usually lack most infrequent tidal marsh species (e.g., *Pluchea odorata, Senecio hydrophilus*, *Glaux maritima*). The failure of these tidal marsh species in diked conditions is probably due to the relatively greater competition by robust "generalist" species with broad ecological amplitude, and physiological intolerance of extremes of inundation and dryness in diked wetlands. Diked salt and brackish marshes in some cases, however, provide refugia for tidal marsh plants of the high tidal marsh which have become (or in some cases have always been) regionally rare or infrequent in the modern tidal marsh ecosystem, such as *Suaeda moquinii*, *Hemizonia pungens* ssp. *maritima*, *Salicornia subterminalis*, *Downingia pulchella*, *Juncus mexicanus*). As such, they may serve to maintain genetically differentiated salt-tolerant populations of species displaced from modern tidal marshes.

Diked brackish and salt marshes are subject to invasion by many non-native species and species which are not typical of tidal marshes, or are typically restricted to marginal conditions in tidal marshes. Non-native pasture grasses with moderate salinity tolerance, such as *Lolium multiflorum* (and hybrids), *Polypogon monspeliensis*, *Lotus corniculatus* and *Hordeum marinum* ssp. *gussoneanum*, and even *Rumex crispus* are also major components of diked salt and brackish marshes, often locally dominating either depressions (*Polypogon, Hordeum)* or mounds (*Lolium*). Exotic halophytic grasses *Parapholis incurva* and *Hainardia cylindrica* are also locally common in diked salt or brackish marsh. *Cotula coronopifolia* is usually only a minor component of tidal salt and brackish marsh, colonizing depressions and marsh pan edges, but is often a major component of diked brackish marshes, particularly in disturbed or winter-ponded brackish depressions where other vegetation has died back after prolonged deep flooding. Other common herbaceous non-native plant species of diked brackish and saline marshes include *Lepidium latifolium*, *Bassia hyssopifolia*, *Beta vulgaris*, *Salsola kali*, and *Salsola soda*. *Lepidium latifolium* is especially invasive in brackish diked marshes, particularly where the soil has been disturbed, but also in areas of marsh with thin or discontinuous vegetative cover.

Diked subsaline and nonsaline Baylands are very seldom the subject of careful floristic surveys (e.g., Rugt 1991, Madrone Associates 1977); vegetation descriptions usually focus on visually dominant ruderal species, often based on summer survey dates when native annual species are not identifiable (Jones and Stokes 1977, Hudson 1980, Werminski 1973). Consequently, the floristic diversity and affinities of diked subsaline to fresh seasonal wetlands has probably in many (perhaps most) cases been underestimated. Diked subsaline and nonsaline wetlands are mixtures of exotic species of ruderal seasonal wetlands and native species typical of vernal pools and swales. Diked wetlands which are mostly subsaline to nonsaline after years of agricultural drainage support a range of marsh plant associations. These are most common around San Pablo Bay and Suisun Bay, where grazing pasture and oat hayfields have been maintained for many decades in diked former tidal brackish marshes. They may have inclusions of relatively brackish indicator species where soil salinity and acidity are locally elevated (e.g., mixtures of *Atriplex triangularis*, *Polypogon monspeliensis*, *Distichlis spicata*) but are dominated by glycophytic wetland plant species, both native and non-native. Composition of the fresh/subsaline diked wetland flora is influenced by disturbance. Annually disked hayfields support wetland "weeds" which are a mixture of native annuals (e.g., *Plagiobothrys* spp., esp. *P. stipitatus*, *P. leptocladus*), *Juncus bufonius*, *Lilaea scilloides, Callitriche marginata, C. spp. Cicendia quadrangularis*, *Elatine brachysperma*, *Eryngium* spp., *Cressa truxillensis*; locally, *Downingia* spp.; non-native annuals (*Lythrum hyssopifolium*, *Cotula coronopifolia*, *Polygonum aviculare, Hordeum marinum ssp. gussoneanum*, *Polypogon monspeliensis*, *)* and non-native perennials *(Lotus corniculatus*, *Agrostis avenacea*) Grazed pasture land in diked Baylands in San Pablo Bay may also support native annuals found in diked disked hayfields, as well as native perennials (*Eleocharis machrostachya*, *Glyceria* spp. *Juncus effusus*, *J. patens*) and naturalized non-native perennials (*Rumex crispus, R. pulcher*, *Cirsium arvense*, *Lolium multiflorum*). The relative abundance of these species in diked pasture and hayfield wetlands is variable and unstable. Some diked wetlands, after relaxation of intensive agricultural manipulation, develop seasonal wetlands with plant species composition highly similar to that of regional vernal pools and swales (locally dominated by *Downingia* spp., *Eryngium* spp. *Eleocharis macrostachya*, *Callitriche* spp. *Lilaea scilloides*, *Plagiobothrys* spp., etc.)

Reference Sites

Reference sites for different types of diked wetlands would generally not be long-lived because of the prevalence of unstable vegetation conditions in diked Baylands. Droughts, wet years, changes in drainage and pumping, disturbances from agricultural practices, and succession can cause profound changes in vegetation in short periods of time. The following reference sites reflect conditions observed in the mid-late 1990s.

1. Diked non-tidal salt marsh (dominant *Salicornia virginica*)
    - Fremont Airport (King and Lyons site; proposed for phased tidal restoration), Alameda Co.
    - Gallinas Creek diked wetlands, Marin Co.
    - Western Marsh and Central Lowlands, Bahia Site, Novato, Marin Co.
    - Dredge pond 3E, Mare Island, Solano Co.
    - Area H, Redwood Shores, San Mateo Co.
2. Diked non-tidal brackish marsh
    - Cullinan Ranch, Solano Co.
    - Suisun Marsh managed marshes, Solano Co.
    - Huichica Unit, CDFG Napa-Sonoma Marsh, Sonoma Co.
3. Diked subsaline to nonsaline seasonal wetlands
    - Black Point/Renaissance Faire site, Novato, Marin Co. (extirpated 1999)
    - Twin House Ranch Site, Lower Petaluma River, Sonoma Co.
    - Leonard Ranch, North Point, Dixon parcels, Sonoma Co., along Hwy 37

Historic and Modern Distribution

Wetlands of diked Baylands are relatively recent historic artifacts. The plant associations they support are analogous to, but distinct from, wetlands along the margins of historic tidal marshes. Brackish non-tidal marshes somewhat similar to diked brackish marshes probably occurred within alluvial deposits at mouths of small streams which discharged into tidal marshes with locally poor drainage, such as near Ignacio (Novato), where riparian areas converged with dense marsh ponds and few or no tidal creeks. Analogous examples of brackish or subsaline marshes with marginal tidal flooding are found today along Drakes Estero and Tomales Bay, particularly near shallow backbarrier lagoons. Salt marsh with restricted tidal influence probably occurred along portions of the Bay where local sand beach ridges were likely to obstruct tidal flows. One modern example exists at Pinole Point (Whittell Marsh), where the proximal end of a sand spit episodically dams small tidal channels, causing seasonal ponding in a small salt marsh cut off from regular tidal flows. Prehistoric examples of "pocket" nontidal salt marsh probably occurred in the vicinity of Richardson Bay, Alameda, Oakland, and the San Francisco Peninsula, where sand beach ridges occurred.

Seasonal freshwater wetlands (vernal pools and swales, springs) occurred within grasslands peripheral to the Bay, particularly in the Petaluma River valley, on alluvial terraces near Fremont, portions of Richmond and Berkeley, and along much of the Suisun Marsh area. Their distribution and abundance, as suggested by soil surveys, were probably not limited to areas mapped as poorly drained; seasonal freshwater wetlands often occur as local inclusions within soil series in which wetlands are not indicated as prevalent. This is indicated by records of vernal pool endemics in locations like San Francisco, where "vernal pool" soil types are not mapped, but winter pools with typical endemic annuals were found.

The historical abundance and distribution of these wetland types is extremely difficult to quantify in terms of area. Quantitative estimates of historic abundance of seasonal wetlands displaced by urbanization depends heavily on interpretation and assumptions about early soil surveys (which were not intended to function as maps of actual or potential native vegetation), historical accounts, and fragmentary information on species occurrences in old floras. The qualitative differences in natural non-tidal wetland types and their diked Bayland analogues further obscures the relevance of quantitative comparisons between historic losses of natural seasonal wetland plant communities and their partial replacement with wetlands of diked Baylands.

Conservation Issues

Plant conservation needs for diked wetlands are dependent on larger-scale wetland management and restoration plans. Diked wetlands usually support less native plant species diversity than mature tidal marshes at equivalent locations, but may in some cases still provide important plant conservation functions. For example, in San Pablo Bay, agriculture and development have eliminated most historic natural seasonal wetlands in supratidal grasslands peripheral to the Bay. The original vernal pool flora which occurred in subsaline to alkaline depressions around the historic edge of the Bay (as in parts of northeastern Suisun Marsh today) has been largely extirpated in its original location, but persists in artificial equivalent topography and edaphic conditions in some diked seasonal wetlands. These populations maintained in subsaline conditions may provide important founder populations for opportunities to restore vernal pool and swale systems in the original soil types and topography along the margins of the Bay, in coordination with tidal restoration. Similarly, one diked salt marsh in the South Bay (former Fremont Airport) provides refugia for *Suaeda moquinii*, otherwise found around the Bay only in remnant alkali vernal pools adjacent to the Bay at one site (Zentner and Zentner 1996). Partial vernal pool floras have also been generated spontaneously after cessation or relaxation of agricultural manipulation at Montezuma Wetlands (Solano County), Sears Point (Sonoma County), and a construction site in Alviso (Santa Clara County). Most diked wetlands are poorly surveyed, and may act as refugia for many populations of plants of conservation significance.

Diked wetlands are also conservation threats to plant species diversity when they provide outposts, reservoirs, or dispersal corridors for invasive wetland weeds, such as *Lepidium latifolium* and *Salsola soda*. By increasing seed rain pressures on adjacent tidal marshes, or adjacent marsh restoration sites, diked wetlands may also cause degradation of tidal marshes.

Sea level rise makes long-term conservation of diked wetlands problematic. In addition to inherent tendencies of diked systems to suffer levee subsidence and erosion, sea level rise imposes increasing risks of levee failure and tidal flooding. Breached diked wetlands spontaneously revert to tidal wetlands, but usually only as low mudflat or marsh to lower middle marsh after even two decades (e.g., White Slough, Vallejo, Solano County) In addition, some high-sulfur diked marsh soils undergo long-term changes in soil chemistry which make them unsustainable for any valuable natural or artificial vegetation.

Dike maintenance and repair may cause degradation to diked and tidal marsh plant communities by favoring spread and dominance of exotic invasive marsh plant species. Dike maintenance practices currently lack any elements which facilitate recolonization by native species.

Restoration of diked marshes is somewhat self-contradictory, since true restoration would entail conversion to the original tidal marsh condition. However, diked wetlands can be significantly enhanced as non-tidal marshes by reducing or eliminating adverse land use practices. Reduction of intensive drainage efforts and elimination of high-frequency disking can enable diked fresh/subsaline wetland plant communities to mature and accumulate greater native species. Pasture management that tolerates some winter inundation in depressions, for example, is more compatible with native wetland plant species diversity than oat crop management.

Conclusions and Recommendations

Diked wetlands considered for conversion to other marsh types, such as tidal wetlands, should be studied individually for site-specific floristic values, particularly for potential functions as refugia for species displaced from historic seasonal wetlands and tidal marsh ecotones. Diked wetlands should not be assumed to have uniformly low native wetland plant species diversity or "ruderal" status. In areas where restoration of seasonal fresh wetland systems (e.g., vernal pools, alkali basins, alluvial *Juncus*/*Scirpus* marsh, etc.) is precluded by development, some diked wetlands should be considered for modification and management to maintain regionally scarce plant communities. Generally, however, priority should be assigned to restore peripheral estuarine plant communities in their proper original soils and topographic position. Where diked wetlands support regionally rare plant populations, they should be given interim conservation priority until suitable population restoration sites are established in more natural or restored habitats. Existing diked marshes should be managed to minimize impacts of exotic invasive plants on adjacent managed or natural tidal marshes. Dike maintenance should include best management practices which favor recolonization of disturbed dike surfaces by native vegetation and suppress re-invasion by exotic species.

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Plants of San Francisco Bay Salt Ponds

Peter R. Baye

Introduction

The term "salt pond," as treated in this discussion, includes both natural and artificial large-scale persistent hypersaline ponds that are intermittently flooded with Bay water, and which occur within tidal salt marsh systems of San Francisco Bay and San Pablo Bay. Historic natural salt ponds were characterized by persistent thick accumulation of salt inundated with concentrated seawater brines. They were restricted to a relatively narrow reach of San Francisco Bay near San Lorenzo Creek. They are distinguished here from related salt marsh features such as pans and which occur at smaller spatial scales, have distinctive physiographic traits, and lack strong persistent (perennial) brines and precipitated crystaline salt deposits. Artificial salt ponds (solar salterns) are diked salt marshes which are managed for the production of concentrated brine and fractional crystallization of sea salts. Natural and artificial salt ponds are presumed to share the same narrowly adapted hypersaline biota.

Information on modern artificially engineered salt pond systems is derived principally from the biological literature on solar salterns and hypersaline environments (Javor 1989, and references within), historic documentation on the salt industry in California from the State Division of Mines (Ver Planck 1958, 1951; Dobkin and Anderson 1994) and regional documentation produced by the local salt industry and government regulatory agencies (Corps of Engineers, San Francisco District, Regulatory Branch permit and compliance files; Office of Counsel files, and references within). Information on historic salt pond systems is limited to descriptive historic accounts and descriptions, detailed topographic maps of natural salt ponds prior to extensive dike construction (U.S. Coast Survey T-charts, 1956), and field investigations by the author comparing modern salt pans, marsh ponds, and artificial salt ponds.

Environmental Setting

Salt ponds are large, shallow, hypersaline impoundments or depressions in tidal salt marsh systems which undergo a sequence of infrequent flooding with saline or brackish Bay water, evaporative concentration, and formation of strong hypersaline brines and deposits of gypsum, calcium carbonate, and crystalline salt (halite; sodium chloride).

Historic salt ponds were mapped with a high degree of resolution in the 1856 U.S. Coast Survey. They were nested within particular portions of the salt marshes along the Alameda shoreline in the vicinity of San Lorenzo Creek and Mount Eden Slough. This reach of salt marsh was distinguished by a relatively straight-edge erosional marsh shoreline, little tidal drainage at the edge of the mudflats, and evidence of drowned marsh topography (mapped as emergent sinuous tidal creek levees). The upland edge was an extensive alluvial lowland, presumably with significant subsurface groundwater discharge. No major freshwater creeks were directly associated with the salt ponds. Atwater et al. (1979) suggested that natural estuarine beach ridges along outer marsh edge were responsible for the impoundments of salt marsh that created salt ponds near San Lorenzo. Some salt ponds at the northern end of the local San Lorenzo distribution were certainly associated with well-defined barrier sand spits (U.S. Coast Survey T-charts, 1850s), which were probably nourished by sand eroded from submerged Merritt sand deposits (Pleistocene marine beach and dune). Less well-defined transgressive berms of sand and coarse organic detritus may have been deposited on top of the erosional marsh edge south of the sand spits themselves. Similar transgressive beach-marsh berms today act as dams enclosing freshwater to brackish ponds and marshes in Drake's Estero, Point Reyes and at one location in San Francisco Bay (Whittell Marsh, Point Pinole, Contra Costa County). U.S. Coast Survey T-charts also indicate numerous sandy barrier beaches which dammed (either permanently or intermittently) lagoons. The impoundment of Crystal Salt Pond by a wave-constructed swash bar or beach ridge would distinguish it morphologically, hydrologically, and topographically from more common salt marsh ponds (pans) which occurred as depressions, sometimes extensive, between tidal creeks. These were widely distributed in salt marshes in the South Bay. Extensive, elongate pans also occurred near and below the upland borders of salt marshes; these have been termed "transitional" pans, although their position and form do not necessarily indicate a gradual ecotonal relationship with alluvial or upland habitats.

Salt ponds today (solar salterns) are artificially managed and engineered diked Baylands converted from tidal salt marsh. The first artificial salt ponds began as extensions and improvements of natural salt ponds which occurred near Hayward (Crystal Salt Pond), but most of the contemporary man-made salt pond system is established in former tidal marsh that included few or no perennial hypersaline ponds. Artificial salt ponds have entirely displaced their natural forerunners; no natural true salt-crystallizing ponds remain in San Francisco Bay today, although related smaller salt pans and marsh ponds containing weak brines in summer and fall do occur.

Classification of Salt Ponds - Javor (1989) placed marine-derived hypersaline aquatic environments in four ecological salinity classes:

The first salinity class (*ca*. 60 - 100 ppt) contains a highly diverse, productive biota dominated by marine species. This class would correspond to "low salinity" ponds (a misnomer, since salinity exceeds seawater concentration), from intake ponds to the next one or two stages that support abundant macroalgae and fish.

The second class (*ca*. 100 - 140 ppt) is dominated by specially adapted halophilic species which are related to freshwater taxa, not marine taxa. The organisms include abundant cyanobacteria, unicellular green algae, brine shrimp, and various halobacteria.

The third class (*ca*. 140 - 300 ppt) is distinguished by marked reduction of species diversity (loss of cyanobacteria, most invertebrates other than brine shrimp), and dominance of *Dunaliella* and brine shrimp.

The fourth class (300 ppt to salt saturation, near 360 ppt) contains only *Dunaliella* and bacteria at low productivity.

The first class predominates in modern marsh ponds. The historic natural salt pond complex probably varied seasonally between Javor's second to fourth hypersaline classes. Other natural marsh pans were most likely predominantly in the first class only, becoming seasonally hypersaline, and supporting relatively weak brines and macroalgal cover. Natural historic salt ponds were distinguished from other types of inundated depressions in salt marshes by the persistent thick halite deposits, indicating perennial hypersaline conditions, and their large lake-like size. In these aspects, they differ from shallow marsh ponds and marsh pans, which are regularly flooded during higher spring tides, and either remain persistently ponded or develop thick algal mats which desiccate in summer (bleaching white in the sun, resembling salt deposits in aerial photographs), or only develop thin, temporary salt films on unvegetated mud and peat.

Various marsh pan features are represented in U.S. Coast Survey maps of the mid-19th century, but only a few have persisted in modern rare remnant tidal marshes, such as Petaluma Marsh, Rush Ranch and Hill Slough (Solano County). Elongate marsh ponds are evident along the upland edge of historic marshes, particularly in eastern and southern parts of San Francisco Bay. Some of these may have been influenced by surface runoff and groundwater seepage from adjacent alluvial uplands, and could have been less saline than other marsh depressions most of the year. Some historic elongate marsh edge pans may also have been the unvegetated upper intertidal surface of alluvial fans and terraces, consistent with small modern "transitional pans" observed at Hill Slough, Solano County. These also lack brine and halite development. Modern elongate marsh pans have formed in recently (100 year) prograded marshes adjacent to Mare Island dredge ponds. These ponds are about 0.3 m deep in winter and spring, and range from brackish (nearly fresh) in winter to hypersaline when ponded areas are highly reduced in summer, but no significant halite precipitation is evident in them. These and similar pans may appear white with sun-bleached dried algal mats, which resemble salt flats. High densities of true natural marsh ponds, also termed "drainage divide ponds" (owing to their position in poorly drained marsh areas between tidal creeks), also occur in the Petaluma Marsh. Marsh ponds are a variation of salt pans which are topographic depressions flooded by spring tides, and support submergent vegetation, typically macroalgae (such as *Enteromorpha* spp.) and beds of widgeon-grass (*Ruppia maritima*), indicating brackish to near-marine salinity. The beds of marsh ponds are usually a soft organic oil-like black muck composed of decayed, waterlogged organic matter.

In contrast with salt ponds in estuaries with strong marine influence, such as San Diego Bay, San Francisco Bay salt ponds are relatively nutrient-rich and sustain high primary productivity (Javor 1989). Nutrient-poor salt pond conditions promote microbial mats, while planktonic microalgae tend to dominate nutrient-rich salt pond systems (Javor 1989). Most salt ponds in San Francisco Bay support richly pigmented and somewhat turbid organic "soups" of *Dunaliella*, halobacteria, cyanobacteria, dissolved organics and organic particulates and, often in ponds between approximately 120 - 200 ppt salinity, large "blooms" of brine shrimp which graze primarily on *Dunaliella*.

Historic natural salt ponds were unlike modern artificial salt ponds in that they were not differentiated geographically into stable hypersaline classes, but varied only seasonally in salinity. Natural salt ponds went through a seasonal "intake" phase during extreme high spring tides (December-January and June-July), when Bay water flooded them and diluted them with brackish to saline Bay water, seldom exceeding 20 ppt, and typically between 2 - 10 ppt in winter. During summer-fall evaporation periods, brines formed *in situ*, ranging in salinity over time up to crystallization (saturation) near 360 ppt. In contrast, the modern engineered salt pond system is based on timed transfers of brines between ponds, resulting in spatial separation of brines at different stages of concentration, and fractional crystallization of various seawater salts (other than sodium chloride, halite), such as magnesium and potassium salts (bitterns), gypsum (calcium sulfate) and lime (calcium chloride) in different ponds. In this system, crystallization is restricted to relatively few ponds engineered to facilitate harvest of halite deposits, and relatively stable hypersalinity regimes are established for individual evaporator ponds in the system (Ver Planck 1958).

The sequential and spatial separation of brines in artificial salt pond systems also produces salt pond "types" which are not fully analogous to natural systems. The late stages of brine production near sodium chloride crystallization produce strong non-sodium brines called "bittern." Bittern brines (or bittern) are a concentrated solution of sodium chloride, magnesium chloride and sulfate, and potassium chloride and sulfate. The ionic balance of highly concentrated bittern is toxic even to bacteria, and saturated bittern is considered sterile (Javor 1989). During winter rains, dilute bittern stratifies on top of the concentrated bittern, and brine shrimp may appear seasonally, indicating algal production (Jim Swanson, Rick Coleman, pers. comm.). Natural salt pond brines did include bittern salts; in fact, the "low quality" of early California solar salt was due to bittern, and the modern solar saltern system is principally devised as a method to fractionate sodium and bittern salts. Crystallizer ponds, which are used to precipitate halite, are also maintained near the limits of halotolerance of *Dunaliella* (which can nonetheless fix carbon up to salt saturation; Javor 1989), but undergo seasonal dilution during winter rains.

Salt Pond Plant Community

Salt ponds support a distinctive and highly specialized halotolerant to halophilic biota consisting of microalgae, photosynthetic bacteria, and invertebrates, but no vascular plants (except along the edges of artificial salt pond levees). The dominant photosynthetic organisms of most hypersaline San Francisco Bay salt ponds are a single-celled green algal species, *Dunaliella salina* (Chlorophycophyta) and numerous species of blue-green bacteria (Cyanobacteria), halobacteria, and purple sulfur-reducing bacteria. The proportions of these organisms vary with salinity. Artificial eutrophic salt ponds with salinities closer to marine concentrations (near 35 ppt; "intake ponds") are dominated by marine macroalgae such as sea-lettuce (*Ulva* spp.), *Enteromorpha* spp., *Cladophora* spp., and also sometimes support *Fucus* spp. and *Codium* spp. where substrate is stable and firm. They also include marine diatoms, dinoflagellates, and cryptomonads. There are no detailed studies of the species diversity, distribution or geographic variation of the halophilic microflora communities of San Francisco Bay.

Managed and engineered contemporary salt ponds are ecologically similar in many respects to their natural precursor salt ponds, and presumably share the same algal and bacterial microflora.

Indicator Species - There are no detailed classifications or analytic studies of salt pond algal communities. Following Javor's (1989) classification of hypersaline environments (see Classification of Salt Ponds, above), two broad hypersaline algal communities may be identified: communities dominated by free-floating marine macroalgae typical of upper tidepools near marine salinities to low-hypersaline conditions, corresponding to intake ponds and young brines in a saltern series (e.g., *Ulva* spp., *Enteromorpha* spp., *Cladophora* spp.; also bottom-mat forming cyanobacterial colonies); and communities dominated by motile unicellular halophilic phytoplankton (principally *Dunaliella salina*), which characterize moderate to high hypersaline conditions. Macroalgal salt pond communities also correspond with fish-dominated animal communities, while phytoplankton-dominated brines are associated with brine shrimp abundance.


Bob Walker

Modern salt ponds are artificially managed and engineered diked baylands converted from tidal salt marsh. (South San Francisco Bay)

Dunaliella spp. is ubiquitous in salt ponds in San Francisco Bay. It is reported to survive, and can be photosynthetically active, in brines which are close to saturated (near 350 ppt), but may be absent in some extremely concentrated brines and bittern (potash-phase, or potassium-magnesium) brines (Javor 1989, Brock 1975). Its optimum salinity for growth is near 120 ppt, about four times the concentration of seawater. *Dunaliella salina* concentrates carotenoid and other pigments in response to various forms of physiological stress, including salinity. It can be used as a crude color-indicator of brine salinity: cells growing in 50-100 ppt are greenish, and turn yellowish-green in 150 ppt brine. Reddish hues occur in brines 200-250 ppt (Javor 1989). Purplish-red hues in brines over 200 ppt may be contributed by halophilic bacteria. A conspicuous mosaic of salt pond hues are readily visible from aerial views of San Francisco Bay, particularly in summer and fall. *Dunaliella* osmoregulates in hypersaline brines by concentrating glycerol as a compatible osmotic solute in its cytoplasm (Javor 1989).

Reference sites

There are currently no reference sites in the San Francisco Bay Estuary for true natural salt ponds (ponds which periodically or chronically produce crystalline salt deposits). The historic salt pond system near San Lorenzo Creek in Alameda was eliminated by diking in the 1850s and 1860s. All modern salt pans and marsh ponds in the Bay Area differ from these historic salt ponds. Most existing marsh ponds are only slightly hypersaline, or briefly hypersaline in late summer, and support algal mats rather than brines and halite beds. Most existing salt pans within small modern Bay Area salt marshes are comparatively small and produce sparse and thin (few mm) salt crusts in summer and fall. In contrast, reference sites for artificial salt ponds are abundant. Examples of (relatively) low salinity intake ponds, which are saline or slightly hypersaline, are found at Pond B1/B2 in Mountain View, Pond 1 near Mowry Slough, and Pond A9 in Alviso. Examples of intermediate hypersaline ponds (known as concentrators or evaporators) are found in ponds A10-14 in Alviso, ponds 2-8 near Coyote Hills, and ponds 2-6 between Mowry Slough and Coyote Creek. High hypersaline ponds (strong brines approaching or reaching salt saturation, "pickle") are found in extensive crystallizer beds near Newark and Redwood City, ponds 10 and 26 near Newark, and periodically in drained evaporators before they are re-filled.

Modern salt marsh (and brackish marsh) pans may be found in few remnant pre-historic tidal marshes at Petaluma Marsh (abundant), China Camp (scarce) and Point Pinole (Whittell Marsh; scarce). Pans vary in topography. Some upper marsh pans are similar to patches of salt flats, while pans in middle marsh zone depressions are normally shallow ponds 10-20 cm deep. Pans which become ponded, either because of depressional topography or marsh surface drainage barriers, develop algae or widgeon-grass. Salt marsh pans also occur in historically accreted marshes at Mowry Marsh. Elongate marsh pans fringing uplands ("transitional" pans) have also formed in the relatively young (20th century) salt marsh at Emeryville Crescent and adjacent to Mare Island dredge ponds. Elongate but diffuse shore-parallel marsh pans, perhaps best regarded as incipient pans, are found along the east end of the fringing salt marsh at Highway 37. Small but well-differentiated semi-circular to semi-linear salt marsh pans occur in peaty coastal salt marshes at Limatour Spit, Point Reyes; Bolinas Lagoon; Morro Bay; Elkhorn Slough; and along Tomales Bay. Morro Bay, Bodega Bay, and Bolinas Lagoon also have elongate shallow salt marsh pans fringing alluvial deposits. Most of these salt marsh pans are brackish in winter and spring, but become moderately hypersaline (usually 40-60 ppt, rarely > 90 ppt) in summer (Baye, unpub. data) when inundated.

Historic and Modern Distribution

The historic (pre-1860) location of natural salt ponds within San Francisco Bay was probably restricted to the Alameda shoreline in the vicinity of San Lorenzo Creek (between the historic Thompsons's Landing and Union City Creek). This area included an extensive complex of both connected and isolated large ponds in a matrix of salt marsh. The complex was labelled as "Crystal Salt Pond" on the 1856 U.S. Coast Survey T-chart of the area. The San Francisco Estuary Institute estimates the acreage of Crystal Salt Pond to be approximately 1660 acres, based on the precise pond outline represented on the 1856 T-chart (R. Grossinger, personal communication). If, however, the pond size fluctuated seasonally (as expected from winter rainfall and tidal flooding), the ponded area may have been several thousand acres from late fall to spring. Two smaller ponds with similar configuration occurred north of San Lorenzo Creek, and were clearly associated with sandy barrier beach deposits at the bayward edge of the marsh. (It is not clear whether these northern satellite ponds produced high concentration brine and halite, or were merely intermittently hypersaline lagoons). Crystal salt pond was used as a salt source by aboriginal inhabitants of the Alameda shoreline, and was exploited by early Mexican, Spanish and U.S. settlers (Ver Planck 1951, 1958). Early descriptions of Crystal Salt Pond indicate that it contained a persistent crust of crystalline salt up to eight inches thick, and the brines and salt contained "impurities" of concentrated non-sodium salts ("bittern" salts, principally magnesium chloride and sulfate; Ver Planck 1958).

The natural halite deposits of Crystal Salt Pond were exhausted rapidly by the infant salt collecting industry; by 1860 they were largely depleted. Artificial enhancement of solar evaporation of brines was initiated around 1853, when salt harvesters (farmers who used salt for tanning leather and curing meats, and expanded into the salt industry) began manual construction of low berms around natural salt ponds to enhance their capacity to retain saline floodwaters and capture and precipitate their salt loads. These artificially enhanced natural salt ponds became the nucleus of the solar salt industry.

By the end of the 19th century, the salt ponds of San Francisco Bay were still confined to the northern portion of the Alameda shoreline, from San Leandro Creek to Alvarado (Union City). They did not comprise a salt pond "system," but were an aggregation of many independently owned and operated enterprises. Extensive conversion of salt marsh to salt ponds in south San Francisco Bay did not occur until the 20th century. This was facilitated by the consolidation of almost all the independent salt operations to a few (dominated by Leslie Salt Company) in the 1930s. Permit requests to the Corps of Engineers to dam numerous sloughs and marshes in the South Bay were not filed until the early 1920s. Actual levee construction would have taken at least several years, and new ponds take about 5 - 7 years to "seal" (become impermeable after gypsum and carbonate precipitation; Ver Planck 1958, Dobkin and Anderson 1994); therefore, the 1920s ponds were probably not fully functional salterns until around 1930. The last extensive marshes in the Alviso and Sunnyvale areas were not diked for conversion to salt ponds until the early 1950s (Pacific Aerial Photo archives). Bair Island was not converted to salt pond until the 1950s, although it had previously been diked for agricultural use. The modern extent of salt ponds in the southern reaches of South Bay, therefore, is relatively recent compared with the northern Alameda salt ponds. The Napa salt ponds are even more recent: the diked Baylands of the Napa marshes were converted from derelict agriculture (seasonal subsaline to brackish wetlands) to salt ponds between 1953 and 1959. Salt production ceased there in the mid-1990s, but most of the system remains hypersaline.

Relative change - The minimum acreage of true natural salt pond in San Francisco Bay was less than 2,000 acres (SFEI 1998); the maximum acreage (assuming seasonal expansion of Crystal Salt Pond by flooding, and assuming that northern satellite ponds were brine/halite ponds) could have been on the order of 3,000 - 4,000 acres. Other marsh pan habitats were not likely to support persistent hypersaline algal communities and were presumably dominated by marine-related macroalgae or *Ruppia*, as are most salt marsh pans today. However, if a significant proportion of the historic extensive elongate lake-size marsh ponds fringing uplands (Redwood City to Palo Alto, and in the Newark vicinity) were seasonally or perennially hypersaline, the total acreage of salt pond habitat could have been on the order of 5,000 - 10,000 acres. There is very weak indication that elongate upland-fringing salt marsh pans ever contained persistent strong brines supporting the narrow hypersaline algal/bacterial community, however. Today, approximately 9,500 acres of derelict salt ponds remain in San Pablo Bay, and over 29,000 acres of artificial salt pond are actively maintained in San Francisco Bay.

Conservation Issues

Exotic Species - Salt pond microbial taxa are widespread geographically, but narrowly distributed ecologically. They are probably subject to dispersal by waterfowl and marine transport. There are no currently recognized exotic species "threats" to salt ponds as there are with vascular plants in salt marshes.

Restoration - The crude technology for creating artificial salt ponds (levee construction, wind-driven pumps, tidegates) has been well developed for over a century. There is little doubt that complete artificial salt pond systems can be created and maintained at a wide range of sizes, from as little as 20 - 50 acre historic "family size" or one-man operations (Ver Planck 1958), to the modern systems in the tens of thousands of acres. Low-salinity "intake" ponds can also be maintained independently, in the absence of a salt-producing system, by balancing influx of Bay water, residence time and redischarge at near-marine salinity. No new salt ponds have been constructed since the 1950s, although ponds have been interconverted from one type to another since then (evaporator ponds to bittern disposal/"storage"). Small and autonomous salt pond systems could be modified to be less "productive" of salt, and more biologically "productive," by reducing the efficiency of brine and salt production. This could be achieved by increasing the flux in intake ponds, and reducing the residence time of brines in each pond transfer. In winter, when brines are diluted by rainwater, they could also be re-mixed with intake Bay water and redischarged to the Bay at near-marine salinities.

There have been recent tidal marsh restoration designs for artificial but naturalistic ponds and pans, but no marsh restoration designs have included equivalents of salt ponds. In principle, naturalistic salt ponds could be artificially created and naturally maintained by replicating the hypothetical historic conditions of Crystal Salt Pond (as inferred by Atwater 1979). This would entail deposition of coarse sediments (sand or shell hash) at the edge of a high-energy marsh shoreline, to be reworked as beach ridges which restrict marsh drainage. In theory, beach ridges would maintain form and size as they retreat with the eroding marsh edge, given ample sediment supply and overwash processes. Under less natural geomorphic settings for salt ponds, artificial naturalistic salt ponds could be created by constructing low, broad berms made of bay mud or sand that would be set at elevations enabling highest spring tides to overtop them. Low, wide berms would be less prone to gullying and breaching than steep levees, but would require some degree of maintenance. Maintenance would be minimized by setting salt pond levees within restored marshes which would shelter them from wave erosion of the open Bay. Restored naturalistic salt ponds would undergo extreme variation of salinity within and between years, depending on rainfall variation, evaporation conditions, and storm surges.

Sea Level Change and Levee Maintenance - The modern salt pond levee system requires periodic maintenance, and levees bordering the open Bay (not sheltered by fringing salt marsh) require frequent maintenance, armoring, or both. The need for levee maintenance (topping with fresh dredged sediment) is likely to become more frequent if storm frequency increases or sea level rises, as would be expected with global warming (Moffatt and Nichol and WRA 1988). Borrow pits along the interior side of salt pond levees become depleted over time, and some old borrow ditches have been widened so much that dredges need to re-handle material to bring it within reach of levees. Dredging tidal marshes as an alternative source of sediment is unlikely, since it causes conflicts with endangered species habitat. Therefore, sea level rise is likely to cause long-term increases in costs and risk of levee failure of the existing salt pond system. Sea level rise could also make naturalistic salt pond restoration more difficult, since beach ridges or low levees are more likely to breach and allow excessive (though restricted) tidal exchange to impounded areas.

Conclusions and Recommendations

The commercial salt pond operations of San Francisco Bay are unlikely to continue indefinitely because of economic changes in the Bay region and in the salt industry, and due to physical changes in the levee and borrow ditch system. Salt ponds are not likely to regenerate spontaneously as a result of natural geomorphic processes when salt marshes are restored. Other more common types of pans and ponds are unlikely to establish in young salt marshes; they are mature marsh features, associated with well-differentiated marsh topography. The environmental setting associated with salt ponds has been radically altered; the combination of steep and relatively high-energy Bay shorelines, coarse sediment supply, and extensive high salt marsh with impeded tidal drainage no longer exists. It is also likely that the feasibility of maintaining the erosion-prone levee system of the artificial salt ponds will decrease over time, as borrow ditches (sources of mud for levee repair) are depleted. Therefore, new and artificial measures will be required to conserve at least historic amounts of salt pond habitats within the Estuary in the long term. The highest priority setting for salt pond restoration of some type would be on the Alameda County shoreline, from approximately San Leandro to the Dumbarton Bridge, where the Bay shoreline profile and wave fetch may be conducive for formation of beach ridges (marsh berms), given appropriate sediment size and supply.

There is no minimal ecosystem size for salt ponds. The basic grazer food chain between *Dunaliella* and *Artemia* can be maintained in extremely small systems. However, the full microbial diversity of San Francisco Bay salt ponds, which has not been analyzed in detail, would probably not persist in small ponds. Also, since the stability of natural salt ponds is inherently low (subject to ordinary natural fluctuations as well as catastrophic changes), microbial diversity would be better conserved with a large system of semi-independent salt ponds. Pre-historic salt pond acreage was probably on the order of 2,000 acres. Aiming at this minimal acreage, in the absence of any experience at restoration of naturalistic salt ponds or "alternative" management of solar salterns, would probably be insufficient to conserve a diverse halophilic microflora.

We therefore recommend that long-term conservation of salt ponds entail the following actions:

1. Pilot projects should be undertaken that incorporate naturalistic salt pond designs as integral components of large-scale tidal marsh restoration on the northern Alameda shoreline;
2. Some existing salt ponds should be divided into smaller, autonomous units away from the open bay, preferably nested in the landward reaches of restored salt marsh areas, and managed to maintain intermediate strength brines rather than salt production;
3. Salt pond restoration and alternative management should aim for temporally variable as well as spatially variable salinity and brine depths;
4. Both artificial and naturalistic salt pond restoration should aim for designs which minimize maintenance requirements; and
5. An initial target acreage for salt ponds should reflect the uncertainty of restoring sustainable salt pond environments after commercial salt production ceases. We suggest that an initial target of approximately 10,000 acres (equivalent to late 19th century acreage) be stipulated and modified based on the results of salt pond restoration and alternative pond management.

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Plant Communities Ecotonal to the Baylands

Glen Holstein

Introduction

The San Francisco Bay estuary wetlands ecosystem historically included vegetated and non-vegetated areas. Dominant among physical factors influencing estuarine vegetation was the semi-diurnal tidal cycle. As a consequence, vegetation exposed to tides differed dramatically from plant communities that existed above the tides. For non-estuarine vegetation diurnal factors were relatively insignificant; annual climate cycles and non-cyclic geological factors were the dominant influences. Substrates in vegetated parts of the Estuary consisted almost entirely of Bay mud (Louderback 1951, Wahrhaftig et al. 1993). Beyond it they were much more heterogenous.

Environmental Setting

Vegetation increases in structural diversity and species richness beyond the estuarine ecosystem boundary in a complex pattern caused by interactions between the physical factors of climate, geology, and hydrology.

Climate - The San Francisco Bay Area, like all the California Floristic Province (Hickman 1993), has a climate characterized by wet winters and dry summers. Such climates are called "Mediterranean" because similar climatic conditions occur in the Mediterranean Basin, but the San Francisco Bay Area's Mediterranean climate is more extreme than much of its namesake since it rarely receives any significant rainfall during the years's warmest five months (Wernstedt 1972). Despite ample water, plant growth is retarded in winter by low temperatures and short days. Growth is maximal in spring when temperature and day length significantly increase and reserves of soil water from winter rains are still abundant (Walter 1979).

The diversity of the San Francisco Bay Area climate is explained, to a great extent, by variation in two factors; winter precipitation and summer marine air flow. Both cause local climates to be relatively mesic, but their maxima rarely coincide and do not identically affect vegetation. High winter precipitation makes abundant soil moisture reserves available for rapid spring and early summer plant growth where low temperatures and fog brought by marine air flow do not limit it. Since rapid plant growth increases biomass, high biomass vegetation types like redwood and mixed evergreen forests are frequently dominant in the Bay Area where rainfall is highest. A popular myth contends redwoods (*Seqouoia sempervirens*) require summer fog. What they actually require (and are limited to) are places with high precipitation that are protected from summer marine air flow and fog. By leaching mineral nutrients from surface soils, high rainfall also retards growth of herbaceous vegetation that could otherwise compete with forest tree seedlings (Holstein 1984a).

Bay Area mean annual precipitation varies from 13 inches at San Jose and Antioch to 47 inches at Kentfield in Marin County (Felton 1965). Not surprisingly, relatively undisturbed upland vegetation consists of redwood and mixed evergreen forests near Kentfield (Shuford 1993) and of grassland near Antioch and San Jose (Critchfield 1971). The Bay Area receives its precipitation from cyclonic storms with predominantly southwest winds arriving from the Pacific Ocean. Consequently stations with large mountains to the southwest lie in rain shadows with reduced precipitation. Antioch, for example, is in the lee of Mount Diablo, and San Jose is in the lee of the Santa Cruz Mountains. Kentfield, paradoxically, is also in the lee of a mountain, Mt. Tamalpais, but is close enough to receive an increase in rainfall caused by its orographic lifting. In most of the bay area, however, mean annual rainfall is between 15 and 25 inches (Gilliam 1962). Within this range, vegetation is controlled more by geologic substrate and slope exposure than relatively minor local differences in mean annual rainfall (Critchfield 1971).

In the San Francisco Bay Area, fog and associated marine air chilled by offshore upwelling reduce summer evapotranspiration and cause local climates to be mesic, where summer marine air flow is strongest and fogs most frequent. Such conditions reduce plant growth and resultant biomass, however, since they limit light and warmth. High biomass forest vegetation also seldom occurs in areas directly exposed to salt-laden winds associated with marine air flow (Holstein 1984a).

Summer water stress causes incomplete cover and much bare ground in most Mediterranean climate vegetation. In parts of the San Francisco Bay Area, however, marine air flow and fog mitigate summer drought sufficiently for occurrence of vegetation types like coastal scrub and prairie characterized by very complete cover and little bare ground despite relatively low biomass (Holstein 1984a).

Summer marine air flow and fog arrive at the Pacific Coast predominantly from the northwest because of anticyclonic origins, but a shallow semi-permanent temperature inversion confines their movement into and through the San Francisco Bay estuary to just a few low altitude gaps in the Coast Range. By far, the most important of these is the Golden Gate (Gilliam 1962).

Since marine air flow and fog suppress summer temperatures, mean July temperature is a reliable indicator of their relative presence or absence in the San Francisco Bay Area. Not surprisingly, San Francisco's July mean of 58.8°F is the lowest around the Estuary because of its location at the Golden Gate. Antioch's July mean of 74.0°F is the highest of any Estuary station since the low hills of northern Contra Costa County protect it from marine air flowing into the Central Valley through the Carquinez Strait. Fairfield's July mean of 72.1°F indicates more direct exposure to that air flow despite its more inland location. Mount Diablo State Park's entrance station has a July mean of 74.3°F because of its location above the inversion that limits marine air to low elevations. Most Estuary stations have July means in the sixties, but a difference of just a few degrees within that range can profoundly effect summer climate. Berkeley (61.5°F), Richmond (62.0°F), and Oakland (62.4°F) have the lowest summer temperatures in the Estuary next to San Francisco because of their location directly east of the Golden Gate. Burlingame (62.3°F) and the San Francisco Airport (62.7°F) are also relatively low because of their location at the east end of the San Bruno coast range gap (Gilliam 1962). Kentfield (65.9°F), in contrast, is relatively warm in July because Mount Tamalpais protects it from summer fog as well as inducing its high winter rainfall. Distance from the Pacific Coast is generally a poor predictor of summer marine air flow. Redwood City (67.9°F) on the west side of the Bay, for example, is warmer than Newark (64.9°F) on the east side since the latter is more directly exposed to air flow through the Golden Gate (Felton 1965, Gilliam 1962). Coastal scrub and coastal prairie, the vegetation types most associated with summer fog, are common on the outer Pacific Coast but relatively scarce in the San Francisco Bay Estuary because the parts of it most exposed to summer fog were also those settled earliest and urbanized most completely (Hoover et al. 1966, Donley et al. 1979).

Geology - Holocene alluvium characterized by abundant clay and level topography surrounds slightly over half the Estuary and is consequently the most abundant geologic substrate beneath its adjacent non-tidal vegetation (Jennings 1977, Wahrhaftig et al. 1993). Bay Area uplands underlain by alluvium were farmed early and are now largely urbanized, but historic accounts and relict stands indicate open grassland was their overwhelmingly dominant vegetation type before settlement (Bryant 1848, McKelvey 1955). An exception was a few oak savannas where widely spaced valley oaks (*Quercus lobata*) occurred in a grassland matrix. Such savannas were most frequent around the northern part of the Estuary where rainfall was relatively high, but even there they were most frequent in areas protected from summer marine air flow.

A specialized feature of California Holocene and older alluvium with level topography is vernal pools, small closed basins that fill in winter and dry during spring. They support a characteristic specialized flora rich in annual forbs (Holland and Jain 1977). Vernal pools were long thought to result from gopher activity (Dalquest and Scheffer 1942), but are better explained as microtopographic patterns arising from ground shaking during earthquakes (Berg 1990) or interaction of localized soil processes and wind erosion (Abbott 1984).

Non-alluvial uplands around the Estuary consist of uplifted hills underlain by a variety of pre-Holocene sedimentary and volcanic rocks. These include the Mesozoic Franciscan formation and Great Valley Beds; Cenozoic sediments consisting of Paleocene, Eocene, Miocene, Pliocene, and Pleistocene marine beds and Pliocene nonmarine deposits; and the Pliocene Sonoma volcanic deposits (Jennings 1977, Norris and Webb 1990). The influence of these rocks on vegetation is most frequently controlled by their clay content. Those with abundant clay like Paleocene, Eocene, Miocene, and Pliocene sediments weather to deep soils much like those on Holocene alluvium and predominantly support similar grassland vegetation. The Mesozoic deposits include areas where clay is abundant and others where it is scarce. As on other clay-rich substrates, deep soils and grasslands dominate the former in contrast to the thin soils and woody vegetation types predominant where clay is scarce. The Franciscan Formation, a melange of soft clay sediments and hard metamorphic rocks, has a particularly complex vegetation pattern since grass dominates the former and trees the latter. Pleistocene marine beds and the Sonoma volcanics are relatively clay poor and consequently largely support woody vegetation types like oak woodland and mixed evergreen forest (Ellen and Wentworth 1995, Critchfield 1971).

Grass is dominant on clay soils because they have a relatively high water holding capacity (Walter 1979). West of Cordelia in Solano County, for example, Dibble-Los Osos and Hambright loams occur on adjacent hills in the same climate. Dibble-Los Osos soils develop on clay-rich Eocene marine sediments and consequently have B2t horizons containing accumulated clay and a water-holding capacity of 5 to 7 inches. Hambright soils, in contrast, develop on Sonoma volcanics, lack a B2t horizon, and have a water holding capacity of only 2 to 3.5 inches (Bates 1977). Despite identical precipitation, Dibble-Los Osos soils support grassland and Hambright soils support oak woodland dominated by coast live oak (*Quercus agrifolia*) because the former's B2t retains soil water that can be used by the shallow fibrous root systems of grasses. Since Hambright soils retain much less water, the excess infiltrates to the fractured rock below where it can be utilized by deep roots of trees but not grasses. In May, evidence of the Dibble-Los Osos B2t's water retention capacity is plain in the hills above Cordelia since grass stays green there several weeks longer on Dibble-Los Osos soils than it does on the Hambright despite the frequent shade of oaks. This phenomenon illustrates that two very different vegetation types can be equally "mesic" and that oak woodland and grassland are competitive enough within this region for slight soil differences to shift dominance from one to the other.

The geologic factor that most influences vegetation around the San Francisco Bay Estuary is the physical effect of clay on soil water holding capacity, but chemical effects are also locally important. Serpentinite, associated with the Franciscan Formation and occurring at the Estuary's edge in Marin and San Francisco counties, is so chemically distinctive because of its high Mg/Ca ratio and frequent heavy metals that it supports unique vegetation types and many endemic plant species (Kruckeberg 1984). Soils beyond the limits of tides are also usually much less saline than those under tidal influence, but salts can locally accumulate to high levels in non-tidal areas where drainage is poor. Salt especially accumulates in non-tidal areas where precipitation is low, relief is subdued, and Cretaceous Great Valley beds provide a salt source (Chapman 1960; Johnson et al. 1993; Harris 1991). Geology also strongly affects microclimate wherever hills have been uplifted since their south slopes receive more sunlight, warmth, and resultant evapotranspiration than their north slopes. Vegetation on Bay Area hills is consequently relatively xeric on south slopes and relatively mesic on north slopes (Bakker 1984).

Hydrology - The influence of geology and climate on soil water is discussed above. Streams also tend to increase in frequency and flow duration as rainfall increases. Since they provide water to plants in greater quantities and different seasons than local climates, they support distinctive riparian vegetation types not found in upland areas. Not surprisingly, riparian and upland vegetation become increasingly distinct as rainfall decreases (Holstein 1984b). Streams and their associated riparian vegetation are usually narrowly linear landscape features, but they can broaden dramatically when streams reach base level and form deltas. A broad willow-composite zone now removed by urbanization that reportedly once occurred around the southern edge of San Francisco Bay (Cooper 1926) undoubtedly represented covergent deltaic riparian vegetation of several creeks that flow into the Bay.

Alluvium in streambeds tends to be coarser and thus better aerated than interfluvial alluvium, and the running water of streams is also relatively well-aerated. Streamsides consequently provide suitable environments for roots of woody riparian vegetation. In freshwater marshes, however, standing water in poorly drained interfluvial areas quickly causes anaerobic reducing conditions to develop at such shallow depths that only herbaceous vegetation with shallow, predominantly fibrous root systems can occur. The herbaceous freshwater marsh vegetation is consequently quite distinct from predominantly woody riparian vegetation (Holstein 1984a).

Freshwater marsh vegetation grades into vernal pool vegetation through a series of transitional seasonal marsh vegetation types and into moist grassland through a transitional series of lowland wet meadow and swale types. Numerous other local hydrological features around the San Francisco Bay Estuary like springs, seeps, and shallow water tables are associated with distinctive local vegetation types. The relatively shallow water table under most valley oak savannas is a notable example.

Ecotonal Plant Communities

Plant communities surrounding the Baylands ecosystem are here classified using the system of Holland and Keil (1995). At present the most widely used and influential classifications of California vegetation are derived from Munz and Keck's (1959) mixed system, which includes taxonomic, physiognomic, and ecological information. Barbour and Major's extensive (1977) review of California vegetation, for example, was organized around a slightly modified and expanded version of Munz and Keck's system. The units of their classification were vegetationally ill-defined, however, since the plant species lists provided for each one lacked even estimates of relative dominance. Some very important plant communities like riparian forests were also missing from both Munz and Keck's system and Barbour and Major's subsequent review. It is doubtful Munz and Keck intended their brief plant community synopsis to so profoundly influence California vegetation science, however, since the primary purpose of their book was clearly floristic. Its success at remaining California's floristic standard for decades undoubtedly strongly contributed to the influence of its community classification.

Sawyer and Keeler-Wolf (1995) have recently tried to overcome the Munz and Keck system's problems by developing a comprehensive alternative that excludes ecological information from community definitions except in the case of certain specialized habitats like vernal pools. The Sawyer and Keeler-Wolf system presents its own new problems, however, since it lumps quite different stable and successional communities when they are dominated by the same species. Excluding most ecological information also causes very different coastal and alpine communities sharing only a generic relationship between their dominant species to be lumped into catch-all groupings like "Sedge series." Many local dominance types present in California's complex vegetation are also missing from their system despite its numerous series and apparent comprehensiveness.

Holland and Keil avoid these problems by greatly increasing the comprehensiveness and consistency of Munz and Keck's limited but fundamentally sound system. The result is a system outstanding for simplicity, ease of use, and realistic description and classification of California vegetation. Beginning with coastal sand dune vegetation and concluding with freshwater vegetation and anthropogenic environments, the plant community descriptions below follow the system developed by Holland and Keil.

1. Coastal Sand Dune Vegetation - Sand is a distinctive substrate for plants since water infiltrates it very rapidly leaving little moisture available for plants with shallow root systems (Walter 1979). Sand differs from other substrates like fractured rock which have similarly high infiltration rates, however, because of sand's high subsurface homogeneity and lack of resistance to root penetration. Large sand deposits are characteristic landscape features of coasts and arid areas. In Holland and Keil's (1995) system, followed here, vegetation on sand deposits of arid areas is classified as desert sand dune vegetation and consequently distinguished from vegetation on coastal sands. In California, however, some dune fields are located in areas neither coastal nor truly arid. Examples occur on the Merced River alluvial fan in Merced County and at Antioch in Contra Costa County (Wahrhaftig et al. 1993). The former was produced by outwash from glacial erosion of granite in the Yosemite Valley (Wahrhaftig and Birman 1965), but extensive Eocene to Pliocene sandstone deposits in nearby hills (Ellen and Wentworth 1995) are a likely source for the latter. Neither the Merced or Antioch dunes are discussed by Holland and Keil, but both occur in semi-arid areas and share more floristic features with their desert sand dune vegetation type than their coastal sand dune vegetation types.

Pioneer dune vegetation occurs where significant aeolian movement of sand limits development of stable soil and vegetation.

Ambrosia chamissonis is its characteristic dominant, and *Abronia latifolia, Achillea millefolium, Atriplex californica, Atriplex leucophylla, Calystegia soldanella, Camissonia cheiranthifolia, Lathyrus littoralis, Leymus mollis,* and *Lupinus chamissonis* are frequent associated species (Barbour and Johnson 1977).

Dune scrub occurs where stable soil and vegetation have developed on sand of dunes usually considerably older than those supporting pioneer dune vegetation. *Ericameria ericoides* is the characteristic dominant of dune scrub, and associated species include *Artemisia californica, Baccharis pilularis, Lotus scoparius, Lupinus arboreus* and *Lupinus chamissonis* (Barbour and Johnson 1977).

Sand is relatively rare around the San Francisco Bay estuary, but a significant deposit, the Pleistocene Merritt sand, is present at Alameda and adjacent parts of Oakland (Radbruch 1957). Since the local climate is marine, some areas with surface deposits of Merritt sand probably once supported pioneer dune and dune scrub communities similar to those now occurring along the outer Pacific Coast. The sandy area at Alameda and Oakland was one of the first places along the Bay to urbanize, however, and any dune vegetation present there was consequently eradicated before it could be described. A modern analogue with similar soils and climate is Elkhorn Slough (Monterey County), which is incised into Pleistocene deposits, the Aromas sand. Agricultural development has removed some natural vegetation around Elkhorn Slough, but remaining relict stands are still numerous. Topographic features recorded prior to development of the port of Oakland and Lake Merritt resemble those along Elkhorn Slough (Wahrhaftig and Birman 1965).

At Antioch, a sandy area is also present immediately east of Broad Slough. It is less urban than Alameda, but most of its dune vegetation was lost to sand mining prior to urbanization. A small protected remnant of such vegetation at Antioch supports several state and federally listed rare animal and plant species (Sawyer and Keeler-Wolf 1995). Antioch is significantly hotter and drier than the outer coast, and its sand probably originated from nearby sand deposits that extend southward along the inner Coast Range. The affinity of its distinctive sand dune flora and vegetation is consequently closer to Holland and Keil's (1995) desert sand dune community than to either of his coastal dune communities. Because a rain shadow occurs along the inner Coast Range, the ranges of several plant and animal species with desert affinities, including the relatively well-known San Joaquin kit fox (*Vulpes macrotis* ssp. *mutica*) (Zeiner et al. 1990), extend north along the western San Joaquin Valley to near Antioch.

2. Coastal Scrub - Coastal scrub refers to communities dominated by small shrubs in non-desert areas of California. Coastal scrub typically develops on soil and friable sediments rather than conglomerate or fractured hard rock and consists of shrubs with relatively shallow root systems.

Northern coastal scrub is a dense shrub-dominated community which most frequently occurs on steep slopes receiving strong prevailing onshore winds and at least 20 inches of precipitation, but can also occur as an ecotone between northern oak woodland and southern oak woodland on slopes with less wind. Most typically, however, it occurs where precipitation and soils are adequate for development of forests, but tree growth is prevented by strong onshore winds. Since moisture is not limiting, cover is typically complete (Heady et al. 1977).

Baccharis pilularis is the characteristic dominant, but *Mimulus aurantiacus, Rhamnus californica, and Toxicodendron diversilobum* can also occasionally be locally dominant. Characteristic understory species include *Achillea millefolium, Anaphalis margaritacea, Eriophyllum staechadifolium, Gaultheria shallon, Heracleum lanatum, Polystichum munitum, Pteridium aquilinum, Rubus ursinus* and *Scrophularia californica.* Northern coastal scrub is most common along the outer Pacific Coast but also occurs at suitable sites around the San Francisco Bay Estuary near the Golden Gate, in the Berkeley Hills, and in San Mateo County. *Baccharis pilularis* frequently invades disturbed grasslands and forms communities which superficially resemble northern coastal scrub but lack most of its characteristic species. Eventually such recently invasive *B. pilularis* stands may develop into stable coastal scrub or oak woodland communities (Heady et al. 1977). A protected example of northern coastal scrub occurs near the estuary at China Camp State Park.

Southern coastal scrub is a relatively open shrub-dominated community occurring most frequently on steep, dry slopes. It is commonest in areas receiving under 20 inches of precipitation but can occasionally occur in wetter areas on sunny south slopes. It typically occurs where soils otherwise suitable for grassland are excessively drained because of steepness. Because water is the primary limiting factor in southern coastal scrub, its dominant shrubs tend to be widely spaced, forming relatively incomplete cover. In spring, when water stress is briefly relieved, a diverse annual forb flora develops in interstices between the dominant shrubs (Mooney 1977).

Artemisia californica is the characteristic dominant, and common associated species include *Eriogonum nudum*, *Eriophyllum lanatum*, *Lotus scoparius*, *Lupinus albifrons*, *Mimulus aurantiacus* and *Nassella pulchra*. Small stands of southern coastal sage scrub occur in hills around the Estuary and are especially frequent east of South San Fracisco Bay and south of Suisun Bay, where precipitation is relatively low. An example occurs along the Estuary shore at Point Richmond.

Sea-bluff coastal scrub occurs where persistent salt-laden onshore winds suppress most other plant communities. Such climatic conditions resemble those in northern coastal scrub but are more extreme. In such sites the only communities are sea-bluff coastal scrub and northern coastal grassland. The former tends to occur on rocky sites with thin soils and the latter on deeper soils that tend to be heavier, but both frequently intermix in a complex mosaic (Holland and Keil 1995).

Eriophyllum stachaedifolium is the characteristic dominant, and frequently associated species include *Artemisia pycnocephala*, *Baccharis pilularis*, *Erigeron glaucus*, *Eriogonum latifolium* and *Lessingia filaginifolia*. Salt-laden winds strong and persistent enough to support this community enter the Estuary through the Golden Gate but rapidly lose their intensely marine character as they move inland. Havlik (1974) described small stands of this community at Yerba Buena Island, Brooks Island, Red Rock, Point Richmond, Point Fleming, and Potrero San Pablo, all places directly exposed to marine winds entering San Francisco Bay through the Golden Gate.

3. Chaparral - Chaparral refers to a widespread and characteristic California community dominated by large shrubs with evergreen sclerophyllous leaves. It is frequent in areas with precipitation between 10 and 20 inches per year and occasional in wetter areas on sunny south slopes. Chaparral occurs where rocky soils with little clay permit rapid infiltration of water and air to relatively great depths. Such conditions are most frequent on steep slopes but can also occur with relatively low relief on stone alluvial fans in valleys.

Holland and Keil (1995) subdivide California chaparral into 11 subclasses, of which six occur in San Francisco Bay counties. These are not separately treated here, however, since relatively little chaparral of any kind occurs in the Estuary's immediate vicinity.

Chaparral is dominated by shrubs in the genera *Adenostoma*, *Arctostaphylos*, *Ceanothus*, *Cercocarpus*, and *Quercus*, which form a functional group characterized by deep root systems adapted for extracting water from deep cavities in fractured rock. The sclerophyllous leaves of chaparral shrubs are adapted for maintaining low levels of evapotranspiration and associated productivity during long growing seasons (Walter 1979, Mooney and Miller 1985). Discussions of chaparral ecology have long emphasized its adaptation to fire since its shrubs use a variety of strategies to rapidly reoccupy burns and an associated functional group of annuals has seeds that remain dormant for decades and only germinate following chaparral fires (Biswell 1974). Extensive research on *Adenostoma*-dominated chaparral suggesting a relatively short fire cycle my not be directly applicable to other chaparral types, however, since some other kinds of chaparral may have a much longer fire cycle (Keeley and Keeley 1988).

The nearest extensive chaparral to the Estuary occurs in Marin County on the slopes of Mt. Tamalpais two miles west of San Francisco Bay (Shuford 1993, Wieslander and Jensen 1945). While chaparral on alluvial fans is rapidly disappearing but still fairly common in parts of southern California (Smith 1980), it is virtually unknown in central and northern California. Cooper (1926), however, reported that chaparral that has since been extirpated formerly occurred near the southern end of San Francisco Bay on Los Gatos Creek's alluvial fan.

4. Grassland - Vegetation dominated by grasses and graminoid sedges was widespread along the shores of the San Francisco Bay Estuary prior to urban development and is still fairly common there (Bryant 1848, McKelvey 1955). It occurs in non-wetlands wherever soils with clay horizons thick enough to hold significant water near the soil surface and to exclude air from deeper horizons are directly exposed to solar radiation. Clay soils are particularly favorable for grasses and other graminoids because the near-surface water they hold is preferentially available to the dense, relatively shallow fibrous root systems of such plants. In wet climates the most mesic conditions occur on soils with high clay content because of their high water holding capacity, but in arid areas that pattern is reversed. In deserts clay holds much water from scarce precipitation near the soil surface, where solar radiation quickly evaporates it (Walter 1979). Conditions intermediate between these extremes prevail in the semiarid climate surrounding most of the Estuary. Clay soils are xeric and grass-covered on plains and south slopes, where they are directly exposed to solar radiation, but mesic and covered by forest and woodland on north slopes, where solar radiation is reduced. Grassland is most prevalent where annual precipitation is between 10 and 20 inches but becomes progressively scarcer as annual rainfall increases. Some grassland is usually present even in very wet areas, however, wherever clay is directly exposed to solar radiation. Soils with sufficient clay for grassland predominate on the recent alluvium that forms the floors of virtually all San Francisco Bay Area valleys; they are also common on hillslopes where clay-rich sediments have been uplifted (Ellen and Wentworth 1995). While direct solar radiation usually keeps grassland free of woody plants on valley floors and south-facing hillslopes, similar grassland frequently dominates understories beneath the oak woodland that occurs on north slopes because of less intense radiation (Holstein 1984a).

Native perennial grassland. Frequent relict stands and clear descriptions by early travelers leave little doubt that most native grassland near the Estuary on both valley floors and hillslopes was dominated by a rhyzomatous and largely sterile hybrid between *Leymus triticoides* and *L. condensatus* (Stebbins and Walters 1949). Hybrids between these species have been called *Leymus xmultiflorus*, but since the hybrid dominant around the Estuary is too small to match descriptions of *xmultiflorus* (Hickman 1993), it is here included in *L. triticoides*. Two frequently associated rhizomatous graminoids were *Carex barbarae* and *C. praegracilis*, the latter being especially frequent at upland-wetland ecotones. *Nassella pulchra*, a non-rhizomatous bunchgrass, has received more attention than any other species as a native grassland dominant. It frequently dominated grassland but mostly did so only near ecotones with coastal scrub and oak woodland where heavy clay grassland soils had begun to thin and dissipate or where specific substrates like serpentinite prevented development of typical grassland soils (Bryant 1848, McKelvey 1955).

Native grassland had numerous local variations ranging from topographic lows where soil water and clay accumulated to topographic highs where clay was thin and water scarce. Species indicating topographic lows (locally called swales) included *Juncus balticus*, *Juncus xiphioides*, *Ranunculus californicus*, and *Sisyrinchium bellum*, while *N. pulchra* and a variety of forbs indicated the highs. Along the Estuary shore at ecotones with tidal marsh, *Distichlis spicata*, another rhizomatous grass, was particularly prominent (Heady 1977, Holland and Keil 1995).

A scarce native grassland type especially significant for its many rare plants occurs on salt-affected soils associated with inland basins and basin rims rather than coastal tidelands (Faber 1997). These inland **alkaline grasslands** share features like the prominence of *Distichlis spicata* with the grassland-tidal marsh ecotone but often differ from it in the presence of more bare ground and many species not occurring at the Estuary shore. Cooper (1926) reported *Hemizonia congesta* and *H. pungens* were formerly dominant on similar soils near the southern end of the Estuary that are now completely covered by urban development. The best presently extant examples of alkaline grassland in the Estuary's vicinity occur near Livermore in Alameda County and near Fairfield in Solano County. Other distinctive grassland types of unusual substrates supporting rare species are **serpentinite grassland** and **sandy soil grassland** (Skinner and Pavlik 1994).

Native annual forbland. Wester (1981) presented evidence that the southern San Joaquin Valley, an area traditionally considered former grassland, was dominated by annual forbs prior to European settlement. California vegetation classification has traditionally called all upland vegetation dominated by herbs grassland, but Wester's work suggests much of the area traditionally mapped as grassland (Kuchler 1964) was actually native annual forbland. Since native annual forbland occurs where rainfall is insufficient for most perennial grasses, it consequently was most extensive far south of the Estuary in the southern San Joaquin Valley. Numerous relict taxa suggest, however, that a narrow native annual forbland corridor extended north from there to near the Estuary shore in Contra Costa County because of a rain shadow along the inner Coast Range's eastern base. Forbland elements also probably occurred even more widely wherever local conditions like soil infertility and trampling by megafauna suppressed otherwise ubiquitous perennial grasses. Even today wildflower displays (i.e., annual forb dominance) are most spectacular locally where soil is relatively infertile (i.e., Bear Valley in Colusa County and Table Mountain in Butte County [Faber 1997]) and most spectacular generally in years, as in 1991, when winter drought suppression of competitive grasses is followed by forb-promoting heavy spring rains. Some forbland species like *Eremocarpus setigerus* have adapted well to anthropogenic land use changes but others have become rare (*Convolvulus simulans, Madia radiata*) or extinct (*Eschscholzia rhombipetala*).

Non-native annual grassland. Introduction of grazing and agriculture during the nineteenth century caused a dominance shift in almost all of California's grasslands from native perennial graminoids to Eurasian non-native annual grasses. Today dominance among such annuals changes spatially in a complex pattern reflecting soil conditions. On catenas from thick, heavy clay soils to thinner, lighter ones a typical annual grass dominance sequence *Lolium multiflorum-Bromus hordeaceus-Avena fatua-Avena barbata* replaces a simpler perennial sequence *Leymus triticoides-Nassella pulchra* still occasionally extant on the same catenas. Another common dominance sequence *Bromus hordeaceus-Bromus diandrus-Hordeum murinum* reflects shifts in soil nitrogen content from low to relatively high. The above species are the most frequently dominant non-native annual grasses, but others also occasionally participate. *Cynosurus echinatus*, for example, frequently dominates annual grassland where rainfall is relatively high. Several exotic forbs are also becoming increasingly important components in a vast exotic herbaceous vegetation type that may only temporarily be called grassland. *Vicia villosa* ssp. *varia* is increasingly planted for forage in the *Avena* zone; *Picris echioides* is important in the *Lolium* zone; and *Centaurea solstitialis*, especially, is a widespread invader of the *B. hordeaceus* zone, where *Erodium botrys* is also important when soil fertility is particularly low (Heady 1977, Holland and Keil 1995). Grazing is particularly important for maintaining replacement of native perennial grasses with exotic annual species. At numerous sites around the Estuary, for example, dominance is shifting back from exotic annual grasses to *Leymus triticoides* and *Carex barbarae* where expanding urbanization has at least temporarily caused the removal of grazing.

<u>Coastal prairie</u>. Where clay soils are directly exposed to marine air flow, a floristically distinct grassland occurs that Holland and Keil (1995) call northern coastal grassland but is widely known in California as coastal prairie. Coastal prairie is most frequent along the outer coast, but small amounts also likely occur near the Estuary where marine air flow is particularly direct.

Much of California's coastal prairie is now dominated by two exotic perennial grasses, *Anthoxanthum odoratum* and *Holcus lanatus*, but many distinctive native perennial grasses like *Agrostis pallens*, *Calamagrostis nutkaensis*, *Danthonia californica*, *Deschampsia cespitosa*, *Festuca idahoensis* and *Festuca rubra* can also frequently be locally dominant. Two other distinctive plant species indicative of coastal prairie are *Iris douglasiana* and *Juncus patens* (Heady et al. 1977).

5. Coastal Coniferous Forest - Forests dominated by large coniferous trees occur along the eastern Pacific Coast in a high rainfall zone extending from central California to Alaska. Holland and Keil (1995) recognize two subdivisions of coastal coniferous forest, but only one of these, redwood forest, occurs near the Estuary.

<u>Redwood forest</u>. Extensive forests dominated by *Sequoia sempervirens*, the well-known redwood and the world's tallest tree species, occur on the southern slopes of Mt. Tamalpais within 1.75 miles of the Estuary (Shuford 1993), but individual redwoods occur in mixed evergreen forest much less than a mile from the shore of San Pablo Bay at China Camp State Park. Redwoods are common up to about 2,000 feet in the California Coast Range wherever annual precipitation is above 40 inches and soil is relatively fertile. Despite sufficient rainfall, sensitivity to cold prevents their occurrence along the Oregon coast beyond a few miles north of the border, at high elevations in the Coast Range, or on inland mountain ranges. Contrary to an enduring myth, redwoods are negatively rather than positively associated with summer fog. Consequently, even at sites protected from onshore winds they are almost completely absent along the immediate coast wherever summer fog is frequent. Redwoods survive summer drought not because of fog drip but by storing surplus water from high winter precipitation in their massive trunks, a strategy that has produced only slightly less dramatic gigantism in other conifer species where large winter water surpluses occur with summer drought. As a consequence northern California and southern Chile, both areas with unusually wet winters and dry summers located at the outer periphery of more typical Mediterranean climate zones, are the world's two greatest centers of tree gigantism (Holstein 1984a, Zinke 1977).

Shade is so intense in the redwood forest understory that only a few plant species survive there. Two that do, *Oxalis oregana* and *Polystichum munitum*, are usually the sole understory dominants.

6. Mixed Evergreen Forest -

<u>Central California mixed evergreen forest</u>. Forests dominated by a mix of broadleaf and conifer evergreen trees are frequent in California where precipitation is relatively high and winter temperatures are mild. In northern California the trees most frequently dominating such mixed evergreen forests are *Arbutus menziesii*, *Lithocarpus densiflorus*, *Pseudotsuga menziesii*, and *Umbellularia californica*. In central California the term mixed evergreen forest as presently used is somewhat anomalous, however, since it often designates forests solely dominated by *Umbellularia californica*, the California laurel. Such laurel-dominated forests are frequent around the Estuary where annual rainfall is between 20 and 40 inches. At the dry end of that precipitation range laurel forests are entirely confined to very shady north slopes and canyons, but they also occur on somewhat sunnier slopes as 40 inches is approached. Above that they are almost entirely replaced by redwood forests (Sawyer et al. 1977, Wainwright and Barbour 1984).

The most commonly associated tree species in central California's laurel forests is a non-evergreen, *Acer macrophyllum*. *Arbutus menziesii* is also a frequent associate but is almost entirely confined to the rockiest slopes. Shade is so intense beneath laurel forest canopies that completely bare ground is common where drought is an added stressor, but as 40 inches is approached *Polystichum munitum* often dominates the understory. *Holodiscus discolor*, a deciduous species, is commonly dominant in shrubby openings frequent in laurel forests (Safford 1995).

7. Oak Woodland - Vegetation with an overstory dominated by oak trees is common throughout California's Mediterranean climate zone including the Estuary's vicinity. Such oak woodlands primarily vary in species and spacing of their overstory oaks. Vegetation is called savannah where oaks are widely spaced and forest where spacing is so close their canopies are closed. Woodland, as a term, describes vegetation with intermediate spacing, but tree separation is so locally variable in California's oak-tree dominated vegetation it is appropriate to use the traditional term oak woodland to refer to all of it. That generalized oak woodland can then be divided into subclasses based on its dominant species (Griffin 1977).

Since woodland oaks and grassland grasses occur in similar environmental conditions, they frequently compete directly for water and other soil resources. Specific aspects of that competition are discussed for each subclass but a few of its consequences are general. Oaks only occur where water is present in deep soil horizons, where it may arrive horizontally through shallow aquifers or vertically when precipitation is abundant enough to infiltrate past dense but relatively shallow grass root systems. Grassland grasses, in contrast, only occur where solar radiation is direct because overstory trees are either absent or so widely spaced their canopies are not contiguous (Walter 1979).

Coast live oak woodland, which is dominated by *Quercus agrifolia*, is distinctive among oak woodland subclasses because it consists almost exclusively of closed canopy forests. As a consequence it is frequently treated as a subclass of mixed evergreen forest rather than oak woodland. It is included here with oak woodland, however, because of the affinities of both its dominant tree and the majority of its fauna (Griffin 1977).

Coast live oak woodland occurs widely around the Estuary where annual precipitation is between 15 and 40 inches and continentality is at least partially moderated by marine influences. Marine air flow through Carquinez Strait even permits occurrence of coast live oak woodland with two isolated Coast Range-related mammal populations (*Sylvilagus bachmani riparius* and *Neotoma fuscipes riparia*) on the Central Valley floor near Lodi (Zeiner et al. 1990).

In hills on clay soils coast live oak woodland is frequently present as an extensive ecotone between grassland and mixed evergreen forest since it occurs on slopes shadier than the former but sunnier than the latter. On slopes where rockier substrates and lighter soils permit infiltration of more water to greater depths, however, coast live oak is less limited by solar exposure and can even occur on south slopes. North of Carquinez Strait, for example, adjacent ridges with identical microclimates differ only in their substrates. Ridges underlain by sediments of the clay-rich Eocene Markley Formation are covered by grassland and have coast live oak woodland only on north slopes and in canyons, while those underlain by hard but fractured rocks of the Pliocene Sonoma volcanics are covered by coast live oak woodland on all exposures but north slopes and canyons, where *Umbellularia*-dominated mixed evergreen forest occurs. The great vegetational difference is a result of the way in which the two substrates respond to precipitation — rain rapidly infiltrates to deep levels on the fractured volcanics where it can be utilized by oak roots, whereas it is held at the surface on the clay-rich Markley where it is more available to grass roots. Rapid infiltration on the volcanics causes such xeric conditions in its surface soils that its few stands of annual grassland cease productivity and dry two weeks earlier than Markley grasslands dominated by the same species (Bates 1977, Ellen and Wentworth 1995).

Coast live oak woodland differs from other oak woodland subclasses in the relative rarity of annual grasses in its understory. The most frequent dominant there is *Toxicodendron diversilobum*, poison oak, but *Rubus ursinus* and *Symphoricarpus mollis* are also often important (Safford 1995).

Valley oak woodland consists of several structurally diverse communities sharing dominance by *Quercus lobata* that include savannah and woodland on clay hillslopes and savannah, woodland, and closed canopy forest on alluvial plains over shallow unconfined aquifers. Alluvial valley oak woodland often occurs on the outer edges of riparian forest corridors (see below) on relatively fine, heavy soils distinct from the coarse alluvial soils under typical riparian stream bank vegetation. Tree spacing in alluvial valley oak woodland is related to water stress since canopies closed when subsurface water is abundant become progressively more open as water stress increases, resulting first in woodland and then savannah. Much alluvial valley oak forest was removed because it coincided with highly desired agricultural soils, but a few stands are extant in the Central Valley and elsewhere. Alluvial valley oak woodland was probably always scarce near the Estuary, however, since it is better adapted to inland Califonia's hot summers than to the outer Coast Range's relatively marine climate. One of the few examples near the Estuary is located along Green Valley Creek near Cordelia in Solano County.

Valley oak woodland is most frequent near the Estuary on clay hillslopes with annual rainfall between 15 and 40 inches, where its range overlaps coast live oak woodland and foothill woodland. It is less abundant than either but more tolerant of clay soils than the former and less resistant to water stress than the latter. The understory of valley oak woodland's savannah and woodland phases typically consists of non-native annual and occasionally native perennial grassland. Vegetation beneath closed canopy valley oak alluvial forest, however, can include both grassland and features shared with riparian forest or coast live oak forest understories. Valley oak reproduction, often low because of competition with annual grass and predation of seeds and seedlings by a variety of herbivores, can be abundant in alluvial woodland when suppression of grass by flooding coincides with large acorn crops. Urban fringes are also favorable sites for valley oak reproduction because their low livestock and wildlife populations result in lowered seed and seedling predation (Holstein 1984b, Holland and Keil 1995).

Foothill woodland is woodland and savannah vegetation wholly or partially dominated by *Quercus douglasii*, blue oak, that is widespread on hillslopes surrounding the Central Valley. Near the Estuary, foothill woodland is largely confined to the inner Coast Range. The foothill woodland environment has a relatively continental climate with cool to cold winters, very hot summers, and annual rainfall from 15 to 40 inches. Winter cold reduces understory grass growth and consequently permits infiltration of a large part of the wet season's water surplus to deep subsoil where it can be utilized by blue oaks during spring and summer. In summer high temperatures and low humidity produce very low water potentials in blue oak leaves that permit withdrawal of water tightly held by clay-rich subsoils.

Blue oak is usually the sole foothill woodland dominant on clay hillslopes, but on slopes with more rock and thinner soils it often shares dominance with *Pinus sabiniana*. Blue oaks occur on a wider range of slope exposures than many other oak species, but foothill woodland dominance often shifts to *Aesculus californicus* on shaded north slopes. In canyons and around rock outcrops *Quercus wislizenii* is also often a local dominant.

Because of foothill woodland's open canopy its understory is almost universally dominated by non-native annual grassland. Native forbs like *Holocarpha virgata*, however, are also usually frequent there. Competition is particularly intense between annual grasses and blue oak seedlings before they develop roots long enough to reach subsoil water. Seedling mortality at this stage is so intense that much foothill woodland consists almost entirely of mature blue oaks that germinated in the 1860's, a decade when severe overgrazing reduced much presumably native perennial grassland from California's rangelands. Subsequent increase of non-native annual grassland has severely restricted reproduction of foothill woodland developing at that time (Griffin 1977, Holland and Keil 1995).

8. Cliffs and Rock Outcrops -Vegetation of cliffs and rock outcrops is usually virtually ignored in surveys of California vegetation including that of Holland and Keil (1995) because its areal extent is small and it consists largely of non-vegetated surfaces. It is particularly important, however, as a habitat for rare plant species. Cliffs are unique environments where soil and competition with other plants is very limited and solar radiation is often abundant. Plants adapted to cliffs (chasmophytes) resemble epiphytes in producing small easily dispersed seeds in such great numbers that the likelihood of reaching rare suitable germination habitats is increased. Seeds reaching these light-rich habitats can afford to be small because they require little stored food. *Dudleya*, the California genus with the most highly adapted chasmophytes, has a few taxa near the Estuary but is much more diverse in Southern California.

Plants of rock outcrops are less specialized than chasmophytes but may be rare since they occur in distinctive microenvironments that consequently are free from competition with surrounding vegetation. Rock outcrops and cliffs are most likely to support rare plants when they are mineralogically different from surrounding landscapes, and one mineral receiving particular attention because of its frequent association with rare plants is serpentine. Soil development is so retarded and vegetation so distinctive on serpentine that its occurrences may be viewed as extended rock outcrops even though they occasionally cover many square miles (Bakker 1984, Skinner and Pavlik 1994, Fiedler and Leidy 1987).

9. Riparian Vegetation - Riparian vegetation refers to the distinctive plant communities of streambanks and ecologically related habitats. Its most salient environmental features are relatively coarse alluvial soils typically associated with streams and root zone water supplies greater than the local climate provides. When mature, California riparian vegetation is closed canopy forest, but early successional riparian vegetation can be shrubby.

Near the Estuary riparian vegetation is overwhelmingly dominated by three species, *Acer negundo, Salix lasiolepis* and *Salix laevigata*, but others may dominate in specialized habitats. *Populus fremontii* and *Salix gooddingii* are important where climate becomes less marine and more continental near the Central Valley; *Salix exigua* is important on sandbars and other habitats where early successional riparian vegetation is developing; *Alnus rhombifolia* and *Salix lucida* ssp. *lasiandra* are important where, as at Niles Canyon, streams with rocky beds flow perennially; and *Platanus occidentalis* and *Baccharis viminea* dominate where ones with sandy and rocky beds flow intermittently.

Typical *Acer negundo-Salix lasiolepis-Salix laevigata* riparian vegetation also is common where ecological conditions simulate streambank environments, as at lakeshores and a variety of places with shallow water tables. On the outer coast non-streambank riparian vegetation is frequent in dune slacks, but around the Estuary it at least formerly was most frequent in sausals, microdeltas occurring where stream channels and their subsurface water tables spread laterally as they entered tidal marsh. Most sausals have been lost to urbanization of the Estuary's periphery, but a small example occurs at China Camp State Park.

Common riparian understory plants near the Estuary include *Baccharis douglasii, Euthamia occidentalis, Rosa californica*, and *Rubus ursinus*. For a short distance these can also replace riparian trees as dominants at the ecotone with tidal marsh where a veneer of coarse stream-side alluvium deposited on tidal mud thins as it nears the Estuary. Like sausals, however, such riparian-tidal marsh ecotones have almost entirely disappeared around the Estuary because of urbanization (Holland and Keil 1995, Holstein 1984b).

10. Freshwater Vegetation - Freshwater wetland vegetation occurs where land surfaces are saturated by freshwater or shallowly covered by it. Its two main phases near the Estuary, freshwater marshes and vernal pools, are very distinctive but also united by intermediate communities.

Freshwater marsh refers to vegetation dominated by plant species emergent from at least semi-permanent shallow freshwater. The most frequently dominant freshwater marsh species near the Estuary is *Scirpus acutus*, but *Scirpus americanus*, *Scirpus californicus*, *Typha angustifolia*, *Typha domingensis*, and *Typha latifolia* can also be important there as dominants. The *Typha* spp., in particular, are often dominant in early successional and nitrogen-enriched freshwater marshes.

Climate and geology have less influence on the distribution of freshwater marsh than they do on the occurrence of other plant communities. When vegetation is primarily limited by precipitation, temperature, and light, its distribution is controlled by climate, and when limited by mineral nutrition and soil texture, its distribution is controlled by geology. The primary limiting factor in freshwater marshes, however, is air, which, while superabundant at the marsh surface, falls to such low concentrations a short distance beneath it that environments too anoxic, reduced, and toxic for root growth are frequent there. All freshwater marsh dominants in California are consequently monocotyledons, which have shallow fibrous root systems readily supplied with air by aerenchyma-rich stems. Many dicotyledons including most trees and shrubs, in contrast, have solid stems and deep, non-fibrous root systems poorly adapted to anoxic conditions. California consequently lacks swamps, vegetation in semi-permanent shallow water dominated by woody plants, since it has no native trees or shrubs capable of completing life cycles in flooded environments. Buttonbush, *Cephalanthus occidentalis*, and several species of *Salix* can tolerate extended flooding, however, and frequently occur at the ecotone between freshwater marsh and riparian vegetation (Holland and Keil 1995, Holstein 1984a,b).

Both tidal and non-tidal freshwater marshes are frequent around the Estuary, but the former are most important in the Sacramento-San Joaquin Delta immediately upstream from the true estuary. The Delta consisted almost entirely of tidal freshwater marsh before it was largely converted to agricultural land, but a few remnant tidal freshwater marshes still occur there. Small non-tidal freshwater marshes often resulting from human alteration of hydrologic conditions are also widespread around the estuary (Bowcutt 1996).

Soils beneath freshwater marshes may be mineral or organic. Despite otherwise similar vegetation freshwater marshes with organic soils are technically fens. Since organic soils derived from *Scirpus acutus* rhizomes were general beneath the Delta's tidal freshwater marshes, they once constituted a single vast fen (Atwater and Belknap 1980). Mineral soils, however, generally occur beneath the many small freshwater marshes around the Estuary. Marshes develop most readily on fine, heavy mineral soils since these exclude air and create the anaerobic conditions suitable for marsh vegetation more readily than the coarse and readily aerated sediments common on streambanks beneath riparian forests. Since waterbirds quickly transport propagules permitting establishment of freshwater marsh plants at sites with suitable hydrological conditions regardless of their climatic and geological environments, freshwater marshes are among the easiest plant communities to restore (Kusler and Kentula 1990).

Continua exist between semi-perennial marshes and both moist grassland swales (see above) and vernal pools (see below). Vegetation of areas with hydrology intermediate between freshwater marshes and vernal pools pond longer than the latter but shorter than the former. These are most frequently dominated by *Eleocharis macrostachya* with normal winter wet season inundation but can also be dominated by *Cyperus eragrostis* when ponding resulting primarily from agricultural and urban runoff occurs in the warm season. Vegetation arising from both kinds of seasonal ponding is properly called seasonal marsh, but wildlife managers also frequently use the term to describe non-tidal mudflat environments extremely important for shorebird foraging. Such non-tidal mudflats have little vegetation and once commonly occurred where flooding temporarily suppressed normal grassland development on stream terraces. Streamflow control and terrace urbanization, however, have greatly reduced traditional episodically flooded shorebird habitat around the Estuary. Most non-tidal seasonal marshes presently occurring there consequently result from seasonal drawdowns of artificial ponds and floodways (SFEP 1991a,b).

Limnetic vegetation refers to floating or submerged vegetation occurring in open freshwater too deep or otherwise unsuitable for marsh vegetation. Important native components of submerged limnetic vegetation near the Estuary include *Ceratophyllum demersum*, *Najas guadalupensis*, *Potamogeton pectinatus* and *Potamogeton pusillus*, while important floating elements are *Azolla filiculoides*, *Lemna gibba* and *Lemna minor*. Non-native species like *Egeria densa* and *Mytiophyllum aquaticum* are now also extremely significant and often predominant elements of submerged limnetic vegetation near the Estuary, but the floating component consists almost entirely of extremely widespread and readily dispersed native species except in and near the Delta, where non-native *Eichornia crassipes* is important (Holland and Keil 1995).

Vernal pool vegetation refers to a distinctive plant community dominated by annual and short-lived perennial forbs that occurs in microtopographic basins flooded in the wet season and dry the rest of the year. Vernal pool plants are consequently adapted for beginning their life cycle like submerged limnetic species but completing it as terrestrial plants in completely dry environments. The vernal pool environment has led to adaptive radiation of numerous species primarily in the genera *Downingia, Eryngium, Lasthenia, Navarretia, Plagiobothrys*, and *Psilocarphus*, and it is these that dominate its vegetation. *Plagiobothrys bracteatus*, in particular, is the most frequent dominant of vernal pool vegetation around the Estuary. Upland vegetation around vernal pools is almost invariably non-native annual grassland (Holland 1977).

The origin of vernal pool basins is obscure but may result from seismic activity or interaction of wind erosion and soil processes (see above). To pond water and create an environment suitable for vernal pool vegetation, however, an aquaclude or barrier to water infiltration that may be a clay horizon, duripan, or bedrock must be present immediately beneath the basin. Most vernal pools and the plants adapted to them occur entirely or almost entirely in California, and few hydrologic features resembling vernal pools occur outside North America even in otherwise similar Mediterranean climates (Thorne 1984).

Vernal pools are at risk even in the Central Valley where they are most common because virtually all human activities except rangeland grazing destroy the microtopography and aquacludes that create the vernal pool environment. Around the Estuary they are even more threatened since they are extremely rare near southern San Francisco Bay and only slightly more frequent north of San Pablo and Suisun bays. Vernal pools north of Suisun Bay are particularly environmentally significant because they are often partially dominated by *Lasthenia conjugens*, a federally listed endangered species extinct throughout much of its range (Skinner and Pavlik 1994).

Artificially created basins often sufficiently resemble natural vernal pools to be colonized by a few wide-ranging and extremely tolerant pool species. More rarely a few rare species may be present in such artificial sites. The full suite of vernal pool taxa including the rarest species almost never develops in such environments, however, because soil characteristics of natural pools can rarely be replicated. As a consequence creation of artificial vernal pools has been the least successful of all wetland restoration efforts (Ferren and Gevirtz 1990, Kusler and Kentula 1990).

Vernal pools typically are freshwater environments since their primary water source is precipitation (Hanes et al. 1990). However, salt diffusion from underlying soils causes some to be slightly brackish. Seasonal pools hydrologically resembling vernal pools but lacking their characteristic biota because of elevated salinity also occur. They are called playas when their surrounding saline environment is inland (Chapman 1960, Waisel 1972) and pans when it is coastal (Adam 1990, Chapman 1960, Long and Mason 1983, Waisel 1972). Both occur in San Francisco Bay Area counties but only the latter near the Estuary shore (SFEP 1991a). Today vegetated pans near the Estuary are ubiquitously dominated by *Cotula coronopifolia*, an exotic annual that may have replaced a now extinct native annual *Plagiobothrys glaber*.

11. Anthropogenic Environments - Anthropogenic environments must be briefly considered because they collectively now dominate non-tidal uplands around the Estuary. The anthropogenic typology used here follows Mayer and Laudenslayer, Jr. (1988) rather than the more complex one of Holland and Keil (1995).

Agricultural environments historically surrounded much of the Estuary but have become increasingly scarce because of displacement by urbanization. Structurally and physiologically different elements like orchards, vineyards, and both irrigated and dry farmed cropland are included here, but all share low plant and animal diversity. Irrigated nursery crops are most important near the southern part of the Estuary; and vineyards, irrigated pastures, and dry farmed oats (*Avena sativa*) predominate near the northern part.

Urban and suburban environments now overwhelmingly dominate non-tidal uplands around the Estuary. They often structurally resemble extended and unusually diverse riparian zones since irrigated non-native trees predominantly in the genera *Acacia, Eucalyptus*, and *Pinus* are ubiquitously present above an even more diverse understory of ornamental shrubs and herbs. As a consequence, urban-suburban communities are probably the landscape unit near the Estuary with the highest plant diversity but the fewest native plants. Some native bird species have adapted to using urban areas as habitat and become common, but far fewer terrestrial species are able to do so.

Rare Plants of Ecotonal Plant Communities

Table 1.4 lists rare plant species found in the nine Bay Area counties. The table is organized using the same classification system (Holland and Keil) as was used in the previous section. It includes, for each species, the state and federal listing status, as well as the status derived from the California Native Plant Society (CNPS) inventory (Skinner and Pavlik 1994). The CNPS inventory is more complete than the state or federal listings and is organized on the following lists:

1a. Presumed extinct
1b. Rare, threatened, or endangered in California and elsewhere.

2. Rare, threatened, or endangered in California but more common elsewhere.
3. Possibly rare, but more information is needed.
4. Distribution limited: a watch list.

Plants with the greatest need for protection are on list 1b, and 1a (presumed extinct) plants are placed there if rediscovered. The CNPS inventories rare plants by county. To prepare Table 1.4, each of the CNPS-identified rare species was assigned to a modal plant community or ecotone based on information provided by state and local floras. An effort was made to place each taxon in the plant community it most frequently (but not necessarily exclusively) occurs(ed) in, however, frequently reference materials regarding a taxon were contradictory. In these cases I sought to develop a consensus view, and weighted local floras and my own field experience most heavily.

The greatest constraint in preparing this table was the frequent sparsity of ecological information regarding rare species. Preparation was easiest in areas with local floras since these are full of observations by botanists with deep knowledge of their region's plants and habitats. Tragically, however, a number of plants near the Estuary went extinct or became extremely rare in an older era when little or no ecological information was provided when plants were collected. We can only speculate regarding the niches of these taxa.

Many species are rare because they occur in rare ecological niches. Historically, these have not been the focus of plant community classification, which is most concerned with the commonest kinds of vegetation. While there was an effort to include some of the rarer niches occurring near the Estuary in Table 1.4, it is not comprehensive, and rare niches distant from the Estuary are not included. Rare plants that occur primarily in plant communities distant from the Estuary were not included in the narrative community descriptions.

It is hoped this table will generate discussion and suggestions for its improvement.

Table 1.4 Rare Plant Species* Found in the Nine Counties Adjacent to the San Francisco Bay Estuary, by Plant Community or Ecotone

1. Sand dune vegetation

A. Pioneer coastal dune vegetation

- 1b. *Abronia umbellata* ssp. *breviflora* - FSC

B. Coastal dune scrub

- 1b. *Agrostis blasdalei* - FSC
  - *Chorizanthe cuspidata* var. *cuspidata* - FSC
  - *Chorizanthe cuspidata* var. *villosa*
  - *Chorizanthe robusta* var. *robusta* - FE
  - *Collinsia corymbosa*
  - *Erysimum ammophilum* - FSC
  - *Horkelia cuneata* ssp. *sericea* - FSC
  - *Horkelia marinensis* - FSC
  - *Layia carnosa* - FE, SE
  - *Lessingia germanorum* - FE, SE
  - *Lupinus tidestromii* - FE, SE
  - +*Gilia capitata* ssp. *chamissonis*
  - +*Gilia millefoliata*
- 4. *Monardella undulata*

C. Inland dune vegetation

- 1b. *Erysimum capitatum* ssp. *angustatum* - FE, SE
  - *Oenothera deltoides* ssp. *howellii* - FE, SE

2. Coastal scrub

A. Northern coastal scrub

- 1b. *Delphinium bakeri* - FPE, SR
  - *Lilium maritimum* - FC
  - +*Lupinus latifolius* var. *dudleyi*
- 3. *Lupinus eximius* - FSC
- 4. *Cirsium andrewsii*
  - *Collinsia multicolor*
  - *Piperia michaelii*
  - *Sanicula hoffmannii*

B. Southern coastal scrub

C. Sea-bluff coastal scrub

- 1b. *Cirsium occidentale* var. *compactum* - FSC
  - *Grindelia hirsutula* var. *maritima* - FSC
  - *Phacelia insularis* var. *continentis* - FSC
  - *Silene verecunda* ssp. *verecunda* - FSC
  - +*Agrostis clivicola* var. *punta-reyesensis*
  - +*Gilia capitata* ssp. *tomentosa*
  - +*Piperia elegans* ssp. *decurtata*
- 4. *Arabis blepharophylla*
  - *Ceanothus gloriosus* var. *gloriosus*
  - *Erysimum franciscanum* - FSC
  - *Hesperevax sparsiflora* var. *brevifolia*
  - +*Agrostis clivicola* var. *clivicola*

3. Chaparral

- 1b. *Arctostaphylos auriculata*
  - *Arctostaphylos densiflora* - FSC, SE
  - *Arctostaphylos imbricata* - FPT, SE
  - *Arctostaphylos manzanita* ssp. *laevigata*
  - *Arctostaphylos montaraensis* - FSC
  - *Arctostaphylos pallida* - FPT, SE
  - *Arctostaphylos stanfordiana* ssp. *decumbens*
  - *Ceanothus confusus* - FSC
  - *Ceanothus divergens* - FSC
  - *Ceanothus foliosus* var. *vineatus* - FSC
  - *Ceanothus masonii* - FSC, SR
  - *Ceanothus sonomensis* - FSC
  - *Malacothamnus hallii*
  - *Plagiobothrys uncinatus* - FSC
- 3. *Calyptridium parryi* var. *hesseae*
  - +*Arctostaphylos manzanita* ssp. *elegans*
- 4. *Ceanothus purpureus*
  - *Dichondra occidentalis*
  - *Lomatium repostum*
  - *Malacothamnus arcuatus*
  - *Malacothamnus helleri*
  - *Orobanche valida* ssp. *howellii*
  - *Plagiobothrys myosotoides*

A. Chaparral burns

- 4. *Calandrinia breweri*
  - +*Malacothrix phaeocarpa*

4. Grassland

A. Native perennial grassland

- 1b. *Amsinckia grandiflora* - FE, SE
  - *Astragalus clarianus* - FE, ST
  - *Blepharizonia plumosa* ssp. *plumosa*
  - *Fritillaria pluriflora* - FSC
  - *Tracyina rostrata*
  - *Trifolium amoenum* - FE
  - +*Calochortus argillosus*
- 3. *Lessingia hololeuca*
- 4. *Androsace elongata* ssp. *acuta*
  - *Fritillaria agrestis*
  - +*Allium peninsulare* var. *franciscanum*
  - +*Microseris paludosa*

Alkaline grassland

- 1a. *Tropidocarpum capparideum* - FSC
- 1b. *Astragalus tener* var. *ferrisiae* - FSC
  - *Astragalus tener* var. *tener*
  - *Atriplex cordulata* - FSC
  - *Atriplex depressa*
  - *Atriplex joaquiniana* - FSC
  - *Cordylanthus mollis* ssp. *hispidus* - FSC
  - *Cordylanthus palmatus* - FE, SE
  - *Delphinium recurvatum* - FSC
  - *Hemizonia parryi* ssp. *congdonii* - FC
  - *Isocoma arguta* – FSC
  - +*Trifolium depauperatum* var. *hydrophilum*
- 3. *Hordeum intercedens*
- 4. *Atriplex coronata* var. *coronata*
  - *Thelypodum brachycarpum*

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* Derived from the inventory of the California Native Plant Society (CNPS) (Skinner and Pavlik 1994)

Key to CNPS list codes:

1a.	Presumed extinct
1b.	Rare, threatened, or endangered in California and elsewhere.
2.	Rare, threatened, or endangered in California but more common elsewhere.
3.	Possibly rare, but more information is needed.
4.	Distribution limited: a watch list
+	Proposed new addition to the CNPS inventory

Key to Federal and State List Codes:

FE	Federally listed as endangered	SE	State listed as endangered
FT	Federally listed as threatened	ST	State listed as threatened
FC	Federal listing candidate	SR	State listed as rare
FPE	Proposed for Federal listing as endangered		
FPT	Proposed for federal listing as threatened		
FSC	Federal species of special concern		

Table 1.4 (continued) Rare Plant Species* Found in the Nine Counties Adjacent to the San Francisco Bay Estuary, by Plant Community or Ecotone

Sandy soil grassland

1a. *Eriogonum truncatum*

4. *Cryptantha hooveri*
Linanthus grandiflorus

Serpentinite grassland

1b. *Acanthomintha duttonii* - FE, SE
Calochortus tiburonensis - FT, ST
Castilleja affinis ssp. *neglecta* - FE, ST
Fritillaria biflora var. *ineziana*
Lessingia arachnoidea - FSC
Streptanthus niger - FE, SE

3. *Eriogonum luteolum* var. *caninum*

4. *Astragalus breweri*
Linanthus ambiguus

Moist grassland

1a. *Plagiobothrys hystriculus*

1b. *Pleuropogon hooverianus* - FSC, SR
Sidalcea oregana ssp. *hydrophila*

2. *Carex californica*

4. *Perideridia gairdneri* ssp. *gairdneri* - FSC

B. Native annual forbland

1a. *Eschscholzia rhombipetala* - FSC

1b. *Madia radiata*

4. *Convolvulus simulans*
+*Erodium macrophyllum*

C. Non-native annual grassland

D. Coastal prairie

1b. *Blennosperma nanum* var. *robustum* - FSC, SR
chorizanthe valida - FE, SE
Erigeron supplex - FSC
Fritillaria lanceolata var. *tristulis*
Fritillaria liliacea - FSC
Holocarpha macradenia - FC, SE
Limnanthes douglasii ssp. *sulphurea* - FSC, SE
Plagiobothrys diffusus - FSC, SE
Sanicula maritima - FSC, SR
Triphysaria floribunda - FSC

3. *Hemizonia congesta* ssp. *leucocephala*
Plagiobothrys chorisianus var. *chorisianus*

5. Coastal coniferous forest

A. Redwood forest

4. *Elymus californicus*

B. Closed-cone coniferous forest

1b. *Ceanothus gloriosus* var. *porrectus* - FSC
Cupressus goveniana ssp. *pigmaea* - FSC
Pinus radiata - FSC

C. North coast coniferous forest

2. *Boschniakia hookeri*

4. *Piperia candida*
Pityopus californicus
+*Galium muricatum*

6. Mixed evergreen forest

A. Central California mixed evergreen forest

1b. +*Quercus parvula* var. *tamalpaisensis*

3. +*Viburnum ellipticum*

4. *Cypripedium montanum*
Dirca occidentalis
Ribes victoris

7. Oak woodland

A. Coast live oak woodland

1b. *Clarkia concinna* var. *automixa*

4. *Amsinckia lunaris*
Isocoma menziesii var. *diabolica*

B. Valley oak woodland

C. Foothill oak woodland

8. Cliffs and rock outcrops

A. Cliffs

3. +*Streptanthus tortuosus* var. *suffrutescens*

4. *Arabis modesta*

B. Rock outcrops

1b. *Arctostaphylos virgata*
Coreopsis hamiltonii - FSC
Penstemon newberryi var. *sonomensis*
Phacelia phacelioides - FSC
Sanicula saxatilis - FSC, SR
Streptanthus callistus - FSC
Streptanthus glandulosus var. *hoffmanii* - FSC
Streptanthus hispidus - FSC

3. *Erigeron biolettii*
Monardella antonina ssp. *antonina*

4. *Antirrhinum virga*
Arabis oregona
Arctostaphylos hispidula
Navarretia subuligera

Serpentinite outcrops

1a. *Arctostaphylos hookeri* ssp. *franciscana* - FSC

1b. *Allium sharsmithae*
Arctostaphylos bakeri ssp. *bakeri* - SR
Arctostaphylos bakeri ssp. *sublaevis*
Arctostaphylos hookeri ssp. *montana* - FSC
Arctostaphylos hookeri ssp. *ravenii* - FE, SE
Astragalus rattanii var. *jepsonianus*
Calochortus raichei - FSC
Campanula sharsmithiae - FSC
Ceanothus ferrisae - FE
Chlorogalum pomeridianum var. *minus*
Clarkia franciscana - FE, SE

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Table 1.4 (continued) Rare Plant Species* Found in the Nine Counties Adjacent to the San Francisco Bay Estuary, by Plant Community or Ecotone

Cordylanthus nidularius - FC, SR
Cordylanthus tenuis ssp. *capillaris* - FE, SR
Cryptantha clevelandii var. *dissita*
Dudleya setchellii - FE
Erigeron angustatus
Erigeron serpentinus
Eriogonum nervulosum - FSC
Fritillaria falcata - FSC
Hesperolinon bicarpellatum - FSC
Hesperolinon breweri - FSC
Hesperolinon congestum - FT, ST
Hesperolinon drymarioides - FSC
Hesperolinon serpentinum
Lessingia micradenia var. *glabrata* - FSC
Lessingia micradenia var. *micradenia* - FSC
Madia hallii - FSC
Navarretia rosulata
Sidalcea hickmanii ssp. *viridis* - FSC
Streptanthus albidus ssp. *albidus* - FE
Streptanthus albidus ssp. *peramoenus* - FC
Streptanthus batrachopus - FSC
Streptanthus brachiatus ssp. *brachiatus* - FC
Streptanthus brachiatus ssp. *hoffmanii* - FC
Streptanthus glandulosus ssp. *pulchellus*
Streptanthus morrisonii ssp. *elatus* - FC
Streptanthus morrisonii ssp. *hirtiflorus* - FC
Streptanthus morrisonii ssp. *kruckebergii* - FSC
Streptanthus morrisonii ssp. *morrisonii* - FSC
+*Hoita strobilina*
+*Streptanthus breweri* var. *hesperidis*

3. *Cardamine pachystigma* var. *dissectifolia*
+*Streptanthus glandulosus* var. *sonomensis*

4. *Acanthomintha lanceolata*
Asclepias solanoana
Aspidotis carlotta-halliae
Calamagrostis ophitidis
Calyptridium quadripetalum
Campanula exigua
Clarkia breweri
Collomia diversifolia
Cordylanthus tenuis ssp. *brunneus*
Eriogonum argillosum
Eriogonum ternatum
Eriogonum tripodum
Fritillaria purdyi
Galium andrewsii ssp. *gatense*
Lomatium ciliolatum var. *hooveri*
Navarretia jepsonii
+*Ceanothus jepsonii* var. *albiflorus*
+*Streptanthus barbiger*

Granite and sandstone outcrops

4. *Arctostaphylos regismontana*

Volcanic outcrops

1b. *Eriastrum brandegeae* - FSC

4. *Madia nutans*

9. Riparian vegetation

1b. *Juglans californica* var. *hindsii* - FSC
+*Triteleia lugens*

4. *Astragalus rattanii* ssp. *rattanii*

10. Freshwater vegetation

A. Freshwater marsh

1a. *Castilleja uliginosa* - FSC, SE

1b. *Alopecurus aequalis* var. *sonomensis* - FE
Arenaria paludicola - FE, SE
Campanula californica - FSC
Carex albida - FE, SE
Lilium pardalinum ssp. *pitkinense* - FE, SE
Potentilla hickmanii - FPE, SE
Rhynchospora californica - FSC
Sidalcea calycosa ssp. *rhizomata*
Sidalcea oregana ssp. *valida* - FE, SE

2. *Calamagrostis crassiglumis* - FSC
Carex comosa
Carex leptalea
Rhynchospora globularis var. *globularis*

3. *Equisetum palustre*

4. *Calamagrostis bolanderi*
Rhynchospora alba
+*Zigadenus micranthus* var. *fontanus*

B. Limnetic vegetation

2. *Potamogeton filiformis*
Potamogeton zosteriformis

4. *Azolla mexicana*
Ranunculus lobbii

C. Vernal pools

1b. *Blennosperma bakeri* - FE, SE
Gratiola heterosepala - SE
Lasthenia burkei - FE, SE
Lasthenia conjugens - FE
Legenere limosa - FSC
Limnanthes vinculans - FE, SE
Navarretia leucocephala ssp. *bakeri*
Navarretia leucocephala ssp. *pauciflora* - FE, ST
Navarretia leucocephala ssp. *plieantha* - FE, SE
Neostapfia colusana - FT, SE
Tuctoria mucronata - FE, SE

2. *Downingia pusilla*

3. *Myosurus minimus* ssp. *apus* - FSC
Pogogyne douglasii ssp. *parviflora*

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Table 1.4 (continued) Rare Plant Species* Found in the Nine Counties Adjacent to the San Francisco Bay Estuary, by Plant Community or Ecotone

4. *Eryngium aristulatum* var. *hooveri* - FC
   Psilocarphus brevissimus var. *multiflorus*
   Psilocarphus tenellus var. *globiferus*

D. Thermal springs

1b. *Dichanthelium lanuginosum* var. *thermale* - FSC, SE
   Plagiobothrys strictus - FE, ST
   Poa napensis - FP, SE

11. Anthropogenic environments

A. Agricultural

B. Urban-suburban

12. Coastal marsh

A. Brackish marsh

1b. *Aster lentus* - FSC
   Cirsium hydrophilum var. *hydrophilum* - FE
   Cordylanthus mollis ssp. *mollis* - FE, SR
   Lathyrus jepsonii var. *jepsonii* - FSC
   Lilaeopsis masonii - FSC, SR

2. *Limosella subulata*

B. Saltmarsh

1b. *Castilleja ambigua* ssp. *humboldtiensis* - FSC
   Cordylanthus maritimus ssp. *palustris* - FSC
   Suaeda californica - FE

3. *Polygonum marinense* - FSC

4. *Eleocharis parvula*
   Grindelia stricta var. *angustifolia*

13. Ecotones

A. Grassland-oak woodland

1b. *Helianthella castanea* - FSC
   Monardella villosa ssp. *globosa*

4. *Linanthus acicularis*

B. Grassland-rock outcrops

1b. *Balsamorhiza macrolepis* var. *macrolepis*
   Clarkia concinna ssp. *raichei* - FSC
   Layia septentrionalis
   Pentachaeta bellidiflora - FE, SE
   Stebbinsoseris decipiens - FSC

4. *Micropus amphibolus*

C. Mixed evergreen-chaparral

1b. *Arctostaphylos andersonii* - FSC
   Arctostaphylos canescens ssp. *sonomensis*
   Cupressus abramsiana - FE, SE
   Eriogonum nudum var. *decurrens*
   Lupinus sericatus
   Penstemon rattanii var. *kleei*

4. *Calystegia collina* ssp. *oxyphylla* - FSC
   Erythronium helenae
   Lilium rubescens
   Monardella viridis ssp. *viridis*

D. Mixed evergreen-serpentinite outcrops

4. *Calochortus umbellatus*

E. Rock outcrops-riparian

1b. *Delphinium californicum* ssp. *interius* - FSC

4. *Trichostema rubisepalum*

F. Serpentinite outcrops-riparian (including serpentine seeps)

1b. *Cirsium fontinale* var. *campylon* - FSC
   Cirsium fontinale var. *fontinale* - FE, SE
   Cirsium hydrophilum var. *vaseyi* - FSC

4. *Astragalus clevelandii*
   Cypripedium californicum
   Delphinium uliginosum
   Helianthus exilis
   Mimulus nudatus
   Senecio clevelandii var. *clevelandii*

G. Coastal coniferous forest-riparian

1b. *Pedicularis dudleyi* - FSC, SR

4. *Cypripedium fasciculatum* - FSC
   Pleuropogon refractus

H. Oak woodland-serpentinite outcrops

1b. *Eriophyllum latilobum* - FE, SE

I. Oak woodland-chaparral

1b. *Calochortus pulchellus*

4. *Eriophyllum jepsonii*

J. Alkaline grassland-pans

1a. *Plagiobothrys glaber*
   Plagiobothrys mollis var. *vestitus* - FSC

K. Coastal coniferous forest-coastal prairie

1b. *Sidalcea malachroides*

L. Freshwater marsh-riparian

1b. *Sagittaria sanfordii* - FSC

2. *Hibiscus lasiocarpus*

M. Grassland-southern coastal scrub

2. *Senecio aphanactis*

N. Coastal prairie-northern coastal scrub

1b. *Delphinium luteum* - FPE, SR

O. Grassland-chaparral

1b. *Clarkia imbricata* - FE, SE
   Horkelia tenuiloba

P. Northern coastal scrub-riparian

4. *Veratrum fimbriatum*

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2

Estuarine Fish and Associated Invertebrates

Opossum Shrimp

Neomysis mercedis

Bruce Herbold

General Information

The opossum shrimp is a native mysid shrimp that is an important food for many estuarine fish, especially young striped bass. Since 1994, their role of dominant planktonic shrimp has been overwhelmed by the introduced species, *Acanthomysis* (Orsi and Mecum 1996).

Reproduction

The common name of the opossum shrimp derives from the fact that females carry their eggs and young in a pouch at the base of the last two pairs of legs. Young are released at a well-developed stage. Fecundity is related both to adult size and season (Heubach 1969).

Reproduction is continuous but the rate is strongly controlled by temperature and food supply. Thus, the rate is high during spring and summer months and slows down as temperature and insolation decline. The wintertime population is composed largely of large adults, whose greater fecundity allows rapid development of high densities as temperatures and phytoplankton densities rise. The autumn decline in density has been variously attributed to seasonal changes in high temperature, low dissolved oxygen, predation, and food supply (Turner and Heubach 1966, Heubach 1969, Siegfried et al. 1979, Orsi and Knutson 1979).

Actual length to 0.8 inches

ARO, M. Roper

Food and Feeding

The diet of *N. mercedis* varies with size. At release, young shrimp eat mostly phytoplankton and rotifers. Adult diets include phytoplankton and rotifers but the diet shifts more to copepods, particularly *Eurytemora affinis* (Herbold et al. 1992).

Distribution

N. mercedis is found in greatest abundance in Suisun Bay and the western Delta, although it occurs as far upstream as Sacramento, the lower reaches of the Mokelumne River, and in the San Joaquin River to above Stockton.

Population Status and Influencing Factors

During most of the 1980s, the opossum shrimp population varied considerably, but remained at a lower level of abundance than existed in the early 1970s. Opossum shrimp abundance fell dramatically after 1986 and remained at very low levels from 1990 to 1993 (CDFG 1994). As a general trend, opossum shrimp populations have declined substantially in Suisun Bay, yet they have occasionally rebounded to high levels (BDOC 1993).

Reasons for the system-wide declines of several zooplankton taxa in the Bay-Delta Estuary are not known. Although the declines occurred at about the same time as declines in phytoplankton and various fish species, no cause-and-effect relationships have been established (CDWR 1992). However, several factors have been identified which are believed to have some influence on the decline of zooplankton in the Estuary.

Decrease in food supply has been associated with the decline in abundance of rotifers and the copepod, *E. affinis*. The decline of rotifers in the Delta appears to be strongly associated with declining concentrations of chlorophyll *a*, which formerly characterized the areas of greatest rotifer abundance (Herbold et al. 1992). However, chlorophyll and many zooplankton species have similar spatial distributions, and correlations between the two groups can arise through movement of the entrapment zone in the Estuary. Also, while it is commonly assumed that chlorophyll is a good measure of food availability for zooplankton, *E. affinis* can subsist on detrital matter and requires larger particles than those that make up total chlorophyll. In addition, small zooplankton could provide food for many of the larger zooplankton species (Kimmerer 1992). Consistently low *E. affinis* abundance in recent years has been named as a factor that has probably contributed to the decline of opossum shrimp (Herbold et al. 1992).

Introduced species have also been named as a potential cause for the decline in zooplankton abundance. For example, the introduction of *Sinocalanus* has been identified as a possible cause of the decline in abundance of *E. affinis* (Kimmerer 1992), although the introduced copepod does not have the same habitat requirements as the native copepods (NHI 1992). However, based on the known feeding habits of a related species of *Sinocalanus, S. doerrii* may prey on native copepods (Herbold et al. 1992). In addition, predation by the introduced Asian clam, *Potamocorbula amurensis*, has been suggested as a factor in the decline of rotifer (Herbold et al. 1992) and *E. affinis* populations. *E. affinis* abundance in Suisun Bay decreased substantially when the clam became abundant there in 1988 (CDWR 1992). Since 1994 *Neomysis* abundance has dropped to less than that of an introduced species of mysid shrimp which has increased in abundance (Orsi 1996). Competition with both the clam and new shrimp are likely to prevent re-establishment of *Neomysis* at the levels of their former abundance.

The decline in the abundance of opossum shrimp and other zooplankton species (e.g., *E. affinis*) that are found in the entrapment zone in relatively high abundances has been correlated with Delta outflow. It is presumed that low outflow reduces opossum shrimp abundance by: (1) restricting the entrapment zone to deeper, more upstream channels which are less likely to promote high densities of opossum shrimp; and (2) producing weaker landward currents along the bottom so that the ability of opossum shrimp transported downstream to return to the entrapment zone is reduced. It has also been presumed that larger numbers of opossum shrimp may be exported through the Central Valley Project and State Water Project pumps as a result of the increased proportion of inflow diverted during drought years when the entrapment zone is upstream in the Estuary. The location of the entrapment zone within the lower river channels during dry years increases the vulnerability of opossum shrimp to such displacement (Herbold et al. 1992). However, analyses by Kimmerer (1992) suggest that exports by the water projects are not a major source of losses for opossum shrimp and *E. affinis* populations, primarily due to the small percentage of entrapment zone volume (and entrapment zone organisms) diverted. Depending on the timing, location, and quantity of withdrawals, in-Delta water diversions, whose net consumption is on the same order of export flows, may result in a higher rate of loss to resident zooplankton populations than export pumping.

Pollutants may be another factor in the decline of zooplankton in the upper Estuary. For example, rice herbicides have been shown to be toxic to opossum shrimp (CDWR 1992). However, rice herbicides are largely confined to the Sacramento River, not the entire Estuary. No Estuary-wide decline in planktonic crustaceans have been associated with the timing of herbicide occurrence in the river (NHI 1992).

Trophic Levels

The opossum shrimp is a primary and secondary consumer.

Proximal Species

Predators: Striped bass, longfin smelt, splittail.
Prey: Various copepods, various phytoplankton.
Competitors: *Potamocorbula amurensis, Acanthomysis* spp.

Good Habitat

Good habitat appears to be similar to that of Delta smelt; a well-dispersed area of open water with salinities in the range of 2 to 6 ppt for most of the year and clean, nontoxic over-wintering habitat in freshwater through the winter and early spring. Dead-end sloughs both in Suisun Marsh and upstream apparently serve as important refuges from predation during the annual period of low abundance and slow growth. With the advent of newly introduced competitors in the open waters of the Estuary it is possible that such refugia will become important for the year-round maintenance of opossum shrimp.

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Dungeness Crab

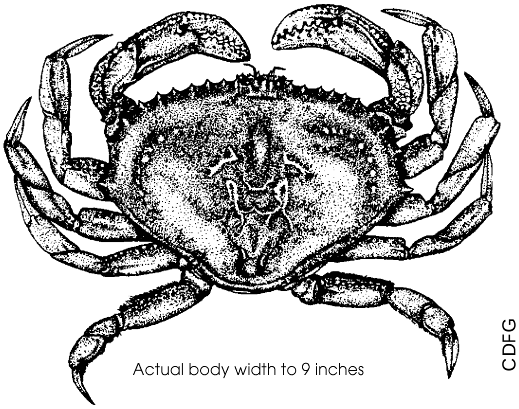
Cancer magister

Robert N. Tasto

General Information

Dungeness crab has been the object of an immensely popular commercial and recreational fishery in the San Francisco region since 1848. The San Francisco fishery, which occurs exclusively outside the Golden Gate, was long a mainstay of statewide commercial landings. However, beginning in the early 1960s, it underwent a severe and longterm decline which persisted until the mid-1980s. The principal causes of the decline have been related to changes in ocean climate, increased predation, and possibly pollution (Wild and Tasto 1983). Landings in the past decade have rebounded to some extent and are generally able to accomodate local market demand, but the northern California fishery (Eureka and Crescent City) continues to be the major provider of Dungeness crabs throughout the rest of California. The value of the Dungeness crab resource extends beyond the traditional economic return to the fishermen, seafood processors, and retail markets, as it is an important element in the tourism industry of San Francisco.

California commercial and recreational fishing regulations pertaining to Dungeness crab have been designed to protect this species from over-harvesting. The standard commercial fishing gear is a baited 3.5-foot diameter metal trap, weighing 60 to 120 pounds (Warner 1992). California regulations set a 6.25-inch carapace width (cw) size limit, prohibit the take of female crabs, and, like most states, have established a specific fishing season to protect reproducing and egg-bearing crabs. A limited recreational fishery allows the take of female crabs and has a smaller size restriction (5.75 inches cw); a 10-crab bag limit is placed on the sportfishers. Recreational gear consists of a variety of traps, hoops, and nets of different sizes, shapes, and materials. It is currently



Actual body width to 9 inches

CDFG

illegal to catch Dungeness crab of any size in San Francisco Bay.

Reproduction

Mating occurs in nearshore coastal waters, from March through May, between hard-shelled males and recently molted, soft-shelled females. Fertilized eggs are extruded in the fall and lay protected beneath the female's abdominal flap in a sponge-like mass until hatching occurs from late December to mid-January (Wild and Tasto 1983). Fecundity ranges from 500,000 to 2,000,000 eggs, depending upon the size of the female (Warner 1992). *C. magister* is capable of about four broods over its reproductive life span (Hines 1991).

Growth and Development

Dungeness crab life stages include the egg, larval, juvenile, and adult. Dungeness crab eggs range in diameter from 0.016 to 0.024 inches (Warner 1992). There are a total of six larval stages (five zoeae and one megalopa) which spend about 3 to 4 months in both nearshore and offshore coastal waters; larval timing is believed to coincide with peak plankton production (Hines 1991). Late-stage megalopae, which have returned to the coast, bays, and estuaries via ocean currents and other mechanisms, settle onto relatively open sandy areas (Oresanz and Gallucci 1988) and subsequently metamorphose to the first bottom-dwelling instar stage generally between April and June. It is at this stage that the young crabs enter San Francisco Bay in large numbers, relative to year-class strength, seemingly aided by strong bottom currents (Tasto 1983). San Francisco Bay-reared crabs molt more frequently than those juveniles found in the near coastal environment and reach sexual maturity (approximately 4 inches wide) after nearly one year (Wild and Tasto 1983). This rate of growth is substantially greater than that found in open areas along the Pacific coast and may be due to increased availability of food and/or overall warmer temperatures of estuaries (Tasto 1983, Gunderson et al. 1990, Wainwright and Armstrong 1993). It is believed that the large number of molts necessary to reach sexual maturity in an estuarine environment is due, in large part, to the demands of osmoregulation (Oresanz and Gallucci 1988).

Food and Feeding

Larval Dungeness crab in the water column are planktivorous, whereas the juvenile and adult crabs are opportunistic foragers on larger bottom-dwelling organisms. In the San Francisco Estuary, juvenile crabs have been shown to feed on clams, crustaceans, and small fishes (Tasto 1983). In Grays Harbor, Washington, juvenile crab diets consisted primarily of *Crangon* shrimp, juvenile fish, and bivalves (Gunderson et al. 1990). By comparison to other cancrid crabs, the small chelae of *C. magister* are better suited for soft-bodied, mobile prey found on sandy bottoms (Oresanz and Gallucci 1988). One study has suggested that size-specific feeding on clams in the laboratory was due to an attempt to minimize handling time of the prey in a competitive situation (Palacios and Armstrong 1990).

The most common predators on juvenile crabs within the San Francisco Estuary include bottom-feeding fishes such as starry flounder, English sole, Pacific tomcod, Pacific staghorn sculpin, white croaker, pile perch, sturgeon, and several elasmobranchs (sharks, skates, and rays) (Reilly 1983a). The principal predator on young-of-the-year Dungeness crab in Gray's Harbor Estuary was found to be the Pacific staghorn sculpin (Fernandez et al. 1993a). In addition, cannibalism is reported to occur among all age groups (Warner 1992).

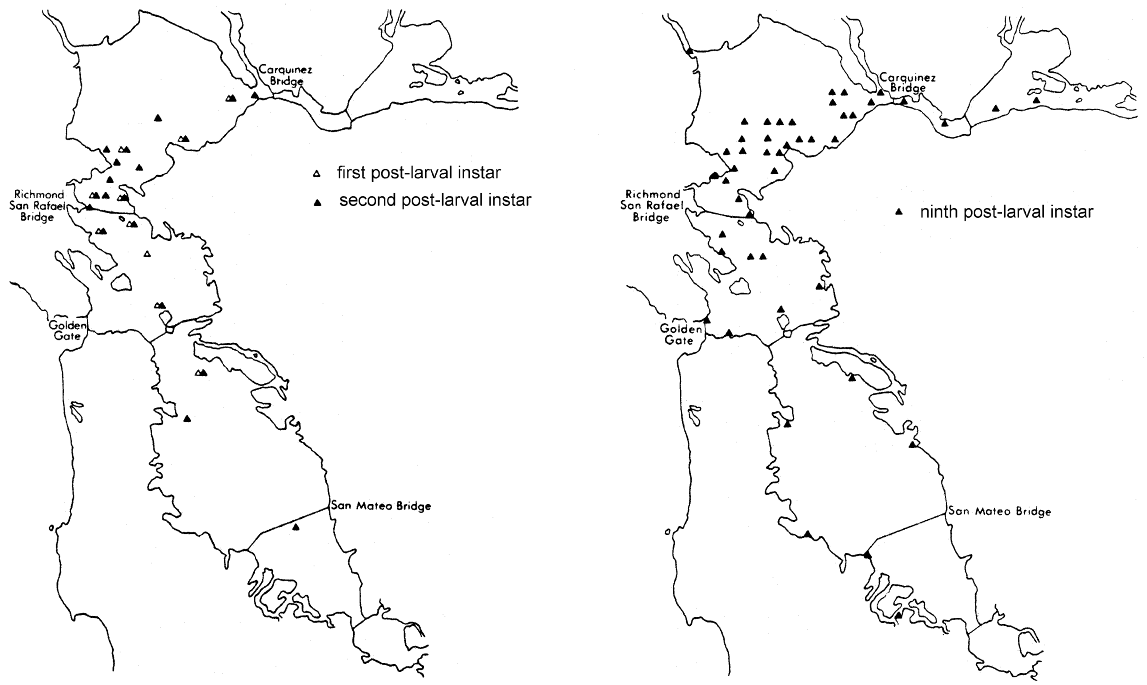
Distribution

Dungeness crab range from the Aleutian Islands to Santa Barbara, but are rare south of Point Conception (Warner 1992). The pelagic larval forms are found distributed widely in both nearshore and offshore waters, but return to the coast, bays, and estuaries where the juvenile and adult stages are mostly found from the intertidal zone to approximately 300 feet (Hatfield 1983, Reilly 1983b, Warner 1992). San Francisco Bay, as is the case with other coastal estuaries, is an important nursery area for the offshore stock. The vast majority of individuals in the Bay are juveniles of a single year-class, having entered in the spring of one year and exited approximately 1 year later (Tasto 1983, McCabe et al. 1988). Juveniles are often found in tidal and navigational channels early in summer, but spread out over mudflats and into protected shoreline areas as they develop over the year (**Figures 2.1** and **2.2**).

Population Status and Influencing Factors

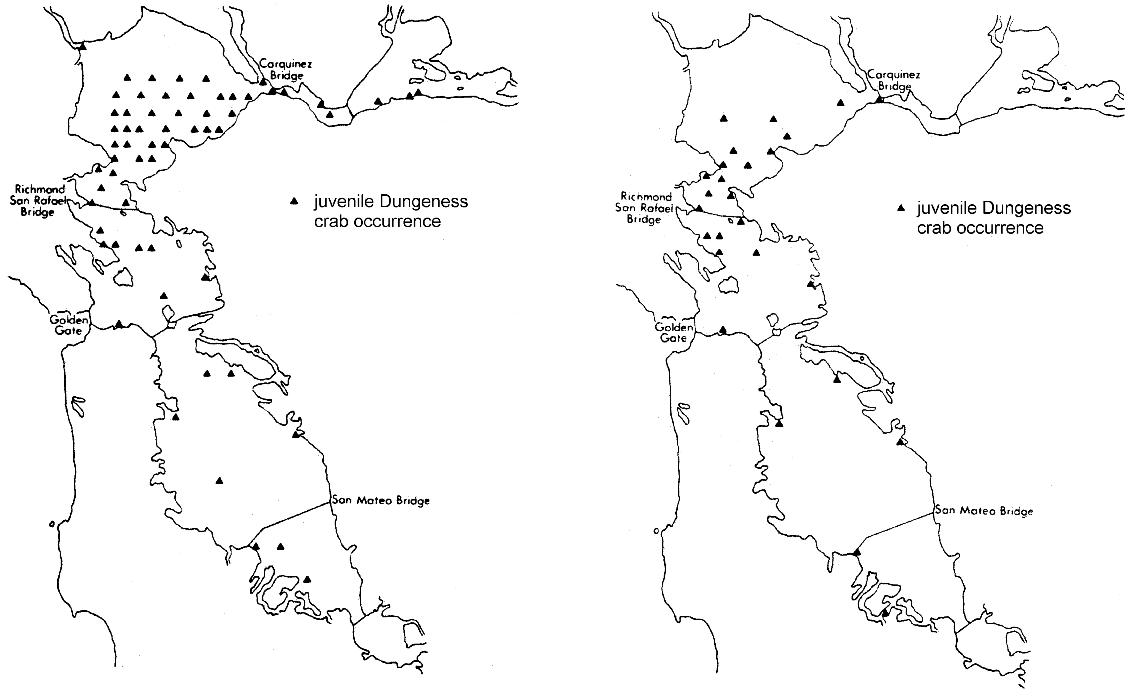
Few population estimates have been made on individual Dungeness crab stocks along the Pacific coast because there is significant variation in year-class strength, purportedly due to environmental conditions and density-dependent factors (Botsford and Hobbs 1995). However, commercial crab landings, monitored annually by state and, in some instances, federal resource agencies, appear to be a reliable indicator of relative abundance.

The most important factors affecting overall population numbers in the San Francisco area (i.e., Half Moon Bay to Bodega Bay) include ocean temperatures (hatching success), ocean currents (larval drift), predation, commercial fishing, and, possibly, pollution of nursery habitat (Wild and Tasto 1983). Although labo-



Bay collection sites for early post-larval instar crabs.

Bay collection sites for ninth post-larval stages.



Bay collection sites for 0-age class crabs. September through December 1975-1979.

Bay collection sites for 1-year-old crabs. April through May 1975-1979.

Figure 2.1 Seasonal Distribution of Juvenile Dungeness Crab Within San Francisco Bay (Tasto 1983)

ratory results show that cannibalism may be an important determinant in the abundance and structure of some populations (Fernandez et al. 1993b), year-class strength and recruitment to the fishery do not appear to be dependent upon success of any particular "critical" stage (McConnaughey and Armstrong 1990). Within the San Francisco Estuary, juvenile abundance varies considerably from year to year, but is often highest in San Pablo Bay and lowest in south Bay (Tasto 1983, CDFG 1987).

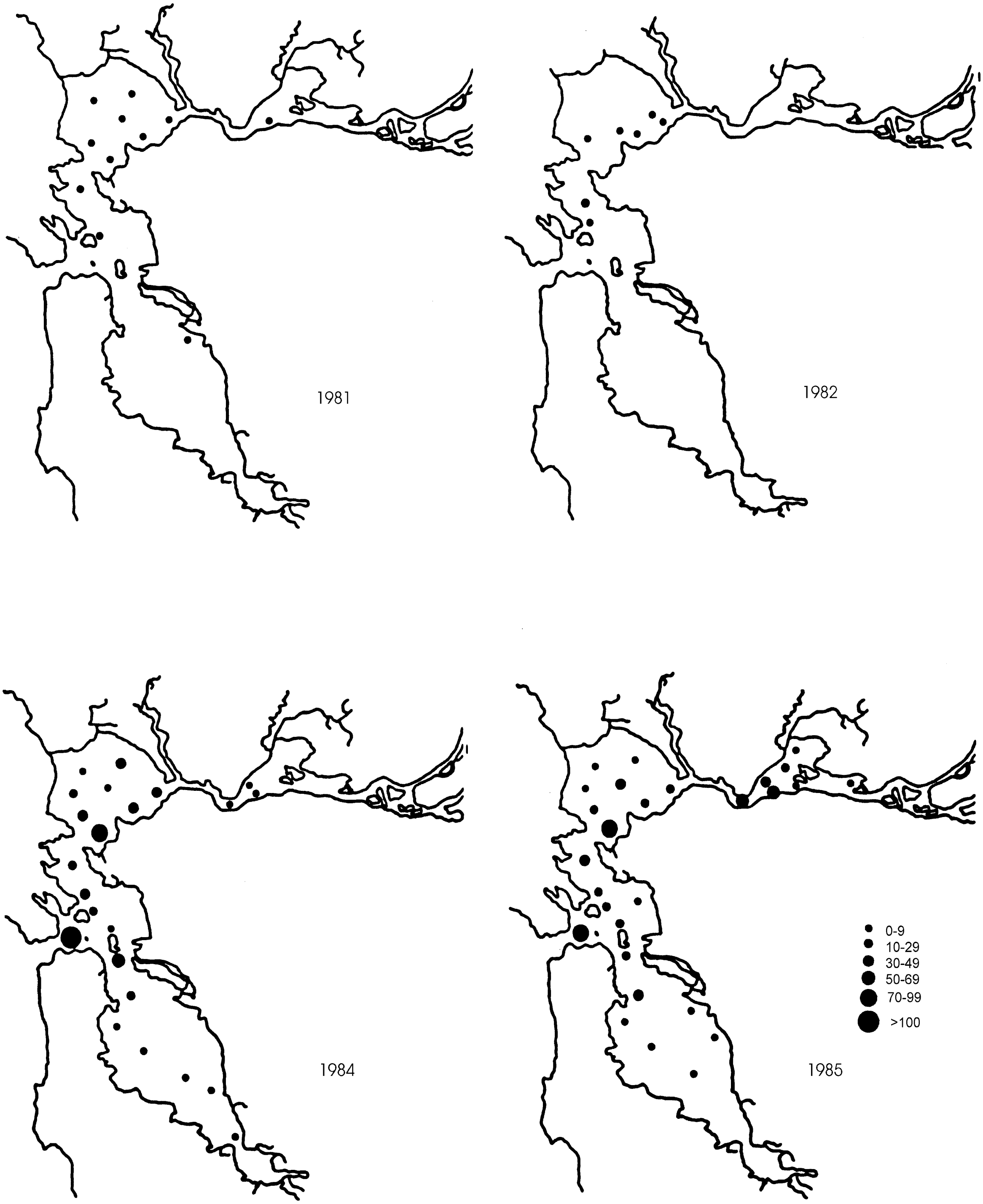


Figure 2.2 Annual Distribution of Juvenile Dungeness Crab Within the San Francisco Bay – Caught by Otter Trawl, May-December (CDFG 1987)

Trophic Levels

Larvae are planktivores making them primary consumers (phytoplankton) and secondary consumers (zooplankton). Juveniles and adults are higher order consumers.

Proximal Species

Predators: Chinook and coho salmon* (prey on late larval stages); *Carcinonemertes errans** (predator worm on egg masses); Dungeness crab (cannibalism by larger instars, principally females, on small juveniles), starry flounder, English sole, Pacific tomcod, Pacific staghorn sculpin, white croaker, brown smoothhound shark, and skate (prey on juveniles); and humans (commercial and recreational fishing for adults*).

* Generally takes place outside of San Francisco Bay.

Prey: Crustaceans, bivalves (clams), small fishes.

Good Habitat

Juvenile crabs appear to prefer sandy or sandy-mud substrate, but can be found on almost any bottom type (e.g., shell debris). Structurally complex habitats that provide protection from predation (e.g., high relief shell, eel grass, drift macroalgae, etc.) are favored over bare mud or open sand (Fernandez et al. 1993a, Iribarne et al. 1995, Eggleston and Armstrong 1995, McMillan et al. 1995).

Chemical and physical characteristics of the water column and sediment are also important habitat features. Juvenile Dungeness crab in the San Francisco Estuary seem to be somewhat intolerant of salinities lower than 10 ppt (Tasto 1983, CDFG 1987). Maximum growth appears to occur at 15°C or above (Kondzela and Shirley 1993, McMillan et al. 1995); and studies in Washington State have shown that juvenile crab have stable metabolic rates at elevated estuarine temperatures (e.g., 14 to 16°C), whereas older crabs were more stable at colder temperatures (Gutermuth and Armstrong 1989). This is consistent with the tendancy for juvenile crabs to emigrate out of estuaries into colder coastal waters as they approach sexual maturity.

Although no single pollutant, or suite of pollutants, has been shown to significantly affect Dungeness crab, various studies on different life stages have shown sensitivity to oiled sediments, dissolved oxygen levels below 5 ppm, low ammonia concentrations, pesticides, and chlorinated wastewater (Wild and Tasto 1983, Emmett et al. 1991). Juvenile crab abundance in the Bay has been shown to be negatively correlated to Delta outflow (CDFG 1987).

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Rock Crabs

Cancer antennarius and *Cancer productus*

Robert N. Tasto

General Information

The brown rock crab *(Cancer antennarius)* is found along the west coast of North America from Washington State to Baja California; the red rock crab *(Cancer productus)* has a slightly more northerly distribution, i.e., Alaska to San Diego (Carroll and Winn 1989). A small recreational fishery exists for brown and red rock crabs in central San Francisco Bay and parts of south Bay and San Pablo Bay. Most rock crabs in this fishery are caught from piers and jetties by a variety of baited hoop nets and traps. A modest commercial fishery also occurs throughout California waters, with the vast majority of the catch taking place from Morro Bay southward (Parker 1992). Ex-vessel value for the commercial fishery approached $2 million in the mid-1980s (Carroll and Winn 1989) and appears to be unchanged since then. Unlike their close relative, the Dungeness crab, which has a significant amount of muscle tissue in the body, rock crabs, generally, have been sought after for their claws only. In recent years, however, live whole crabs have become a larger part of the retail market. California Department of Fish and Game regulations prohibit the commercial take of crabs less than 4.25 inches carapace width (cw), require that sport-caught crabs must be 4.0 inches cw or greater, and impose a bag limit of 35 crabs per day.

Reproduction

Mating takes place between a soft-shelled (recently molted) female and hard-shelled male. Male brown rock crabs have been reported to outnumber females by a ratio of 1.6/1 (San Mateo County coast) during all seasons (Breen 1988), although studies by Carroll (1982) at Diablo Cove showed that females were more abundant in the fall, with no other seasonal trends for either sex. Unfertilized eggs remain within the female for approximately three months, following mating, and then are fertilized by the stored sperm as they are released (Parker 1992). The fertilized eggs are then carried until hatching (6 to 8 weeks) in a sponge-like mass beneath the female's abdominal flap (Parker 1992). Female body size is the principal determinant of reproductive output and fecundity, with red rock crab having 172,600 to 597,100 eggs per brood and brown rock crab having 156,400 to 5,372,000 eggs per brood (Hines 1991). Like the Dungeness crab, ovigerous female rock crabs have been observed buried in the sand at the base of rocks in shallow waters protecting their eggs (Reilly 1987). Also, some red rock crab females have been detected emigrating out of estuaries prior to spawning to avoid osmotic stress (Oresanz and Gallucci 1988).

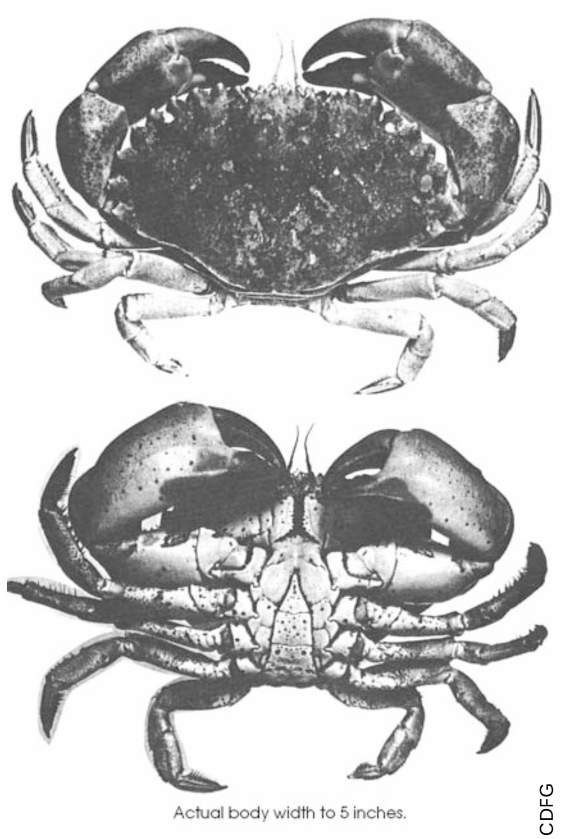
Hatching takes place in spring and early summer in central California (Carroll 1982). The planktonic larvae then settle to the bottom before beginning the juvenile stage. Juvenile abundance is highest in San Francisco Bay during the summer months (CDFG 1987). Much like other cancrids, larval release in spring coincides with peak plankton production, and settlement in the summer is optimal for growth (Hines 1991). The reproductive life span for the red rock crab is approximately four years with four broods, and for the brown rock crab it is approximately seven years with up to 10 broods (Hines 1991).

Growth and Development

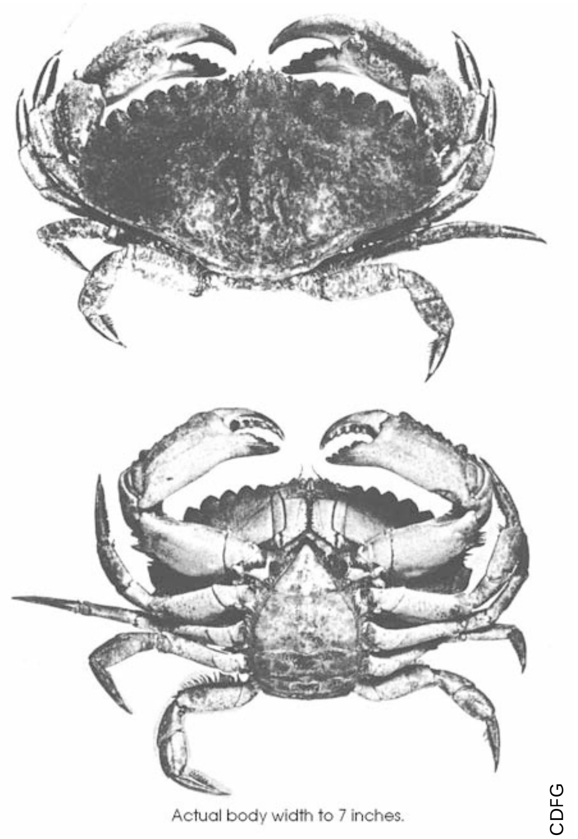
Brown rock crabs are known to go through 10 to 12 molts before reaching sexual maturity at about 3 inches cw, and will likely molt one to two times per year thereafter (Parker 1992). The average number of red rock crab instars is 13 over the total life span (Oresanz and Gallucci 1988). Studies in Humboldt Bay (O'Toole 1985) found ovigerous red rock crab as small as 3.7 inches cw. Brown rock crabs have reached a maximum 6.5 inches cw and red rock crabs, the larger of the two species, at 8 inches cw (Carroll and Winn 1989, Parker 1992). Maximum life span of the brown rock crab has been estimated at 5-6 years (Carroll 1982).

Food and Feeding

Rock crabs are both nocturnal predators and scavangers and have been shown to feed upon hard-shelled organisms such as clams, snails, and barnacles (Parker 1992). The large chelae of these crabs is well-suited to forage on the hard shells of more sedentary prey of their rocky habitats (Oresanz and Gallucci 1988). Red rock crab feed upon intertidal mussels and barnacles (Robles et al. 1989). Juvenile rock crabs are preyed upon by other macroinvertebrates and demersal fishes, whereas adults are prey items for marine mammals (Carroll 1982). Very little is known about the specific food habits of, or predators upon, these two species of rock crabs within San Francisco Bay; however, the sportfishery within the Bay accounts for the loss of an indeterminate number of adult crabs.



Brown Rock Crab, *Cancer antennarius*.
Top and bottom: Views of 5 in. male crab.



Red Rock Crab, *Cancer productus*.
Top: top surface of 6.5 in. male. Bottom: under surface of 5.75 in. female.

Distribution

Both rock crab species inhabit the low intertidal zone to depths of 300 feet or more (Parker 1992) and, although their microhabitat utilization patterns are similar, they appear to be different in how they utilize estuaries (Oresanz and Gallucci 1988). The brown rock crab is principally a marine species and does not osmoregulate well in brackish waters, whereas the red rock crab can successfully inhabit brackish areas. All stages of the red and brown rock crab have been collected in San Francisco Bay, including larvae and ovigerous females (**Tables 2.1** and **2.2**). Areas of peak abundance appear to be in Central Bay, the northern portion of South Bay, and the southern portion of San Pablo Bay, with the red rock crab having a somewhat greater distribution than the brown rock crab (CDFG 1987). In general, rock crab movement is local (Breen 1988, Carroll and Winn 1989). At Fitzgerald Marine Reserve along the San Mateo County coast, studies demonstrated that juvenile brown rock crab are most abundant in July, although no seasonal trend in the settlement of early instars was evident (Breen 1988). In Santa Barbara County, Reilly (1987) found all stages of rock crabs to be most abundant in the fall.

Population Status and Influencing Factors

There are no known estimates of the overall population size or knowledge of recruitment mechanisms for San Francisco Bay rock crabs. Most studies have shown that population densities of rock crabs were well below 1/m^2 (Carroll 1982, Breen 1988). Small, local populations of rock crab can be overfished, although there is no evidence suggesting that overfishing occurs in the Bay. Data from the Interagency Ecological Study Program indicate that there is a negative relationship between abundance of both rock crab species and outflow from the Delta (CDFG 1987).

Trophic Levels

Rockcrab larvae are planktivores and, as such, are both primary consumers (phytoplankton) and secondary consumers (zooplankton). Juveniles and adults are higher order consumers.

Proximal Species

Predators: Marine mammals, humans (recreational fishery).
Prey: Bay mussels, barnacles.

Good Habitat

Not surprisingly, both species have been shown to prefer rocky shore, subtidal reef, or coarse gravel and sand substrate (Carroll and Winn 1989). Opportunity for concealment appears to be an important feature of red rock crab habitat in British Columbia studies (Robles et al. 1989). Juvenile brown rock crab, when settling from the last larval stage, appear to accept both sand and rock as suitable substrate (Carroll and Winn 1989), and red rock crab also tend to settle out onto structurally complex substrates (Oresanz and Gallucci 1988).

Table 2.1 Annual Abundance of Rock Crabs Caught by Otter Trawl (crabs/tow) in the San Francisco Estuary (CDFG 1987)

Species and Size Class	1980	1981	1982	1983	1984	1985	1986
C. antennarius (all sizes)	0.101	0.047	0.010	0.015	0.071	0.033	0.007
C. antennarius (<50mm)	0.098	0.037	0.005	0.015	0.067	0.024	0.007
C. gracilis (all sizes)	0.035	0.103	0.044	0.182	0.333	0.240	0.174
C. gracilis (<20mm)	0.003	0.005	0.034	0.080	0.079	0.064	0.095
C. productus (all sizes)	0.014	0.032	0.005	0.010	0.055	0.071	0.088
C. productus (<50mm)	0.014	0.027	0.002	0.005	0.040	0.050	0.081

Table 2.2 Annual Abundance of Rock Crabs Caught by Ring Net (crabs/tow) in the San Francisco Estuary (CDFG 1987)

Species and Size Class	1980	1981	1982*	1983	1984	1985	1986
C. antennarius (all sizes)	-	-	0.113	0.095	0.296	0.491	0.407
C. antennarius (<50mm)	-	-	0	0.009	0.028	0.009	0.176
C. gracilis (all sizes)	-	-	0.014	0.019	0.037	0.009	0.130
C. productus (all sizes)	-	-	0.155	0.067	2.509	4.315	0.806
C. productus (<50mm)	-	-	0	0	0.185	0.148	0.157

* Ring net survey started in May 1982

Rock crabs appear to be influenced by both temperature and salinity. In various laboratory studies, both brown and red rock crab were adversely affected by exposure to water temperatures above 20°C (Carroll and Winn 1989, Sulkin and McKeen 1994). The brown rock crab is considered primarily a marine species, whereas red rock crabs can osmoregulate in more brackish water; although the latter have been shown to be adversely affected by salinities below 13 ppt (Oresanz and Gallucci 1988, Carroll and Winn 1989).

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Bat Ray

Myliobatus californica

Kurt F. Kline

General Information

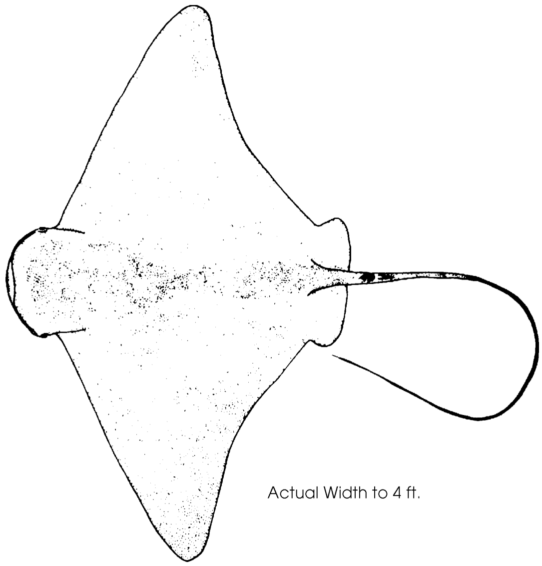
The bat ray is a member of the family Myliobatidae (eagle rays). The family is found worldwide in tropical and temperate shallow seas. Bat rays are very common and are found in sandy and muddy bays and sloughs, as well as in rocky areas and kelp beds. In shallow bays they can be found feeding in the intertidal zone during high tide.

Reproduction

Mating occurs during the summer months followed by an estimated gestation period of nine to 12 months (Martin and Cailliet 1988). The young are born alive at 220 to 356 mm wing width and weigh about 0.9 kg (Baxter 1980, Martin and Cailliet 1988). Males are mature at 450 to 622 mm wing width and two to three years, while 50% of the females are mature at 881 mm wing width and five years.

Growth and Development

The growth of juvenile bat rays is not well documented, but is likely at least 100 mm per year. They can grow to



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a wingspan of six feet (>2000 mm) though individuals this large are uncommon. The largest bat ray reported was a 95 kg female from Newport Bay (Baxter 1980).

Food and Feeding

Bat rays are opportunistic bottom feeders, feeding primarily upon benthic and epibenthic invertebrates. In Elkhorn Slough, bat rays feed primarily on clams and the echiuroid worm, *Urechis caupo*; in La Jolla kelp beds, they feed on shellfish including abalone and snails; and in Tomales Bay, they feed on polychaete worms, large clams and echiuroid worms (Karl and Obrebski 1976, Karl 1979, Talent 1982). Studies done along the southern California coast (Van Blaricom 1982) found that pits dug by feeding bat rays were an important controlling factor of infaunal community organization, opening areas for infauna recolonization and uncovering food items for other fish.

Distribution

The bat ray ranges from the Gulf of California to Oregon, and is found from shallow subtidal water to 46 m. It is common in bays and shallow sandy areas along the coast (Miller and Lea 1976).

Population Status and Influencing Factors

The current status of the bat ray in San Francisco Bay is unknown. Its distribution is likely influenced by salinity; it has occaisionally been collected in San Pablo Bay at salinities lower 20 ppt (Flemming 1999).

Trophic Levels

Bat rays are primary consumers, feeding primarily on benthic invertebrates. They are taken by fishermen using cut fish as bait, however natural feeding on fishes has not been documented.

Proximal Species

Prey: Benthic mollusks, polychaetes, crustaceans, *Urechis caupo*.

Good Habitat

Sandy to muddy shallow bottoms with abundant mollusk and polychaete populations.

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Leopard Shark

Triakis semifasciata

Michael F. McGowan

General Information

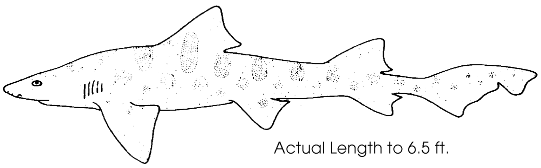
The leopard shark (Family: Elasmobranchs) is one of the most common sharks in California bays and estuaries (Talent 1976). It is the most abundant shark in San Francisco Bay (Ebert 1986) being found especially around piers and jetties (Emmett et al. 1991). The leopard shark is an important recreational species in San Francisco Bay and a limited commercial long-line fishery has targeted it in the bay (Smith and Kato 1979). Juveniles and adults are demersal and sometimes rest on the bottom (Feder et al. 1974). Although other elasmobranchs occur in euhaline bays and estuaries of the U. S. Pacific coast, the leopard shark was the only shark or ray included among 47 fish and invertebrate species in the life history summaries of west coast estuarine species prepared by the National Oceanic and Atmospheric Administration's Estuarine Living Marine Resources (ELMR) program (Emmett et al. 1991). These species were selected on the basis of commercial value, recreational value, indicator species of environmental stress, and ecological importance. That the leopard shark was selected is an indication of its importance in estuaries in general and in San Francisco Bay where it is the most abundant shark.

Reproduction

The leopard shark is a live bearer with internal fertilization, but no yolk-sac placenta. Mating occurs in the spring, primarily during April and May soon after the females give birth to from 4-29 pups (Compagno 1984). Pupping can occur from March through August with a peak in April or May (Ackerman 1971). In San Francisco Bay leopard sharks pup almost exclusively in South Bay (CDFG Bay Trawl data). The center of abundance of pups <300 mm long is south of, and just north of the Dumbarton Bridge.

Growth and Development

Embryonic development is direct and internal and takes 10-12 months. At birth pups are 18-20 cm long. Females mature when 12-14 years old at a length of 110-129 cm. Males mature earlier and at smaller sizes than females. Growth rates are slow. In San Francisco Bay tagged leopard sharks grew 1.4 cm/yr (Smith and Abramson 1990).



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Food and Feeding

Primary foods of the leopard shark are benthic and epibenthic crustaceans, clam siphons, echinuroid worms, and small fishes.

Distribution

The leopard shark is found from Mazatlan, Mexico including the Sea of Cortez to Oregon (Miller and Lea 1976). In California it is most common in estuaries and bays south of Tomales Bay (Monaco et al. 1990). Leopard sharks are apparently resident in San Francisco Bay, although some move out in fall and winter (Smith and Abramson 1990) and several size classes appear in the California Department of Fish and Game length data.

Population Status and Influencing Factors

The leopard shark probably has no predators except larger sharks and humans. Its broad dietary range should protect it from food limitation. Heavy fishing mortality poses a threat to the leopard shark, as it does to all sharks, because of its slow growth, long time to maturity, and low fecundity. The minimum size limit recommended by Smith and Abramson (1990) for sustainable fishing in San Francisco Bay was 100 cm (40 in). Areas of high freshwater input causing low salinity are largely avoided by leopard sharks.

Trophic Levels

Juveniles and adults are secondary and higher carnivores.

Proximal Species

Predators: Larger sharks, humans.
Prey: Yellow shore crab, *Urechis caupo*, ghost shrimp, rock crabs, octopus, shiner perch, arrow goby, Pacific herring, northern anchovy, topsmelt.
Cohabitors: Smoothhound sharks form mixed schools with leopard sharks.

Good Habitat

Leopard sharks are primarily a marine species which occupies bays and estuaries unless freshwater flows lower salinity excessively. Sandy and muddy bottom areas are preferred, although they may be found near rocky areas and kelp beds along the coast. Estuaries are used as pupping and rearing areas for young sharks. Shallow mud and sand flats are used for foraging during high tide (Compagno 1984).

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Pacific Herring

Clupea pallasi

Robert N. Tasto

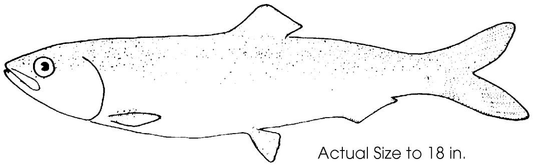
General Information

The Pacific herring (Family: Clupeidae) resource in the San Francisco Estuary is widely recognized for its commercial, recreational, and ecological values. The commercial fishery concentrates on ripe females for their roe (eggs) which are then exported to Japan, although there is some limited effort for the fresh fish market and for live bait by recreational salmon trollers (Spratt 1981, Lassuy 1989). Fishermen traditionally catch herring in nearshore areas of the Bay with gillnets or in deeper waters with round-haul nets, and there also is a relatively new roe-on-kelp fishery operated from rafts (Spratt 1981, CDFG 1992). The economic value of the fishery based upon ex-vessel prices paid to the fishermen in 1995-96 was approximately 16.5 million dollars (CDFG, unpub. data).

Reproduction

Adult herring congregate outside of San Francisco Bay before entering and generally spend about 2 weeks in the Bay before spawning (CDFG 1987). Spawning takes place from early November through March, with peak activity in January (Spratt 1981, CDFG 1992). The timing of spawning is believed to coincide with increased levels of plankton production as a food source for larvae (Lassuy 1989), as well as the presence of freshwater flows (Emmett et al. 1991). Pacific herring spawn primarily on vegetation, rock rip-rap, pier pilings, and other hard substrates in intertidal and shallow subtidal waters (Spratt 1981, Lassuy 1989, Emmett et al. 1991). Spawning occurs in waves of 1 to 3 days, occasionally up to a week in length, and often at night in conjunction with high tides (Spratt 1981). Waves are separated by one to several weeks over the length of the season with larger fish tending to spawn first (Lassuy 1989). The number and size of the waves is related to the distribution of the dominant year classes (CDFG 1992).

Egg-deposition is thought to be facilitated by the brushing of the female's vent up against the substrate, and, while there is no pairing of the sexes, the spawning area will be white with milt from the males so that the rate of fertilization is usually high (Hart 1973). Pa-



Actual Size to 18 in.

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cific herring eggs adhere to the substrate in amounts ranging from a few eggs to as many as eight layers thick (Spratt 1981). The fecundity of herring is approximately 4,000 to 134,000 eggs per female, depending upon its distribution and size (Hart 1973, Emmett et al. 1991). As with spawning, most hatching takes place at night, and will occur in 10 to 15 days under 8.5° to 10.7°C temperatures; longer if the water is colder (Emmett et al. 1991). The average in San Francisco Bay is 10.5 days at 10.0°C (CDFG 1992).

Growth and Development

Pacific herring eggs are approximately 1.0 mm in diameter, and 1.2 to 1.5 mm after fertilization (Hart 1973). A newly hatched larva, with yolk sac, is about 6 to 8 mm total length (TL) and will develop swimming powers at about 20 mm TL (CDFG 1992). Metamorphosis to the juvenile stage occurs from 25 to 35 mm TL and takes place over two to three months (Emmett et al. 1991). They are free-swimming at this stage and begin to form shoreline-oriented schools (CDFG 1992). Juveniles are 35 to 150 mm TL depending upon regional growth rates, which in turn are affected by population size and environmental conditions (Emmett et al. 1991). In the Bay Area, there are no apparent differences in the growth rates of males and females (Spratt 1981). Adults range in size from 130 to 260 mm TL, and locally it takes two to three years to reach maturity (Spratt 1981, Emmett et al. 1991). The San Francisco Bay population ranges from 110 to 250 mm TL (CDFG 1992; Ken Ota, Pers. Comm.) It is possible that some Pacific herring in more northern climates may exceed 15 years in age, but few have been noted to live longer than nine years (Emmett et al. 1991).

Food and Feeding

Pacific herring larvae, juveniles, and adults are selective pelagic planktonic feeders and move toward the water's surface to feed at dusk and dawn (Emmett et al. 1991). Generally, prey items will change with growth and geographic distribution. Larvae feed on diatoms, invertebrate and fish eggs, crustacean and mollusc larvae, bryzoans, rotifers, and copepods (Hart 1973). Juveniles consume a variety of crustaceans, as well as mollusc and fish larvae; while adults eat mostly planktonic crustaceans and fish larvae (Hart 1973, Emmett et al. 1991). In winter, there is an overall reduction in adult Pacific herring feeding as stored energy is used for ripening reproductive products and, during their spawning migration and inshore "holding" period, herring may severely limit or stop feeding entirely (Lassuy 1989).

Herring eggs are eaten by various species of fish (e.g., sturgeon), ducks (e.g., surf scoter), and gulls (CDFG 1992). Larvae are often prey for large pelagic invertebrates and various fishes, while juveniles and adults are consumed by a variety of fishes (e.g., spiny dogfish shark, Chinook salmon, Pacific staghorn sculpin, and striped bass), seabirds (e.g., Brandts cormorants, brown pelicans, and western gulls), and marine mammals, such as harbor seals (Hart 1973, Lassuy 1989, Emmett et al. 1991). Predation is considered to be the greatest source of natural mortality for juvenile and adult Pacific herring (CDFG 1992).

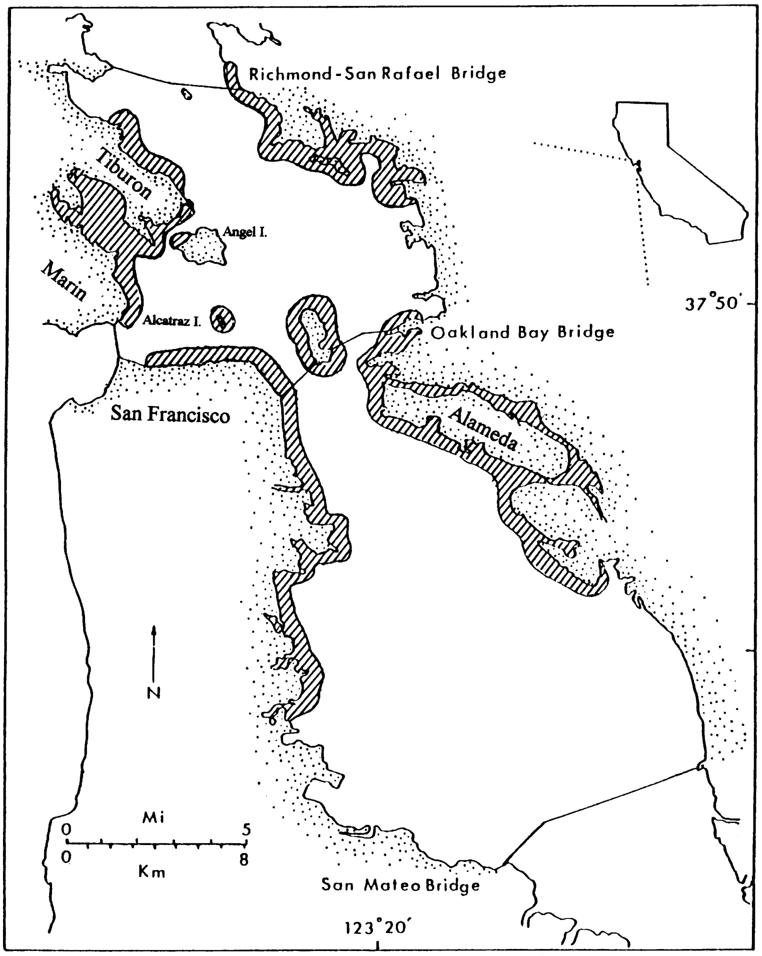
Distribution

Major populations exist in the eastern Pacific between San Francisco Bay and central Alaska (Hart 1973). Within San Francisco Bay, the principal spawning areas are found along the Marin County coastline (i.e., Sausalito, Tiburon Penninsula, and Angel Island), at the San Francisco waterfront and Treasure Island, on the east side of the Bay from the Port of Richmond to the Naval Air Station at Alameda, and on beds of vegetation in Richardson Bay and South Bay (**Figure 2.3**) (Spratt 1981, CDFG 1992). After hatching, the larvae are clumped and controlled largely by tidal factors, and following disappearance of the yolk sac and the onset of feeding, their distribution becomes patchy (CDFG 1992). Larvae and young juveniles are found in the Bay between November and April and their greatest densities are in the shallow waters of upper South Bay, Central Bay, and San Pablo Bay. Juveniles are found in the deeper areas of the Bay (peak in Central Bay) between April and August, and, for the most part, have left the Bay by late June at sizes that approach 80 mm TL (CDFG 1987). They eventually move to offshore or nearshore areas and do not return to the Bay until they are mature and ready for spawning. There is conflicting evidence of a strong correlation between juvenile abundance, as measured by young-of-the-year surveys, and recruitment to the adult spawning population two years later (Herbold et al. 1992)

Population Status and Influencing Factors

San Francisco Bay population levels fluctuate widely and have ranged between approximately 6,000 tons and 100,000 tons spawning biomass, as measured by spawn deposition surveys and hydroacoustic monitoring of fish schools (CDFG 1992). 1995-96 season estimates were approximately 99,000 tons, second highest on record (CDFG, unpub. data). Year-class strength is often determined in the first six months of life (Hart 1973, Lassuy 1989, Emmett et al. 1991). Egg mortalities can result from tidal exposure and dessication, abrubt or severe temperature or salinity changes, low oxygen levels, wave action, suffocation by high egg densities or siltation, pollution, and predation (Lassuy 1989, Emmett et al. 1991). Factors related to natural mortality of larvae

Figure 2.3 Traditional Pacific Herring Spawning Areas in Central San Francisco Bay



in the Bay include competition and other density dependent mechanisms, as well as starvation during their initial feeding period and changes in dispersal patterns. Juveniles and adult survival is affected by competition, predation, disease, spawning stress, and fishing (Emmett et al. 1991).

Predation appears to be the single most important factor affecting population levels (Lassuy 1989). In addition to commercial and recreational fishing, humans influence herring survival by impacting water and habitat quality. Spawning habitat quantity and Delta outflows are not thought currently to be limiting factors in determining the Bay's herring population size (CDFG 1987 and 1992).

Trophic Levels

Larvae are planktivores (primary and secondary consumers). Juveniles and adults are primary and higher order consumers.

Proximal Species

Egg Predators: Gulls, diving ducks, white sturgeon, atherinids (topsmelt and jacksmelt), surf perches, rock crabs.

Larvae predators: Young salmonids, pelagic invertabrates.

Juvenile Predators: California halibut, young salmonids, harbor seals, harbor porpoise.

Adult Predators: California halibut, California sea lion, harbor seals, harbor porpoise.

Habitat: Eel grass (spawning substrate).

Prey: Striped bass, copepods.

Good Habitat

It is frequently stated that herring prefer sea grasses (e.g., *Zostera marina*) or algae (e.g., *Gracilaria* sp.) as spawning substrate (Lassuy 1989, Emmett et al. 1991); however, a variety of seemingly less attractive surfaces have proven to be very successful in the Estuary. Rigidity, smooth texture, and the absence of sediment appear to be important components of suitable substrates (Lassuy 1989). Larvae and juveniles need quiescent and productive shallow subtidal areas as rearing habitat.

In northern waters, the optimal salinity range for spawning is reported to be 8 to 22 ppt and 13 to 19 ppt for eggs and larval survival (CDFG 1987). Also in these areas, temperatures in the range of 5.5 to 8.7° C have been shown to be best for egg development (Emmett et al. 1991); however, 10 to 12°C temperatures are about average for the spawning grounds in San Francisco Bay (Lassuy 1989). Optimal temperatures for juveniles and adults appear to be a few degrees higher than for eggs or larvae (Lassuy 1989). It has been suggested that eggs need a minimum dissolved oxygen concentration of 2.5 mg/L at the surface and, therefore, eggs elevated from the bottom on vegetation or other structures avoid siltation and receive better circulation for waste removal and oxygenation (Lassuy 1989). Water quality is an important factor as eggs are vulnerable to high levels of suspended particulate matter, particularly if the sediments are laden with contaminants (e.g., dredged material from urban ports). Additionally, larvae have been shown to be sensitive to the water-soluble fraction of hydrocarbons from spilled oil or other sources (Lassuy 1989).

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Personal Communications

Ken Ota. Ca. Dept. of Fish and Game, Pacific Herring Research Project, 1996.

Northern Anchovy

Engraulis mordax

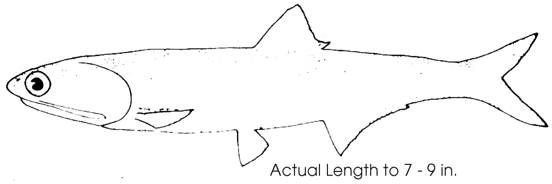
Michael F. McGowan

General Information

The northern anchovy (Family: Engraudidae) has the largest biomass and is the most abundant fish in San Francisco Bay (Aplin 1967). It is an important forage species for larger predators and consumes substantial amounts of phytoplankton and zooplankton (McGowan 1986). There is a bait fishery for northern anchovy at the mouth of the Bay. Most of the stock occurs outside the Bay in the California Current. Although northern anchovy can be found inside the bay throughout the year, their seasonal peak is generally April to October. The spring influx may be associated with the onset of coastal upwelling (P. Adams, pers. comm.). Their exodus in the autumn may be linked to cooling water temperatures inside the bay (McGowan 1986).

Reproduction

Northern anchovy spawn oval, pelagic eggs approximately 1.5 x 0.75 mm in size. Peak spawning is thought to occur at night at about 10 pm. Females can produce up to 130,000 eggs per year in batches of about 6,000. The eggs hatch in approximately 48 hours depending on temperature. Larvae were collected in Richardson Bay within San Francisco Bay by Eldridge (1977). Spawning was documented in San Francisco Bay in 1978 by collections of eggs and larvae from south of the Dumbarton Bridge to San Pablo Bay (McGowan 1986). Based on differential distributions of eggs and larvae, spawning occurs in the channels while larvae seek out the productive shallows. Although the biomass of northern anchovy within the bays is small relative to that in the California Current, the bay is a favorable habitat for reproduction because of ample food for adults to produce eggs, abundant zooplankton prey for larvae, and protection of eggs and larvae from offshore transport to less productive areas by coastal upwelling.



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Growth and Development

Larvae grow from 2.5 to 25 mm in about two months, at which time they are considered juveniles. Growth is rapid within the warm productive bay environment. Based on analysis of length frequencies, some juveniles that were spawned late in the summer overwinter in the bay (McGowan 1986). The others apparently depart at the same time as the adults in autumn.

Food and Feeding

Larvae eat dinoflagellates and zooplankton, while adults filter-feed in dense patches of large phytoplankton or small zooplankton, but selectively pick larger zooplankters from the water (O'Connell 1972).

Distribution

The northern anchovy occurs from Queen Charlotte Islands, Canada to Cabo San Lucas, Baha California and into the Sea of Cortez. It can be found in all estuaries within this range. There is a subpopulation which occupies the Columbia River plume, an "offshore estuary." In San Francisco Bay, they occur from Suisun Bay to South Bay, but are most abundant downstream of the Carquinez Strait (Herbold et al. 1992). There is a seasonal influx of northern anchovy into the bay in spring when water temperatures and plankton production begin to rise in the bay and when nearshore upwelling generally begins. Adults exit the bay in autumn, but some late-spawned juveniles may overwinter within the bay.

Population Status and Influencing Factors

Northern anchovy populations off California range in the hundreds of thousands of tons. Their biomass increased dramatically following the decline of the sardine stock, suggesting that competitive interactions might control population fluctuations. Historical records of fish scales in sediments suggests that large fluctuations in both anchovy and sardine populations have occurred in the past and were not strongly correlated with each other.

Variable survival of eggs and larvae due to environmental factors probably influences population size more than predation or fishing. Active research into the causes of northern anchovy population dynamics has contributed immensely to our understanding but without resolving whether starvation, predation, advection, or other cause is the key limiting factor.

Trophic Levels

First-feeding larvae may eat phytoplankters, larger larvae selectively pick copepods and other zooplankters from the water, juveniles and adults pick or filter plankton, fish eggs, and fish larvae, depending on food concentrations. Larvae and older stages should be considered as secondary and higher consumers.

Proximal Species

Predators: California halibut, Chinook and coho salmon; rockfishes, yellowtail, tunas, sharks, and almost all California current fish; harbor seal; northern fur seal; sea lions; common murre; brown pelican; sooty shearwater; cormorant spp.

Potential Competitors: Sardine. Jacksmelt, topsmelt, and other schooling planktivores are potential competitors and predators on young life stages.

Good Habitat

Northern anchovy occupy near surface waters where the water temperature should be between 10° and 25° C. Eggs tend to be in water with salinities from 32-35 ppt, but juveniles and adults are abundant in fresher bays and estuaries as well as marine waters. Spawning in San Francisco Bay occurs at higher temperatures and lower salinities than spawning in coastal areas. Northern anchovy are typical species of areas with high production such as coastal upwelling regions and estuaries.

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Personal Communications

P. Adams, National Marine Fisheries Service, Tiburon.

Sacramento Splittail

Pogonichthys macrolepidotus

Ted R. Sommer

General Information

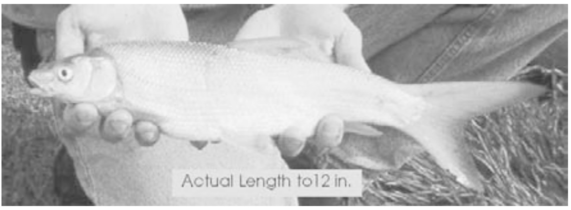
The Sacramento splittail (Family: Cyprinidae) is one of California's largest native minnows and is the only surviving member of its genus. In 1994 it was proposed for listing as a Threatened species by U.S. Fish and Wildlife Service based on concerns about reduced abundance and distribution (Meng and Kanim 1994, Meng and Moyle 1995). The species supports a small sport fishery in winter and spring, when it is caught for human consumption and live bait for striped bass angling.

Reproduction

Adult splittail generally reach sexual maturity at about 2 years of age (Caywood 1974). Some males mature at the end of their first year and a few females mature in their third year. An upstream spawning migration occurs November through May, with a typical peak from January-March. Spawning is thought to peak during February-June, but may extend from January-July. Although submerged vegetation is thought to be the preferred spawning substrate, egg samples have not yet been collected on any substrate. Reproductive activity appears to be related to inundation of floodplain areas, which provides shallow, submerged vegetation for spawning, rearing and foraging (Caywood 1974, Sommer et al. 1997). Splittail have high fecundity like most cyprinids. Reported fecundities range from 5,000 to 266,000 eggs per female, depending on age (Daniels and Moyle 1983). Generally, female splittail will have more than 100,000 eggs each year.

Growth and Development

The morphological characteristics of splittail eggs, larvae, and juveniles have been described and recent culturing studies (Bailey 1994) are providing preliminary information on early life history requirements and development. Very little is known about factors that influence splittail egg and larval development.



Ted Sommer

Mature splittail eggs are 1.3 to 1.6 mm in diameter with a smooth, transparent, thick chorion (Wang 1986 cited in CDWR and USBR 1994). The eggs are adhesive or become adhesive soon after contacting water (Bailey 1994). The eggs appear to be demersal and it is assumed that they are laid in clumps and attach to vegetation or other submerged substrates. Under laboratory conditions, fertilized eggs incubated in fresh water at 19°C (±0.5°C) start to hatch after approximately 96 hours. Asynchronous hatching of egg batches from single females has been observed in preliminary culturing tests.

Early hatched larvae are 6 mm long, have not developed eye pigment, and are physically underdeveloped. The last larvae to hatch have developed eye pigmentation and are morphologically better developed. Larvae are 7.0 to 8.0 mm total length (TL) when they complete yolk-sac absorption and become free swimming; postlarvae are up to 20 mm (±4.2 mm) TL. First scale formation appears at lengths of 22 mm standard length (SL) or 25 mm to 26 mm TL. It is unknown when exogenous feeding actually begins, but preliminary observations indicate that newly hatched larvae may have undeveloped mouths. Well-developed mouths are observed in postlarvae between 8.1 mm and 10.4 mm TL.

Sacramento splittail are a relatively long-lived minnow, reaching ages of 5, and possibly, up to 7 years. Studies from Suisun Marsh indicate that young-of-the-year (YOY) grow approximately 20 mm per month (mm/month) from May through September and then decrease to < 5 mm/month through February (Daniels and Moyle 1983). In their second season they grow at about 10 mm/month until the fall when somatic growth declined and gonadal development began. The adult growth rate ranges from 5 to 7 mm/month. During gonad development, which occurs primarily between September and February, the growth rate slows to less than 5 mm/month. The largest recorded splittail measured between 380 mm and 400 mm.

Food and Feeding

Feeding studies describe splittail as opportunistic benthic foragers. Splittail feeding appears highest in the morning and early afternoon. Studies from the Sacramento River found that their diets were dominated by oligochaetes, cladocerans, and dipterans (Caywood 1974). Samples from the lower San Joaquin River included copepods, dipterans, detritus and algae, clams (*Corbicula*) and amphipods (*Corophium* spp.). Copepods were the dominant food items. These findings were similar to results of feeding studies from Suisun Marsh (Daniels and Moyle 1983), where the diet consisted predominantly of detritus in both percent frequency of occurrence (74%) and percent volume (57%). A smaller portion of the stomach contents (41% by volume) consisted of animal matter, mostly crustaceans (35% by volume). Opossum shrimp (*Neomysis mercedis*) were the dominant crustacean food item (37% frequency; 59% volume less detritus) both daily and seasonally for splittail in Suisun Marsh. Other minor prey items included molluscs, insects, and fish.

Food selection studies from Suisun Marsh suggest that splittail specifically select *Neomysis* as their main prey item in the Estuary (Herbold 1987). Fullness indices data indicate that condition factors of splittail are linked to *Neomysis* abundance. Splittail did not switch to alternate and more prevalent food items, as was observed for other native resident species.

Distribution

The historical range of splittail included all low gradient portions of all major tributaries to the Sacramento and San Joaquin rivers, as well as some other freshwater tributaries to San Francisco Bay (Meng and Moyle 1995). A confounding issue is that the collection season and life stage for most of the early observations are unknown, so the relative importance of each location to different age classes of splittail cannot be established.

Splittail are presently most common in the brackish waters of Suisun Bay, Suisun Marsh, and the Sacramento-San Joaquin Delta. The data suggest that splittail inhabit much of their historical range and have been located in previously unreported sites (**Table 2.3**). Much of the loss of splittail habitat is attributable to migration barriers, but loss of floodplain and wetlands due to diking and draining activities during the past century probably represents the greatest reduction in habitat.

Within the San Francisco Estuary, splittail were collected from southern San Francisco Bay and at the mouth of Coyote Creek in Santa Clara County around the turn of the century. To our knowledge, no other splittail have been collected in this part of San Francisco Bay (Aceituno et al. 1976). However, splittail are caught in San Francisco Bay and San Pablo Bay in wet years. Adults and young are abundant in two tributaries to San Pablo Bay, the Napa and Petaluma rivers. The core of distribution of adult splittail during summer appears to be the region from Suisun Bay to the west Delta. Splittail are also present in some of the smaller tributaries and sloughs of Suisun Bay, including Peyton Slough, Hastings Slough, and Pacheco Creek.

Population Status and Influencing Factors

Abundance estimates for YOY and adult splittail were developed recently (Sommer et al. 1997) from several Interagency Ecological Program surveys. The survey equipment for the Program includes otter trawls, midwater trawls, beach seines, and townets.

Abundance of YOY declined in the Estuary during the six-year drought, which commenced in 1987 (**Figure 2.4**). There was a strong resurgence in YOY in 1995, when abundance estimates were the highest on record for State Water Project, Central Valley Project, beach seine, Outflow/Bay otter trawl, and Outflow/Bay study midwater trawl. The midwater trawl index was the second highest on record. The response

Table 2.3 Historical and Recent Collections of Splittail(a)

River	Distance (km) from Mouth of River to Collection Site			Distance (km) to first dam
	Rutter (1908)	Caywood (1974)	Sommer et al. (1997)	
Sacramento	483	387	331	387 (Red Bluff)
Feather	109	(b)	94	109 (Oroville)
American	49	37	19	37 (Nimbus)
San Joaquin	435(c)	(b)	201	295 (Sack)
Mokelumne	n/a	25	63	63 (Woodbridge)
Napa	n/a	21	10	n/a
Petaluma	n/a	25	8	16(d)

(a) For the purposes of comparing present and historical distribution, we assumed that collection of any life stage of splittail constituted evidence that a given location was part of the range of the species. The results should be considered as the minimum range only; there had not been sufficient sampling in sites farther upstream to conclusively show that they were not present. To illustrate the fact that much of the loss of channel habitat is attributable to migration barriers, the location of the first dam on each river is included.

(b) Records indicate that splittail were collected, but it is unclear where.

(c) Rutter (1908) was cited by FWS (1994) as the source of an observation of splittail at Fort Miller (km 435), near the current site of Friant Dam on the San Joaquin River . However, Rutter's distribution was based on Girard (1854), who reported two Pogonichthys species, *P. symetricus* and *P. inaquilobus* in the San Joaquin system. *P. symetricus*, collected from Fort Miller, is unlikely to have been a splittail (*P. macrolepidotus*) because Girard reported the "lobes of the caudal fin are symmetrical". Girard's description of *P. inaequilobus* had an asymmetrical tail and other features similar to that of splittail, but the collection location is listed as "San Joaquin River" without reference to a specific site.

(d) Dam was removed in 1994.

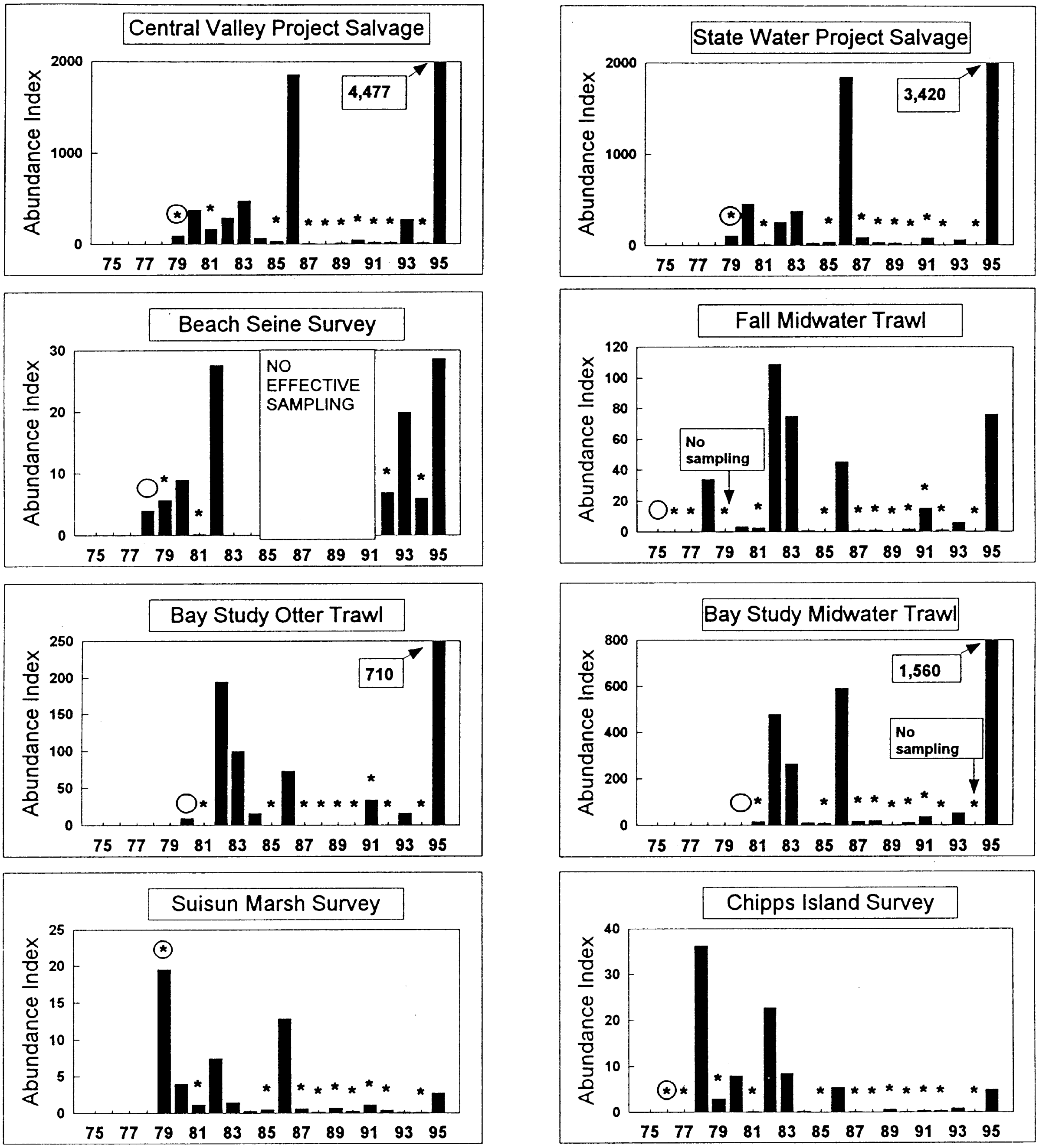


Figure 2.4 Trends in Age-0 Splittail Abundance for 1975-1995 as Indexed by Eight Independent Surveys. The first data point in each series is marked with a circle. Dry years are identified with asterisks above the data points- all other years are wet.

was not as dramatic for the Suisun Marsh, Chipps Island, or townet surveys, but there was a clear increase in abundance for each relative to the previous nine years.

There appears to be no consistent decline in adult abundance for most of the surveys (**Figure 2.5**). However, both the Suisun Marsh and Chipps Island surveys show significantly lower abundance in the early to mid-1980s (Sommer et al. 1997).

Floodplain inundation appears to be a key factor responsible for strong year classes, based on both statistical and limited observational data (Sommer et al. 1997). Higher flows increase inundation of floodplain areas, such as the Yolo Bypass, which provides spawning, rearing, and foraging habitat. The species has little or no stock recruitment relationship. This is best illustrated from data collected in 1995, when exceptionally large numbers of young splittail were produced by a stock

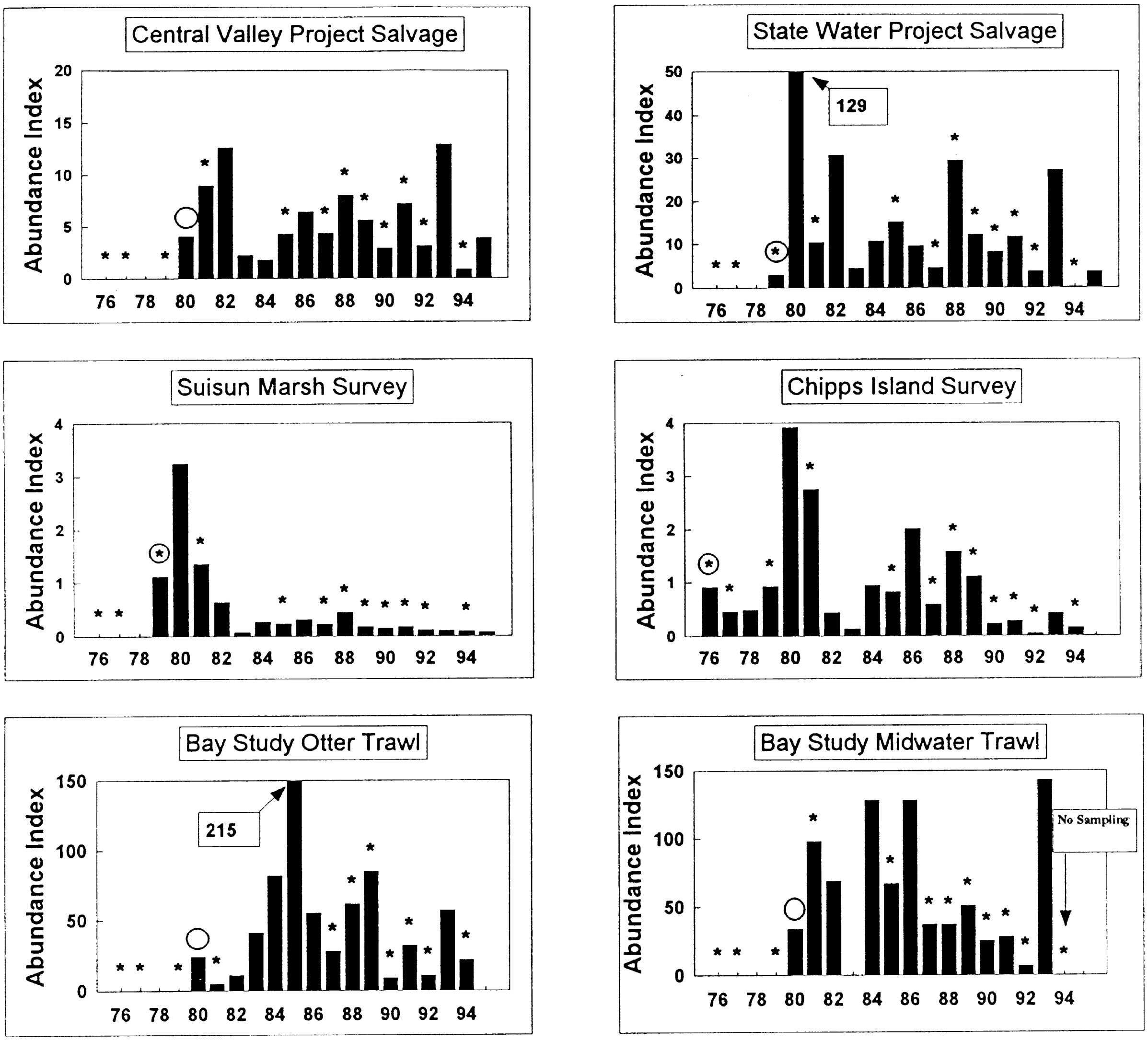


Figure 2.5 Trends in Adult Splittail Abundance for 1976-1995 as Indexed by Six Independent Surveys. The first data point in each series is marked with a circle. Dry years are identified with asterisks above the data points- all other years are wet.

that should have been depleted by drought conditions in seven of the previous eight years.

Attributes that help splittail respond rapidly to improved environmental conditions include a relatively long life span, high reproductive capacity, and broad environmental tolerances (Sommer et al. 1997). Additional factors that may affect population levels include habitat loss, recreational fishing, entrainment, and toxic compounds.

Trophic Levels

Splittail are secondary consumers.

Proximal Species

Predators: Striped bass, centrarchids.

Prey: Oligochaetes, zooplankton (cladocerans and copepods), terrestrial insects, opossum shrimp (*Neomysis mercedis*), mollusks.

Good Habitat

Sacramento splittail are one of the few freshwater cyprinids that are highly tolerant of brackish water. Although they have been collected at salinities as high as 18 ppt, abundance is highest in the 0-10 ppt salinity range (Sommer et al. 1997). Physiological studies show that splittail have critical salinity maxima of 20-29 ppt (Young and Cech 1996). Splittail also tolerate a wide range (7-33° C) of water temperatures in the laboratory, which fits well with thermal fluctuations associated with its habitat. Depending upon the acclimation temperature (range 12-20° C), critical thermal maxima ranged from 22-33° C. As further evidence of the general hardiness of the species, splittail appear to be tolerant of low dissolved oxygen levels and strong water currents.

Splittail are numerous within small dead-end sloughs, those fed by freshwater streams, and in the larger sloughs such as Montezuma and Suisun (Daniels and Moyle 1983). Juveniles and adults utilize shallow edgewater areas lined by emergent aquatic vegetation. Submerged vegetation provides abundant food sources and cover to escape from predators. Shallow, seasonally flooded vegetation is also apparently the preferred spawning habitat of adult splittail (Caywood 1974).

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Chinook Salmon

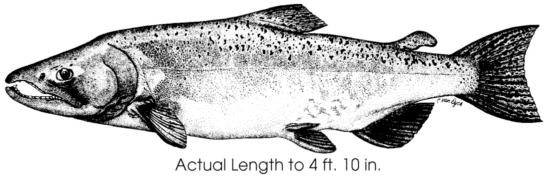
Oncorhynchus tshawytscha

Lt. Dante B. Maragni

General Information

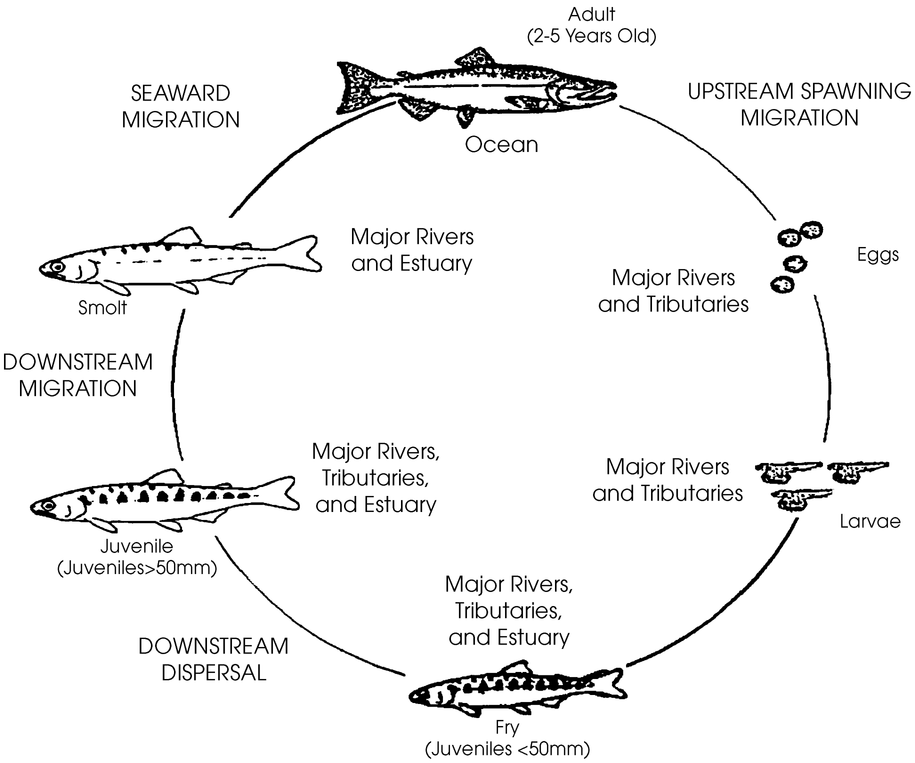
The Chinook salmon (Family: Salmonidae) is morphologically distinguished from other *Oncorhynchus* species of the northern Pacific Ocean by its large size, small black spots on both caudal fin lobes, black pigment along the base of the teeth (McPhail and Lindsey 1970 as cited in Healey 1991), and varying shades of flesh color from white through shades of pink and red (Healey 1991). The Chinook salmon life history (**Figure 2.6**) is characterized by adult migration from the ocean to natal freshwater streams to spawn, and juvenile migration seaward as smolts in their first year of life. During the smoltification process, juvenile Chinook salmon undergo physiological, morphological, and behavioral changes that stimulate emigration and prepare them for life in the marine environment (Healey 1991).

The Sacramento-San Joaquin Chinook salmon of California exists as four races—winter, spring, fall, and late-fall—as defined by the timing of adult spawning migration (Mason 1965, Frey 1971, Moyle 1976, Healey 1991). In 1989, the Sacramento River winter-run Chinook salmon was listed as threatened under the federal Endangered Species Act by the National Marine Fisheries Service (NMFS) (54 FR 32085). NMFS reclassified the winter-run as endangered in 1994 (59 FR 440) based on: 1) the continued decline and increased variability of run sizes since its listing as a threatened species in 1989, 2) the expectation of weak returns in certain years as a result of two small year classes (1991 and 1993), and 3) continuing threats to the population. The State of California listed the winter-run as endangered under the California Endangered Species Act in 1989. In 1995, the Oregon Natural Resources Council and R. Nawa petitioned NMFS to list Chinook salmon along the entire West Coast, including the States of California, Idaho, Oregon, and Washington, under the federal Endangered Species Act (54 FR 32085). The State of California presently includes on its list of species of special concern the late-fall (Class 2- special concern) and the spring-run (Class 1- qualified as threatened or endangered) Chinook salmon. Spring-run Chinook salmon


Actual Length to 4 ft. 10 in.

Moyle 1976

Figure 2.6 Life History of Chinook Salmon (USFWS 1995)



have also been given a special category by the state and are considered a "monitored" species.

Chinook salmon support commercial, recreational, and tribal subsistence fisheries. However, due to the state of Pacific Coast Chinook salmon populations, the U. S. Department of Commerce declared the U.S. Pacific Coast salmon commercial fishery, excluding Alaska, a disaster and has provided emergency relief funding for displaced fisherman in 1995 and 1996 (59 FR 51419, 60 FR 5908). Also, the federal Central Valley Project Improvement Act requires restoration actions to double the Chinook salmon population in the Sacramento-San Joaquin River system in California by the year 2002 estimated from average population levels from 1967 to 1991 (CDFG 1993).

Reproduction

The Chinook salmon is anadromous; that is, it spends most of its adult life in the ocean and returns to freshwater streams to spawn. Chinook salmon typically spend 3-6 years maturing in the ocean before returning as adults to their natal streams to spawn (Moyle 1976, Eschmeyer et al. 1983). Historically, most Sacramento-San Joaquin Chinook salmon returning to spawn have been four years of age (Clark 1929). The Chinook salmon is also semelparous in its reproductive strategy in that it dies after it spawns. Thus, the life span of the Chinook salmon is 3-6 years. All adults die after spawning except some "jacks" (i.e., precocious males that mature early in freshwater) (Miller and Brannon 1982).

Chinook salmon can be grouped into two types based on variations in their life histories: stream-type and ocean-type. Stream-type Chinook salmon populations are most commonly found north of 56° N latitude along the North American coast and characterized by long freshwater residence as juveniles (1+ years). Ocean-type Chinook salmon populations are most commonly found south of 56° N latitude and characterized by short freshwater residence as juveniles (2-3 months). Chinook salmon of the Sacramento-San Joaquin River system are predominantly ocean-type (Healey 1991). Adult upstream migration and juvenile downstream migration of the Sacramento-San Joaquin Chinook salmon differ among the four races. Sacramento-San Joaquin Chinook salmon populations' migration characteristics are listed in **Table 2.4** (Bryant, pers. comm.).

The Chinook salmon normally spawns in large rivers and tributaries, and typically in deeper water and larger gravel than other Pacific salmon (Scott and Crossman 1973). In preparation for spawning, a female Chinook salmon digs a shallow depression in the gravel of the stream bottom in an area of relatively swift water by performing vigorous swimming movements on her side near the bottom (Emmett et al. 1991, Healey 1991). This depression is referred to as a "redd," and can be 1.2-10.7 m (3.9-35.1 ft) in diameter (Chapman 1943). The female then deposits a group or "pocket" of eggs in the redd (Emmett et al. 1991, Healey 1991). From 2,000 to 14,000 eggs are laid per female, with 5,000 eggs per female being average (Rounsefell 1957, Moyle 1976, Bell 1984). The eggs are in turn fertilized by one or more males. During spawning, a female will be attended by one dominant male and occasionally other subdominant males. The female then buries the eggs by displacing gravels upstream of the redd (Emmett et al. 1991, Healey 1991).

Growth and Development

Chinook salmon eggs are spherical, non-adhesive, and the largest of all the salmonids (6.0-8.5 mm (0.24-0.33 in) in diameter) (Rounsefell 1957, Scott and Crossman 1973, Wang 1986). The incubation range is from 4-6 weeks, depending on levels of dissolved oxygen, biochemical oxygen demand, water temperature, substrate, channel gradient and configuration, water depth, water velocity and discharge (Reiser and Bjornn 1979, Alaska Department of Fish and Game 1985).

Larval sizes range from 20-35 mm (0.79-1.38 in) in length (Wang 1986). Yolk sac fry, termed "alevins," remain in the gravel from 2-3 weeks until the yolk sac is absorbed (Scott and Crossman 1973, Wydoski and Whitney 1979), whence they emerge from the gravel as fry. Fry develop into parr beginning the smoltification process as they encounter increasing salinities during their migration from freshwater to the ocean. Parr acquire a silver color as they transform into smolts during the smoltification process (Healey 1991). Fry and smolts can stay in freshwater from 1-18 months (Beauchamp et al. 1983), with residency periods differing with race (**Table 2.4**). Outmigration periods vary with outflow conditions. High outflows will carry fry downstream, while seasons with low outflow cause fry to rear longer in upstream areas where they grow much larger. Juvenile Chinook salmon in these two differing scenarios have substantially different habitat requirements (Kjelson et al. 1982). The fry to smolt life stages' size range is 2-152 cm (0.6-42.9 in), but is usually less than 91 cm (25.7 in), in length (Wydoski and Whitney 1979).

Juvenile Chinook salmon migration into estuaries has been reported to occur at night (Seiler et al. 1981) and during daylight (Dawley et al. 1986). Juveniles may move quickly through estuaries (Dawley et al. 1986) or reside there for up to 189 days (Simenstad et al. 1982). Juvenile Chinook salmon gain significant growth in estuarine habitats as they smolt and prepare for the marine phase of their life (MacDonald et al. 1987). The juveniles of most stocks of Chinook salmon appear to migrate north upon entering the ocean (Wright 1968, Healey 1991). Chinook salmon produced in streams from the Rogue River (Oregon) and south appear to rear in the ocean off northern California-southern Oregon (Cramer 1987). The stream-type Chinook salmon move offshore early in their ocean life, whereas ocean-type Chinook salmon remain in sheltered coastal waters. Stream-type Chinook salmon maintain a more offshore distribution throughout their ocean life than do ocean-type (Healey 1991). Chinook salmon reach maturity in 3-6 years (Moyle 1976).

Food and Feeding

Chinook salmon larvae and alevins feed on their yolk. Chinook salmon juveniles and adults are carnivorous, "opportunistic" feeders, feeding on a variety of terrestrial and aquatic insects, crustaceans, and fish (Emmett et al. 1991).

Juveniles in freshwater consume primarily terrestrial and aquatic insects, amphipods and other crustaceans, and sometimes fish (Becker 1973, Higley and Bond 1973, Scott and Crossman 1973, Craddock et al. 1976, Muir and Emmett 1988, Sagar and Glovea 1988).

Table 2.4 Migration Characteristics of Sacramento-San Joaquin Chinook Salmon Runs (Bryant 1997)

Characteristic	Winter	Spring	Fall	Late-fall
ADULT				
Immigration Period	December - July	March - July	June - December	October - April
Peak Immigration	March	May -June	September - October	December
Spawning Period	late April - early August	late August - late October	late September - December	January - late April
Peak Spawning	early June	mid September	late October	early February
JUVENILE				
Emergence Period	July - October	November - March	December - March	April - June
Freshwater Residency Period	5 - 10 months July - April	3 - 15 months November - January (year 2)	4 - 7 months December - June	7 - 13 months April - April (year 2)
Estuarine Emigration Period	November - May	March - June & November - March	March - July	October - May

In estuaries, juveniles feed in intertidal and subtidal habitats of tidal marshes. In these habitats, juveniles prey upon insects, gammarid amphipods, harpacticoid copepods, musids, chironomids, decapod larvae, and small (larval and juvenile) fish (Levy and Levings 1978, Levy et al. 1979, Northcote et al. 1979, Healey 1980a, Levy and Northcote 1981, Healey 1982, Kjelson et al. 1982, Simenstad et al. 1982, Simenstad 1983, McCabe et al. 1986). In low flow years when juveniles are larger, their food source will include crab megalops, squid, and small fish (e.g., northern anchovy, Pacific herring, rockfish) (Beauchamp et al. 1983).

Smaller juvenile Chinook salmon having recently migrated into the marine environment feed on amphipods, euphausiids, and other invertebrates, and small (larval and juvenile) fish (Healey 1980b, Peterson et al.1983, Emmett et al. 1986). Larger juvenile and adult Chinook salmon in the ocean feed primarily on fish (e.g., northern anchovy, Pacific herring, and Pacific sandlance), as well as squid, euphausiids, decapod larvae, and other invertebrates (Silliman 1941, Merkel 1957, Prakash 1962, Ito 1964, Hart 1973, Fresh et al. 1981). Immigrating adult Chinook salmon do not actively feed in freshwater (Emmett et al. 1991).

Distribution

Chinook salmon eggs and alevins are benthic and infaunal. Fry and parr are benthopelagic. Parr become pelagic as they enter smoltification. Smolts, ocean-dwelling and maturing juveniles, and adults are pelagic (Alaska Department of Fish and Game 1985). Adults are bottom-oriented in freshwater (Emmett et al. 1991).

Chinook salmon eggs, alevins, fry, and parr occur in riverine areas from just above the intertidal zone to altitudes of 2,268 m (7,441 ft) above sea level (Allen et al. 1991). Smolts are riverine and estuarine. Ocean-dwelling juveniles are neritic and epipelagic, and found within 128 m (420 ft) of the surface (Fredin et al. 1977). Adults may be neritic and estuarine, but are riverine during their spawning migration and may travel upstream more than 4,700 km (2,920 mi) from the ocean (Emmett et al. 1991) as flows and passage allow. Most tributaries are now dammed for water supply, which limits the extent of upstream migration (USFWS 1995).

The Chinook salmon is the least abundant of the major Pacific salmon species (Emmett et al. 1991, Healey 1991). However, it is the most abundant salmon in California (McGinnis 1984). The Chinook salmon is recorded as far north as the Coppermine River in Arctic Canada, and south to northeastern Hokkaido, Japan, and southern California (Ventura River) (Hart 1973, Scott and Crossman 1973). It is, however, rarely found in freshwater south of the Sacramento-San Joaquin River system of California (Eschmeyer et al. 1983).

While Chinook salmon are found in all estuaries north of San Francisco Bay in California, except Tomales Bay (Monaco et al. 1990), California's largest populations of Chinook salmon originate in the Sacramento-San Joaquin River system (Fry 1973). Spring-run Chinook salmon are extinct in the San Joaquin River and only remnant runs remain in a few Sacramento River tributaries. Historically, spring-run Chinook salmon spawned in small tributaries that have essentially all been blocked to migration by large dams. Fall and late-fall Chinook salmon are main stem spawners. Winter-run Chinook salmon are unique to the Sacramento River and spawned in coldwater tributaries above Shasta Dam prior to its construction (Sacramento River Winter-Run Chinook Salmon Recovery Team 1996). While distribution of outmigrating juvenile Chinook salmon is not well known in the San Francisco Bay, they have been found throughout, including the South Bay on high outflow years.

Population Status and Influencing Factors

Chinook salmon populations have declined substantially, with winter-run at the point of near extinction and spring-run at severely depressed population levels (**Table 2.5**). Whereas spring-run historically outnumbered all other runs, fall-run comprises the bulk of the present Chinook salmon population. The remnant " endangered" population of winter-run now depend on cold water releases from Shasta Reservoir, and the protection of the federal Endangered Species Act.

No single impact can be attributed to the decline of Chinook salmon populations and the important Chinook salmon fishery. High mortality for Chinook salmon occurs during the early freshwater life stages (eggs, fry, parr) (Emmett et al. 1991). This mortality is caused by redd destruction, siltation and destruction of spawning grounds, extremely high or low water temperatures, low dissolved oxygen, loss of cover, disease, food availability and competition, and predation (Reiser and Bjornn 1979). Besides the above factors, human impacts such as river flow reductions, the construction of dams and the consequent creation of reservoirs, water diversions, logging practices, and pollution have affected population abundances (Raymond 1979, Netboy 1980, Stevens and Miller 1983). Factors influencing survival of adult Chinook salmon are equally numerous. In the ocean, Chinook salmon are impacted by oceanographic conditions, disease, food availability and competition, predation, and overfishing (Fraidenburg and Lincoln 1985, Emmett et al. 1991). In freshwater, adults are subject to natural factors such as drought and flood, and human impacts including fishing, dams, road construction and other development, flood protection, dredging, gravel mining, timber harvest, grazing, and pollution (USFWS 1995).

Trophic Levels

Chinook salmon are primary and secondary consumers as juveniles and secondary consumers as adults.

Proximal Species

Juvenile Predators: Sacramento squawfish (*Ptychocheilus grandis*), riffle sculpin (*Cottus gulosus*), channel catfish (*Ictalurus punctatus*), steelhead trout (*Oncorhynchus mykiss*), striped bass (*Morone saxatilis*), centrarchids, rockfish (*Sebastes* spp.), kingfishers, egrets, herons, terns, grebes, pelicans.

Adult Predators: Pacific lamprey (*Lampetra tridentata*), harbor seal (*Phoca vitulina*), California sea lion (*Callorhinus ursinus*), killer whale (*Orcinus orca*), North American river otter (*Lutra canadensis*), American black bear (*Ursus americanus*), bald eagle (*Haliaeetus leucocephalus*).

Juvenile Prey: Terrestrial insects, aquatic insects, chironomids, copepods, amphipods, mysids, euphausiids, decapod larvae, bay shrimp.

Adult Prey: Euphausiids, decapods, squid, Pacific herring (*Clupea pallasi*, northern anchovy (*Engraulis mordax*), osmerids, rockfish (*Sebastes* spp.), Pacific sandlance (*Ammodytes hexapterus*).

Good Habitat

Chinook salmon eggs develop only in freshwater, but larvae can tolerate salinities of up to 15 ppt at hatching. Three months after hatching juvenile Chinook salmon can tolerate full seawater, with faster growing individuals better able to handle salinity changes (Wagner et al. 1969). Juveniles and adults occur in freshwater to euhaline waters. Successful egg incubation occurs from just above freezing to 20.0°C (68.4°F) (Olsen and Fos-

Table 2.5 Estimated Number of Sacramento-San Joaquin Chinook Salmon Returning to Spawn: 1967-1991 (Mills and Fisher 1994) (Continued on next page.)

Year	Sacramento Fall-run Chinook[1]			San Joaquin Fall-run Chinook[2]			Sacramento Late-fall-run Chinook[3]		
	grilse	adult	total	grilse	adult	total	grilse	adult	total
1967	38,410	104,790	143,200	1,176	21,359	22,535	5,730	31,478	37,208
1968	18,181	155,859	174,040	11,211	6,577	17,788	1,910	32,823	34,733
1969	48,528	208,289	256,817	1,935	49,662	51,597	1,747	35,431	37,178
1970	30,121	147,279	177,400	8,539	28,550	37,089	1,823	17,367	19,190
1971	35,775	140,691	176,466	2,986	38,580	41,566	2,277	12,046	14,323
1972	43,795	80,622	124,417	2,454	12,321	14,775	2,398	29,155	31,553
1973	40,640	197,193	237,833	674	6,438	7,112	711	21,493	22,204
1974	25,364	185,953	211,317	762	3,625	4,387	329	6,116	6,445
1975	29,691	141,884	171,575	968	6,258	7,226	816	15,847	16,663
1976	21,926	155,767	177,693	505	3,894	4,399	581	14,699	15,280
1977	22,831	139,971	162,802	60	990	1,050	873	8,217	9,090
1978	23,635	115,363	138,998	254	2,473	2,727	959	7,921	8,880
1979	46,397	152,982	199,379	456	3,897	4,353	44	8,696	8,740
1980	25,472	110,833	136,305	702	5,600	6,302	566	7,181	7,747
1981	42,575	145,503	188,078	8,022	20,295	28,317	168	1,429	1,597
1982	43,396	129,388	172,784	2,681	14,214	16,895	186	955	1,141
1983	41,714	88,676	130,390	32,312	10,970	43,282	1,221	12,053	13,274
1984	41,030	115,509	156,539	18,335	37,641	55,976	2,357	3,550	5,907
1985	41,563	211,695	253,258	4,311	71,873	76,184	1,670	5,990	7,660
1986	27,356	212,739	240,095	3,117	18,588	21,705	490	6,220	6,710
1987	66,364	150,965	217,329	18,269	6,689	24,958	780	13,663	14,443
1988	26,517	197,841	224,358	1,138	20,798	21,936	2,094	8,589	10,683
1989	24,060	116,726	140,786	282	3,489	3,771	286	9,589	9,875
1990	9,443	83,499	92,942	312	663	975	1,536	5,385	6,921
1991	11,546	87,070	98,616	207	647	854	888	5,643	6,531
AVERAGE	33,053	143,083	176,137	4,867	15,844	20,710	1,298	12,861	14,159

[1] Escapement data for the Sacramento River and its tributaries north of and including the American River.
[2] Escapement data for the Mokelumne, Cosumnes, Calaveras, Stanislaus, Tuolumne and Merced rivers.
[3] Escapement data for the main stem Sacramento River above Red Bluff Diversion Dam.

ter 1955), however, best incubation temperatures are 5.0-14.4°C (41.0-57.9°F) (Bell 1984). The upper lethal temperature for Chinook salmon is 25.1°C (77.2°F) (Brett 1952), but may be lower depending on other water quality factors (Ebel et al. 1971). Eggs and alevins are found in areas with flow of 20-150 cm/sec (0.7-5 ft/sec) and juveniles where flows are 0.5-60.0 cm/sec (0.02-2 ft/sec) (at pool edges). Adults can migrate upstream in flows up to 2.44 m/sec (8 ft/sec) (Thompson 1972). Successful egg development requires redds to have adequate dissolved oxygen (≥5.0 mg/L), water temperatures (4-14°C [39-57°F]), substrate permeability, sediment composition (≤25% fines, ≤6.4 mm [0.25 in] in diameter), surface flows and velocities, and low biochemical oxygen demand (Reiser and Bjornn 1979).

Juveniles in freshwater avoid waters with ≤4.5 mg/L dissolved oxygen at 20°C (68°F) (Whitmore et al. 1960). Migrating adults will pass through water with dissolved oxygen levels as low as 5 mg/L (Hallock et al. 1970). Excessive silt loads (≥4,000 mg/L) may halt Chinook salmon movements or migrations. Silt can also hinder fry emergence, and limit benthic invertebrate (food) production (Reiser and Bjornn 1979). Freshwater inflow into estuaries is critical for providing adequate water temperatures, food production, and overall beneficial environmental conditions for juvenile outmigration. High freshwater flows allow for cooler water temperatures, while also stimulating and sustaining production of food. High river flows improve juvenile survival and enable active migration into estuaries and on to the ocean.

In addition to specific hydrologic components, physical habitat requirements of interrelated instream gravel, riparian, and tidal marsh habitats comprise the healthy ecosystem in which Chinook salmon spawn and rear. Chinook salmon eggs and alevins require clean, loose gravel and occur in spawning gravel or cobble that

Table 2.5 (continued) Estimated Number of Sacramento-San Joaquin Chinook Salmon Returning to Spawn: 1967-1991 (Mills and Fisher 1994)

YEAR	Sacramento Springl-run Chinook[4]			Sacramento Winter-run Chinook[5]			Central Valley Total Chinook Salmon		
	grilse	adult	total	grilse	adult	total	grilse	adult	total
1967	11,397	12,297	23,694	24,985	32,321	57,306	81,698	202,245	283,943
1968	3,317	11,827	15,144	10,299	74,115	84,414	44,917	281,202	326,119
1969	2,843	24,492	27,335	8,953	108,855	117,808	64,006	426,729	490,735
1970	1,420	6,017	7,437	8,324	32,085	40,409	50,228	231,297	281,525
1971	2,464	6,336	8,800	20,864	32,225	53,089	64,366	229,878	294,244
1972	1,343	7,053	8,396	8,541	28,592	37,133	58,531	157,743	216,274
1973	2,082	9,680	11,762	4,623	19,456	24,079	48,729	254,261	302,990
1974	2,538	5,545	8,083	3,788	18,109	21,897	32,782	219,347	252,129
1975	7,683	15,670	23,353	7,498	15,932	23,430	46,656	195,591	242,247
1976	4,067	22,006	26,073	8,634	26,462	35,096	35,712	222,829	258,541
1977	5,421	8,409	13,830	2,186	15,028	17,214	31,372	172,614	203,986
1978	1,093	7,063	8,156	1,193	23,669	24,862	27,134	156,489	183,623
1979	707	2,203	2,910	113	2,251	2,364	47,717	170,029	217,746
1980	3,734	8,081	11,815	1,072	84	1,156	31,545	131,780	163,325
1981	8,249	13,066	21,315	1,744	18,297	20,041	60,757	198,591	259,348
1982	4,528	21,644	26,172	270	972	1,242	51,061	167,947	219,008
1983	672	3,809	4,481	392	1,439	1,831	76,311	116,947	193,258
1984	4,373	3,988	8,361	1,869	794	2,663	67,965	161,481	229,446
1985	3,792	7,631	11,423	329	3,633	3,962	51,665	300,822	352,487
1986	1,606	17,290	18,896	451	2,013	2,464	33,020	256,850	289,870
1987	4,177	7,330	11,507	236	1,761	1,997	89,826	180,408	270,234
1988	2,132	9,521	11,653	708	1,386	2,094	32,589	238,136	270,725
1989	884	6,304	7,188	53	480	533	25,566	136,587	162,153
1990	948	4,376	5,324	16	425	441	12,256	94,347	106,603
1991	433	1,208	1,641	38	153	191	13,112	94,721	107,833
AVERAGE	3,276	9,714	12,990	4,687	18,421	23,109	47,181	199,955	247,136

[4] Escapement data for the main stem Sacramento River above Red Bluff Diversion Dam.
[5] Escapement data for the main stem Sacramento River above Red Bluff Diversion Dam.

is 1.3-10.2 cm (0.5-10.2 in) in diameter (Reiser and Bjornn 1979). Juveniles in freshwater are found within areas of shallow riffles and deep pools over various substrates, ranging from silt bottoms to large boulders (Chapman and Bjornn 1968). Juveniles in estuaries occur in intertidal and tidal habitats over mud, sand, gravel, and eelgrass (*Zostera* spp.) (Healey 1980a). Adults in marine waters show no sediment preference, but may be associated with gravel-cobble bottoms in rivers and streams during upstream migration (Alaska Department of Fish and Game 1985).

In riverine areas, both submerged cover, such as boulders, woody debris, and aquatic vegetation, and overhead cover, such as continuous riparian vegetation canopies, undercut banks, and turbulent water, provide shade, food, and protection against predation to juvenile Chinook salmon. Estuaries appear to play a vital role in Chinook salmon life history as well, and specifically, tidal marsh habitat is of great importance to juvenile salmonids (Dorcey et al. 1978, Levy et al. 1979, Meyer 1979, Levy and Northcote 1981, Healey 1982, MacDonald et al. 1987, 1988). Juvenile Chinook salmon forage in the intertidal and shallow subtidal areas of tidal marsh mudflat, slough, and channel habitats, and open bay habitats of eelgrass and shallow sand shoal areas. These productive habitats provide both a rich food supply and protective cover within shallow turbid waters (McDonald 1960; Dunford 1975, cited from Cannon 1991). The distribution of juvenile Chinook salmon changes tidally, with fry moving from tidal channels during flood tides to feed in nearshore marshes.

Tidal marshes are most heavily used by fry, whereas smolts tend to utilize deeper waters. Fry disperse along the edges of marshes at the highest points reached by the tide, then retreat into the tidal channels with the receding tide. Smolts congregate in surface waters of main and secondary sloughs and move into shallow subtidal areas to feed (Levy and Northcote 1981, Levings 1982, Allen and Hassler 1986, Healey 1991).

In addition to good water quality, adequate flows, and productive spawning and rearing habitat, state-of-the-art positive barrier screens on water diversions, protection from excessive harvest, and free access to upstream migration or well-designed ladders for adult passage offers promising overall habitat for healthy Chinook salmon populations.

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Steelhead

Oncorhynchus mykiss irideus

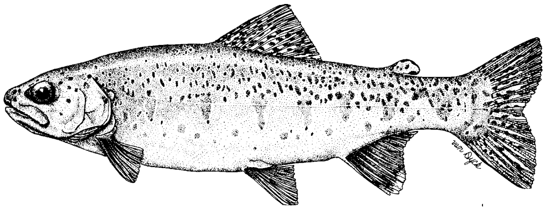
Robert A. Leidy

General Information

Steelhead (Family: Salmonidae) are the anadromous (sea-run) form of resident rainbow trout. Behnke (1992) proposed classification of steelhead on the west coast of the United States into a coastal subspecies, *O. m. irideus*, and an inland subspecies, *O. m. gairdneri*. California is considered to have only coastal steelhead (Behnke 1992). In California steelhead may be classified into two races, summer and winter steelhead, based upon the timing of upstream migration into freshwater. The San Francisco Estuary and its tributary streams support winter steelhead. Steelhead are a polymorphic species and as such populations within a stream may be anadromous, resident, or mixtures of the two forms that presumably interbreed (Titus et al., *in press*). Steelhead do not support a commercial fishery within the San Francisco Estuary and its tributaries. It is illegal for commercial salmon trollers to possess steelhead (McEwan and Jackson 1996). There is a inland recreational sportfishery for steelhead that is dependent largely on hatchery operations to sustain populations. The estimated net annual economic benefit of doubling steelhead stocks within the Sacramento/San Joaquin river systems is estimated at 8.0 million dollars (Meyer Resources Inc. 1988).

Reproduction

Polymorphic salmonids exhibit a high degree of life history variation (Titus et al., *in press*). Steelhead within the San Francisco Estuary may be classified as "ocean-maturing" or "winter" steelhead that typically begin their spawning migration in the fall and winter, and spawn within a few weeks to a few months from when they enter freshwater (McEwan and Jackson 1996). Ocean maturing steelhead enter freshwater with well-developed gonads and spawn shortly after entering a river or stream. Steelhead begin upstream migration after one to four growing seasons at sea (Burgner et al. 1992). A small number of immature fish (i.e., grilse) may also move upstream after spending only a few months in the ocean. Releases of cold water from several large Central Valley reservoirs on the Sacramento River system may induce steelhead to begin to move into upstream tributaries as early as August and September. This means that upstream migrating steelhead may be observed within San Francisco Bay and Suisun Marsh/Bay between August and March. Ocean-maturing steelhead typically spawn between December and April, with most spawning occurring between January through March.



Moyle 1976

Actual Length to 2 ft.

Steelhead are iteroparous and do not die after spawning as do other Pacific salmon; therefore, they may return to the ocean and spawn again the following year. The frequency of return spawning for a given population is generally unknown. Steelhead spawn in redds constructed by the female over a gravel/cobble substrate. Eggs are deposited in the redd and then fertilized by the male. The number of eggs produced is largely a function of the size of the female, and may range from 200 to 12,000 eggs over the geographic range of steelhead (Scott and Crossman 1973, Moyle 1976). Steelhead within the Sacramento River drainage average between 1,000 to 4,500 eggs (Mills and Fisher 1994).

Growth and Development

Steelhead eggs are spherical to slightly irregular in shape, non-adhesive, demersal, and range in diameter from 3-6 mm (Wang 1986). Incubation of eggs is dependent upon water temperature in the redd. Wales (1941) observed hatching at approximately 19 days at an average water temperature of 15.5° C and 80 days at about 4.5° C. For Waddell Creek in coastal San Mateo County, steelhead hatching time was estimated at 25 to 35 days, with emergence beginning at 2-3 weeks following hatching (Shapovalov and Taft 1954). Steelhead length at hatching ranges between 14 to 15.5 mm total length (TL), with alevins ranging between 23-26 mm TL (Wang 1986). Alevins emerge from the gravel following yolk sac absorption as fry or juveniles ready to actively feed.

Steelhead remain in freshwater for one to four years (usually two years) before downstream migration as "smolts", at an average size ranging between 13 cm and 25 cm TL (Moyle 1976). Age at emigration is highly variable, but may occur earlier in warmer, more productive streams where juveniles can reach smolt size at a younger age (Moyle et al. 1995). Most Sacramento River juvenile steelhead emigrate as 1-year-old fish during spring and early summer (Barnhart 1986, Reynolds et al. 1993), although Shapovalov and Taft (1954) found that steelhead moved downstream in Waddell Creek during all months of the year. While steelhead may spend up to four years in the ocean, most only survive to age two. In the ocean steelhead may grow at a rate of 1.2 inches per month and reach a length of 23 inches in two years.

Food and Feeding

Rearing juvenile steelhead are primarily drift feeders utilizing a variety of terrestrial and aquatic insects, including emergent aquatic insects, aquatic insect larvae, snails, amphipods, opossum shrimp, and various species of small fish (Moyle 1976). Larger steelhead will feed on newly emergent steelhead fry. Emigrating adult and juvenile steelhead may forage in the open water of estuarine subtidal and riverine tidal wetland habitats within the Estuary, although the importance of these areas as rearing habitat for juveniles is not well documented. Apparently upstream migrating steelhead rarely eat and therefore exhibit reduced growth (Pauley and Bortz 1986).

Distribution

Steelhead populations are native to Pacific Ocean coastal drainages of the Kamchatka Peninsula and scattered mainland locations of Asia and in the western Pacific from the Kuskokwim River in Alaska to Malibu Creek in southern California (Titus et al., *in press*, McEwan and Jackson 1996, Moyle 1976). Although the life-history characteristics of steelhead are generally well known, the polymorphic nature of the subspecies has resulted in much confusion over the status and distribution of steelhead in San Francisco Estuary and its tributaries. Historically, the Sacramento-San Joaquin River systems supported large runs of steelhead (McEwan and Jackson 1996). Presumably, most streams with suitable habitat within the San Francisco Estuary also supported steelhead, however accurate population estimates for individual streams are not available (Skinner 1962, Leidy 1984).

Currently, small steelhead runs of unknown size are known to exist in South San Francisco Bay in San Francisquito Creek, San Mateo County; Guadalupe River and Coyote and Upper Penitencia creeks, Santa Clara County; Alameda Creek, Alameda County; and possibly San Leandro Creek, Alameda County (R. Leidy, unpub. data). Within Central San Francisco Bay steelhead runs are believed to occur in Corte Madera Creek and its tributaries, Miller Creek, Novato Creek, and possibly Arroyo Corte Madera del Presideo Creek, Marin County (R. Leidy, unpub. data). Within San Pablo Bay, steelhead make spawning runs in the Napa River and several of its tributary streams and Huichica Creek, Napa County; and the Petaluma River and Sonoma Creek and several of their tributary streams, Sonoma County (R. Leidy, unpub. data). Tributaries to Suisun Bay and adjacent drainages that support steelhead runs of unknown size include the Sacramento and San Joaquin rivers; Green Valley and Suisun creeks, Solano County; and Walnut Creek and possibly Alhambra, Pinole, Wildcat, and San Pablo creeks, Contra Costa County (R. Leidy, unpub. data). Steelhead may also be present in other tributary streams below migration barriers within the Estuary, but currently there is little or no data on their status in many streams. Steelhead adults and smolts may be found foraging in and migrating through estuarine subtidal and riverine tidal habitats within all areas of the San Francisco Estuary.

Population Status and Influencing Factors

Nehlsen et al. (1991) identified at least 43 steelhead stocks at moderate to high risk of extinction, with more than 23 stocks believed to have been extirpated, on the west coast of the United States. Steelhead in California are estimated to number roughly 250,000 adults, which is one half the adult population of 30 years ago (McEwan and Jackson 1996). As a result of this precipitous decline, the National Marine Fisheries is currently reviewing the status of steelhead to determine if they warrant listing under the Endangered Species Act. Estimates of the average annual steelhead run size for the Sacramento-San Joaquin River system, including San Francisco Bay tributaries, range between 10,000 and 40,000 adults (Hallock et al. 1961, McEwan and Jackson 1996). The *California Fish and Wildlife Plan* (CDFG 1965) estimated an annual run size for the Sacramento above the mouth of the Feather River of approximately 30,000 fish, and a total for the reminder of the entire Central Valley of 40,000 steelhead, including tributaries to San Francisco Bay. This likely places the size of steelhead runs in San Francisco Bay tributaries at well below 10,000 fish, however, the fact remains that reliable estimates for individual streams tributary to San Francisco Estuary do not exist.

General factors influencing steelhead population numbers during upstream migration, spawning, and incubation include barriers to passage, diversions, flow fluctuations, water temperature, and other water quality parameters, such as sedimentation of spawning habitats. Factors affecting juvenile rearing habitat and emigration within the San Francisco Estuary and its tributary streams include low summer flows combined with high water temperatures. Within Suisun Bay/Marsh the downstream migrating steelhead are adversely affected by altered flows, entrainment, and mortality associated with trapping, loading, and trucking fish at state and federal pumping facilities. In addition, dredging and dredged material disposal within the San Francisco Estuary may contribute to degradation of steelhead habitat and interference with migration, foraging, and food resources (LTMS 1996).

Trophic Levels

Larvae are primary consumers. Juveniles and adults are primary and higher order consumers.

Proximal Species

Egg Predators: Freshwater sculpins.
Juvenile and Smolt Predators: Other large freshwater, estuarine, and marine piscivorous fish.
Juvenile and Adult Predators: Harbor seals and other pennipeds.
Habitat/Cover: Riparian, emergent, and palustrine wetland vegetation.
Major Prey Items: Aquatic and terrestrial insects, amphipods, snails, mysid shrimp, small fish.

Good Habitat

The preferred water depth for steelhead spawning ranges from six to 24 inches, while fry and parr prefer water depths of between two to 14 inches and 10 to 20 inches, respectively (Bovee 1978). Steelhead prefer to spawn in areas with water velocities of approximately two ft/sec (range = 1-3.6 ft/sec), although optimal spawning velocity is partially a function of the size of fish; larger fish can successfully spawn in higher water velocities (Barnhart 1986). Optimal spawning substrate is reported to range from 0.2 to 4.0 inches in diameter, but steelhead will utilize various mixtures of sand-gravel and gravel-cobble (Bovee 1978, Reiser and Bjornn 1979). Optimal temperature requirements for steelhead vary as follows: adult migration, 46° to 52° F; spawning, 39° to 52° F; incubation and emergence, 48° to 52° F; fry and juvenile rearing, 45° to 60° F, and smoltification, < 57° F (Bovee 1978, Reiser and Bjornn 1979, Bell 1986). While egg mortality begins to occur at 56° F and fish are known to have difficulty extracting oxygen from the water at temperatures exceeding 70° F (Hooper 1973), steelhead populations are often adapted to local environmental conditions where preferred temperature conditions are regularly exceeded for prolonged time periods (McEwan and Jackson 1996).

Some other important factors that are critical to maintaining optimal steelhead habitat include water quality and quantity, habitat heterogeneity, migration barriers, and introduced salmonids. Steelhead require relatively "good" water quality (e.g., low suspended sediment and contaminant loads and other forms of pollution), as well as sufficient flows for spawning, rearing, and migration. Diverse stream habitats consisting of shallow riffles for spawning and relatively deep pools, with well-developed cover, for rearing are important factors. The importance of estuarine or riverine tidal wetlands within the San Francisco Estuary for rearing/foraging or migrating steelhead are not well understood.

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Delta Smelt

Hypomesus transpacificus

Ted R. Sommer
Bruce Herbold

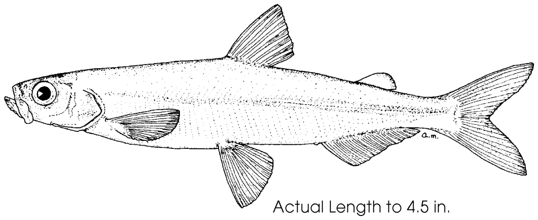
General Information

The Delta smelt (Family Osmeridae) is a small, short-lived native fish which is found only in the Bay-Delta Estuary. The species was listed as threatened in 1993 under the Federal Endangered Species Act. Habitat loss is thought to be one of the most important elements in causing its decline. New water quality standards adopted by the state in 1995 are aimed in part at improving habitat conditions (SWRCB 1995).

Reproduction

The Delta smelt has low fecundity and is primarily an annual species, although a few individuals may survive a second year (Herbold et al. 1992). The location and season of Delta smelt spawning varies from year to year. Spawning, which occurs in shallow freshwater (CDFG 1992b, USFWS 1994), has been known to occur at various sites within the Delta, including the lower Sacramento and San Joaquin rivers and Georgiana Slough, and in sloughs of the Suisun Marsh (USFWS 1994). In 1996, newly emerged Delta smelt larvae were found in the Napa River, Cordelia Slough, Montezuma Slough, and in the San Joaquin River up to Stockton (CDFG unpub. data). Based on egg and larval trawls in recent low flow years, it appears that a significant portion of Delta smelt spawning now takes place in the northern and western Delta (CDWR 1992).

Spawning may occur from late winter (December) to early summer (July). In 1989 and 1990, two spawning peaks occurred, one in late-April and another early-May (USFWS 1994). Spawning has been reported to occur at about 45° to 59° F (7-15° C) in tidally influenced rivers and sloughs, including dead-end sloughs and shallow edge waters of the upper Delta. Most spawning occurs in fresh water, but some may occur in brackish water in or near the entrapment zone (Wang 1991). The demersal, adhesive eggs sink and attach to hard substrates, such as submerged tree branches and roots, gravel



Actual Length to 4.5 in.

Moyle 1976

or rocks, and submerged vegetation. Survival of adhesive eggs and larvae is probably significantly influenced by hydrology at the time of spawning (CDWR and USBR 1994). Moyle et al. (1992) found no correlation between female length and fecundity. Females of 59-70 mm standard length (SL) ranged in fecundity from 1,247 to 2,590 eggs per fish, with an average of 1,907.

Spawning stock does not appear to have a major influence on Delta smelt year class success. However, the low fecundity of this species, combined with planktonic larvae which likely have high rates of mortality, requires a large spawning stock if the population is to perpetuate itself. This may not have been an important factor in the decline of Delta smelt, but it may be important for its recovery (CDFG 1992b).

Growth and Development

Newly hatched larvae are planktonic and drift downstream near the surface to the freshwater/saltwater interface in nearshore and channel areas. Maeger (1993) found that larvae hatched in 10 to 14 days under laboratory conditions and started feeding on phytoplankton at day four and on zooplankton at day six. Growth is rapid through summer, and juveniles reach 40 to 50 mm fork length (FL; the measure to the bottom of the fork of the tail fin) by early August. Growth slows in fall and winter, presumably to allow for gonadal development. Adults range from 55 to 120 mm FL, but most do not grow larger than 80 mm FL. Delta smelt become sexually mature in the fall at approximately seven to nine months of age. The majority of adults die after spawning.

Food and Feeding

Newly hatched larvae feed on rotifers and other microzooplankton. Older fish feed almost exclusively on copepods. Prior to 1988, Delta smelt ate almost solely the native *Eurytemora affinis* (Herbold 1987). During the 1980s *Eurytemora affinis* was displaced by the introduced copepod *Pseudodiaptomus forbsii* throughout Suisun Bay, and Delta smelt shifted to a diet of *Pseudodiaptomus forbsii* (P. Moyle, pers. comm.).

Distribution

Delta smelt are endemic to the Sacramento-San Joaquin Estuary. They have been found as far north as the confluence of the American and Sacramento rivers and as far south as Mossdale on the San Joaquin River. Their upstream range is greatest during periods of spawning. Larvae subsequently move downstream for rearing. Juvenile and adult Delta smelt commonly occur in the surface and shoal waters of the lower reaches of the Sacramento River below Isleton, the San Joaquin River below Mossdale, through the Delta, and into Suisun Bay (Moyle 1976, Moyle et al. 1992). Downstream distribution is generally limited to western Suisun Bay. During periods of high Delta outflow, Delta smelt populations do occur in San Pablo Bay, although they do not appear to establish permanent populations there (Herbold et al. 1992). Recent surveys, however, show that Delta smelt may persist for longer periods in Napa River, a tributary to San Pablo Bay (IEP, unpub. data).

Rearing and pre-spawning Delta smelt generally inhabit a salinity range of less than 2 ppt (parts per thousand), although they have been collected at salinities as high as 10 to 14 ppt (CDFG 1992b). Abundance of pre-spawning adults typically peaks upstream of the entrapment zone (CDWR and USBR 1994).

Population Status and Influencing Factors

Seven surveys, although not specifically designed to gather data on Delta smelt populations in the Estuary, have charted the abundance of Delta smelt. The summer townet survey, which began in 1959 and was primarily designed to measure striped bass abundance, is considered one of the best measures of Delta smelt abundance because it covers much of the species' habitat and represents the longest historical record. Although the abundance indices vary considerably, they generally remained low between 1983 and 1993. In recent years moderately wet conditions have produced relatively high abundances in the summer townet survey. The reduced population levels during the 1980s appear to have been consistent throughout the Delta and Suisun Bay, but declines may have occurred as early as the mid-1970s in the eastern and southern portions of the Delta (CDWR and USBR 1993).

The midwater trawl survey provides one of the best indexes of smelt abundance because it covers most of the range of Delta smelt (CDWR and USBR 1994). From 1967 through 1975, fall catches were generally greater than 10 smelt per trawl per month (in 6 of 8 years); from 1976 through 1989, catches were generally less than 10 smelt per trawl per month (in 13 of 14 years). Since 1986, catches have averaged considerably less than one smelt per trawl per month. The frequency of occurrence of Delta smelt in the trawls has also declined. Prior to 1983, Delta smelt were found in 30% or more of the fall trawl catches. In 1983-1985, they occurred in less than 30% of the catches, and since 1986, they have been caught in less than 10% of the trawls (Herbold et al. 1992). In 1993, the midwater trawl index was the sixth highest of the 25 years of record. In 1994, the index dropped to a 28-year low, but it rebounded again in 1995. Unlike the summer townet survey indices, the mean catches of Delta smelt have not declined in the midwater trawl survey. The smelt population is more dispersed in the summer than in the fall. The summer populations have decreased in average densities while the fall populations have decreased in numbers of schools (CDFG 1992b). Data from the Bay Study and the Suisun Marsh study show sharp declines in Delta smelt at about the same time. The exact timing of the decline is different in most of the sampling programs, but falls between 1982 and 1985 (Herbold et al. 1992).

As a result of the sharp decline in abundance in the 1980s, the Delta smelt was listed as a federal "threatened" species by the U.S. Fish and Wildlife Service in March 1993 and as a State "threatened" species by the California Department of Fish and Game in December 1993.

No single factor appears to be the sole cause of the Delta smelt decline; however declines have been attributed primarily to restricted habitat and increased losses through entrainment by Delta diversions (CDWR 1992, Herbold et al. 1992, USFWS 1994). Reduced water flow may intensify entrainment at pumping facilities as well as reduce the quantity and quality of nursery habitat. Outflow also controls the location of the entrapment zone, an important part of the habitat of Delta smelt. A weak, positive correlation exists between fall abundance of Delta smelt and the number of days during spring that the entrapment zone remained in Suisun Bay (Herbold 1994). The number of days when the entrapment zone has been in Suisun Bay during the February through June period is one of only two parameters found so far that predicts Delta smelt abundance (Herbold 1994). Reduced suitable habitat and increased entrainment occurs when the entrapment zone moves out of the shallows of Suisun Bay and into the channels of the lower Sacramento and San Joaquin rivers as a result of low Delta outflow. The movement of the entrapment zone to the river channels not only decreases the amount of area that can be occupied by smelt, but also decreases food supply (Herbold et al. 1992).

Delta smelt in the western delta are vulnerable to entrainment by the pumps of the State Water Project and the Central Valley Project, as well as local agricultural diversions (CDWR 1992, NHI 1992, Herbold et al. 1992). Diversions in the northern and central Delta, where smelt are most abundant, are likely the greatest source of entrainment (USFWS 1994). Larvae and juveniles appear to be particularly vulnerable to pumping because screens are not effective for these life stages (CDWR and USBR 1994). Whether entrainment, as estimated by salvage, affects abundance remains to be demonstrated statistically. However, the relative effects of entrainment are higher in dry years, when the abundance of Delta smelt is typically lowest and the distribution of the species shifts closer to the pumps in the interior Delta. Water diversions such as Contra Costa Canal, PG&E's power plants, and in-Delta agricultural diversions, potentially entrain Delta smelt in numbers comparable to or greater than at the Central Valley Project and State Water Project pumps. However, initial results from Interagency Ecological Program studies have found few Delta smelt in agricultural diversions.

Although the effects of the recent high diversions of fresh water, especially when coupled with drought conditions from 1987-1992, are the most likely causes of the decline in the Delta smelt population, other contributing factors may include: the presence of toxic compounds in the water, competition and predation, food supply, disease, very high outflows, and low spawning stock.

Toxic contaminants have been identified as a factor that could affect Delta smelt survival (USFWS 1991). Possible pollutants include heavy metals, pesticides, herbicides, and polycyclic aromatic hydrocarbons. An inverse relationship has been found between copper applications to ricefields and Delta smelt abundance (Herbold, unpub. data), but no toxicity studies have been conducted to verify the degree to which pollutants in water and sediments affect Delta smelt.

Research conducted by Bennett (1995) suggests that competition with inland silversides, a non-native fish that arrived in the Bay around 1975, working synergistically with low flows, has contributed to Delta smelt decline. Inland silversides were found to be voracious predators of larval fish in both field and laboratory experiments. In addition, smelt and silversides may compete for copepods and cladocerans. Hatching and larval smelt may be extremely vulnerable to schools of foraging silversides, especially in low-outflow years when Delta smelt are forced into narrower, upstream channels, where silverside competition and predation may be increased. Evidence suggests that other non-native species, such as chameleon goby and striped bass, are either direct predators or compete with Delta smelt for food or habitat (CDWR and USBR 1994). However, it is questionable if striped bass is an important factor when both striped bass and Delta smelt were abundant in the 1960s, and the smelt was not a significant prey of the bass (CDFG 1992b).

Exact food requirements of Delta smelt are not known, but prey densities in the Estuary appear low relative to other systems in the United States, creating the potential for food limitation (Miller 1991). Moreover, there have been several changes in the species composition of zooplankton, with unknown effects on Delta smelt. The 1988 decline of *Eurytemora affinis*, a copepod which has been the primary food supply of Delta smelt, has been identified as a possible factor in the decline of smelt in the Estuary (CDFG 1992b). However, it may be that declines in *E. affinis* abundance, due to the introduction of other copepod species, is not an important factor because the smelt has shifted its diet and now consumes *Pseudodiaptomus forbesi*, which was introduced into the Estuary in 1986. The clam, *Potamocorbula amurensis*, may have an indirect effect on smelt populations by reducing its food supply (Herbold et al. 1992).

In some years disease is thought to cause widespread mortality of some fish species in the Estuary, but mortality of Delta smelt has not been specifically observed (Stevens et al. 1990). *Mycobacterium*, a genus of bacteria known to cause chronic infections in fish and other species, has been the major cause of mortality of Delta smelt held in the laboratory, and it may cause deaths among wild fish as well (Hedrick 1995).

The period of the Delta smelt decline includes unusually wet years with exceptionally high outflows. Very high outflows may be detrimental to the planktonic smelt larvae, which may be transported out of the Delta and into San Pablo and San Francisco bays with no way to get back upstream (CDFG 1992b).

It is possible that the size of the spawning stock influences population levels. However, there is not a statistically significant stock-recruitment relationship for Delta smelt, so this factor is not considered a primary factor regulating abundance (CDWR and USBR 1994).

Trophic Levels

Delta smelt are secondary consumers.

Proximal Species

Egg and larvae predators: Inland silversides, *Menidia beryllina.*
Juvenile and adult predators: Striped bass, *Morone saxatilis* (likely).
Prey: *Eurytemora affinis*, *Pseudodiaptomus forbsii*, rotifers (e.g., *Trichocerca).*

Good Habitat

Spawning habitat has been as widely dispersed as the Napa River to Stockton in 1996. The predominate feature appears to be shallow, freshwater conditions with some sort of solid substrate for the attachment of eggs. Spawning has been reported to occur at about 45-59° F (7-15° C) in tidally influenced rivers and sloughs including dead-end sloughs and shallow edge waters of the upper Delta.

Juvenile and adult Delta smelt commonly occur in the surface and shoal waters of the lower reaches of the Sacramento River below Mossdale, through the Delta, and into Suisun Bay (Moyle 1976, Moyle et al. 1992). Rearing and pre-spawning Delta smelt generally inhabit a salinity range of less than 2 ppt, although they have been collected at salinities as high as 10 to 14 ppt (CDFG 1992a). Analysis of the salinity preferences using midwater trawl data indicate that Delta smelt distribution peaks upstream of the entrapment zone (Obrebski 1993)[1]. It should be noted, however, that the distribution of Delta smelt is fairly broad, particularly in years when abundance levels are high (CDWR and USBR 1993). Evidence from the 1993 year class also demonstrates that salt field position does not necessarily regulate Delta smelt distribution in all years. In late 1993 and early 1994, Delta smelt were found in Suisun Bay region despite the fact that X2[2] was located upstream. Samples collected in this area demonstrated that high levels of the copepod *Eurytemora* were present, suggesting that food availability may also influence smelt distribution (CDWR and USBR 1994).

Although these results show that the Delta smelt is not an entrapment zone specialist, there is evidence that their abundance is correlated with X2. Herbold (1994) found a significant relationship between the number of days X2 was in Suisun Bay during February through June versus midwater trawl abundance. Furthermore, when the entrapment zone is in Suisun Bay and both deep and shallow water exists, Delta smelt are caught most frequently in shallow water (Moyle et al. 1992).

Results from the University of California, Davis provide an indication of environmental tolerances of Delta smelt (Swanson and Cech 1995). The study found that although Delta smelt tolerate a wide range of water temperatures (<8° C to >25° C), warmer temperatures apparently restrict their distribution more than colder temperatures.

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[1] The entrapment zone, also referred to by a variety of other discriptive terms, such as the "mixing zone," the "null zone," and and the "zone of maximum turbidity," is the area within an estuary where the freshwater from a stream meets with the salt water of the ocean. This zone is biologically highly productive, and considered to be of critical importance to the aquatic food web of the Estuary.

[2] "X2" is the geographic location, measured in kilometers above the Golden Gate, of the entrapment zone. X2 is largely a function of outflow, such that when outflow is high, X2 is closer to the Golden Gate. X2 was used by U.S. Fish and Wildlife Service in defining Delta Smelt's critical habitat under the Endangered Species Act (USFWS 1994).

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Longfin Smelt

Spirinchus thaleichthys

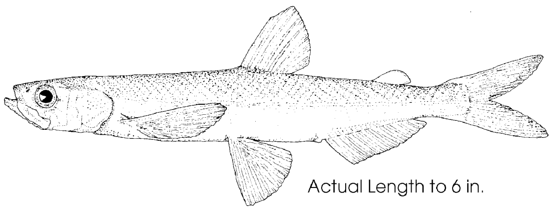
Frank G. Wernette

General Information

The longfin smelt (Family: Osmeridae) is a three to seven-inch long silvery fish (Moyle 1976). Longfin smelt were the most abundant smelt species in the Bay-Delta Estuary prior to 1984 and have been commercially harvested (Wang 1986). In 1993, the U.S. Fish Wildlife Service (USFWS) was petitioned to list the longfin smelt under the federal Endangered Species Act. In January 1994, however, USFWS determined that the longfin smelt did not warrant listing because other longfin smelt populations exist along the Pacific Coast, the Bay-Delta Estuary population does not appear to be biologically significant to the species as a whole, and the Bay-Delta Estuary population may not be sufficiently reproductively isolated (Federal Register Vol. 59 No. 869, January 6, 1994). Still, longfin smelt are typically addressed in Biological Assessments because of the decline in their abundance after 1982 and the relatively small increase in abundance following a wet year in 1993. The species may also be considered in the future for listing under the California Endangered Species Act.

The longfin smelt is an euryhaline species with a 2-year life cycle. Spawning occurs in fresh water over sandy-gravel substrates, rocks, or aquatic plants. Spawning may take place as early as November and extend into June, although the peak spawning period is from January to April. After hatching, larvae move up into surface water and are transported downstream into brackish-water nursery areas. Delta outflow into Suisun and San Pablo bays has been positively correlated with longfin smelt recruitment because higher outflow increases larval dispersal and the area available for rearing. The longfin smelt diet consists of mysids, although copepods and other crustaceans also are eaten. Longfin smelt are preyed upon by fishes, birds, and marine mammals (Federal Register Vol. 59 No. 4, January 3, 1994).

In the Bay-Delta Estuary, the decline in longfin smelt abundance is associated with freshwater diversion from the Delta. Longfin smelt may be particularly sensitive to adverse habitat alterations because their 2-year life cycle increases their likelihood of extinction after consecutive periods of reproductive failure due to drought or other factors. Relatively brief periods of reproductive failure could lead to extirpations (Federal Register Vol. 59 No. 4, January 3, 1994).



CDFG

Although the southernmost populations of longfin smelt are declining, little or no population trend data are available for estuaries in Oregon and Washington. Longfin populations may not be isolated since there is little genetic variation between northern and southern populations. Under prolonged drought conditions however, only the Colombia River and San Francisco Bay stocks may survive.

Reproduction

Maturation of longfin smelt begins late in the second summer of their life in August and September. As they mature, the smelt begin migrating upstream from San Francisco and San Pablo bays toward Suisun Bay and the Delta. Longfin smelt spawn in fresh water, primarily in the upper end of Suisun Bay and in the lower and middle Delta. In the Delta, they spawn mostly in the Sacramento River channel and adjacent sloughs (Wang 1991). During the recent drought, when saline water intruded into the Delta, larval longfin smelt were found near the Central Valley Project and State Water Project export facilities in the southern Delta (Wang 1991). Ripe adults, larvae, and juveniles are salvaged at the export facilities in every below normal or drier water year (Baxter, pers. comm.). The eggs are adhesive and are probably deposited on rocks or aquatic plants. Longfin smelt eggs hatch in 37-47 days at 45° F.

Growth and Development

Shortly after hatching, longfin smelt larvae develop a gas bladder that allows them to remain near the water surface (Wang 1991). The larvae do not vertically migrate, but instead remain near the surface on both the flood and ebb tides (CDFG 1992). Larvae are swept downstream into nursery areas in the western Delta and Suisun and San Pablo bays with larval dispersal farther downstream in years of high outflow than in years of low outflow (CDFG 1992; Baxter, pers. comm.). Early development of gas bladders by longfin smelt causes the larvae to remain near the surface much longer than Delta smelt larvae. That factor and earlier spawning period help explain why the longfin smelt larvae are dispersed much farther downstream in the Estuary than are Delta smelt larvae (Baxter, pers. comm.). Larval development occurs primarily in the February through May period and peaks during February-April (CDFG 1992).

Metamorphosis of longfin smelt from the larval to juvenile form begins 30-60 days after hatching, depending on temperature. Most longfin smelt growth occurs during the first summer, when length typically reaches

6 to 7 cm. During their second summer, smelt reach 9 to 11 cm in length (NHI 1992). Most longfin smelt spawn and die at two years of age (CDFG 1992).

Food and Feeding

The main prey of adult longfin smelt is the opossum shrimp, *Neomysis mercedis* (NHI 1992). There is little information on food habitats of longfin smelt larvae, but fish larvae of most species, including Delta smelt, are known to feed on phytoplankton and small zooplankton, such as rotifers and copepod nauplii (Hunter 1981, USBR 1993). Juvenile longfin smelt feed on copepods, cladocerans, and mysids. The mysid *Neomysis mercedis* is the most important prey of larger juveniles.

Distribution

Longfin smelt are widely distributed in estuaries on the Pacific Coast. They have been collected from numerous river estuaries from San Francisco to Prince William Sound in Alaska (Moyle 1976).

Longfin smelt are euryhaline meaning they are adapted to a wide salinity range. They are also anadromous. Spawning adults are found seasonally as far upstream in the Delta as Hood, Medford Island, and the Central Valley Project and State Water Project fish collection facilities in the southern Delta. Historically, before construction of Shasta Dam in 1944, saline water intruded in dry months as far upstream in the Delta as Sacramento, so longfin smelt may have periodically ranged farther upstream than they do currently (Herbold et al. 1992).

Except when spawning, longfin smelt are most abundant in Suisun and San Pablo bays, where salinity generally ranges between 2 ppt and 20 ppt (NHI 1992). Pre-spawning adults and yearling juveniles are generally most abundant in San Pablo Bay and downstream areas as far as the South Bay and in the open ocean.

Population Status and Influencing Factors

Abundance estimates were developed from otter trawl and midwater trawl sampling conducted by the Outflow/Bay study as part of the Interagency Ecological Program. Fall midwater trawl surveys provide the longest index of longfin smelt abundance.

Results of the fall midwater trawl surveys indicate that, like Sacramento splittail abundance, longfin smelt abundance has been highly variable from year to year, with peaks and declines coinciding with wet and dry periods. Longfin smelt abundance has steadily declined since 1982. Abundance continued to be suppressed during the drought years beginning in 1987. Longfin abundance was very low from 1987 to 1992, with 1992 having the lowest index on record. Abundance increased moderately in 1993 following the drought during a period of improved Delta outflow.

Year-class abundance of longfin smelt appears to depend on the environmental conditions experienced by the eggs and young fish. Generally, year-class abundance is positively related to Delta outflow (i.e., high abundance follows high outflow during winter and spring). Factors possibly contributing to the recent decline in longfin smelt abundance are reduced Delta outflow, entrainment in diversions, introductions of exotic species, loss of habitat, and the recent drought.

Delta Outflow - Higher outflows result in higher longfin smelt survival. An index of survival computed as the ratio of the index of abundance from fall midwater trawl surveys to an index of larval abundance in previous springs was strongly correlated (r=0.95) with December-August outflow. Delta outflow or factors associated with outflow affect survival of larvae and early juveniles. Delta outflow may be the single most important factor controlling longfin smelt abundance. High outflows increase dispersion downstream, available habitat, and possibly, food availability. High outflow may also reduce predation and the effects of other adverse factors (i.e., toxin concentrations). Low outflow conditions reduce downstream dispersion and increase vulnerability to entrainment in Delta diversions.

Longfin smelt abundance (according to the fall midwater trawl survey index) is positively related to Delta outflow (Stevens and Miller 1983, CDFG 1992). Regression analysis indicated that 79% of variability in the midwater trawl survey index is explained by changes in January and February Delta outflow. The significant relationship between the index of abundance from the fall midwater trawl surveys and Delta outflow may reflect the effect of outflow on survival of larvae and early juveniles. Year-class strength may be largely determined by survival of the early life stages.

High Delta outflow may increase the amount of suitable brackish water rearing habitat; reduce salinity in the Estuary, reducing competition and predation by marine organisms; reduce predation because young smelt are more dispersed and turbidity is higher; increase phytoplankton and zooplankton production; and increase transport of larvae out of the Delta and away from diversions (CDFG 1992; Stevens and Miller 1983; Baxter, pers. comm.). Any of these mechanisms may be responsible for the observed relationship between Delta outflow and longfin smelt abundance.

The position of the entrapment zone[1], location of X2[2], and volume of critical nursery habitat are determined by Delta outflow. In addition to the relationship with outflow, the fall midwater trawl survey index has a positive relationship with the location of X2 and the volume of critical nursery habitat (Jassby 1993, Herrgesell 1993).

Delta smelt abundance tends to be highest when X2 has an intermediate value (i.e., X2 is located in upper Suisun Bay). The location of X2 is also a good predictor of longfin smelt abundance. Since X2 and the volume of critical nursery habitat are largely determined by Delta outflow, the relationship between longfin smelt abundance and the location of X2 or volume of critical habitat may simply reflect effects of outflow or other correlates of outflow on longfin smelt abundance.

Lower San Joaquin River - Reverse flow in the lower San Joaquin River usually transports relatively fresh water drawn from the Sacramento River and may increase upstream migration of adults to the southern Delta. Reverse flow may also transport larvae to the southern Delta. In the southern Delta, adults, larvae, and juveniles are vulnerable to entrainment, predation, and other sources of mortality.

Entrainment - Entrainment of longfin smelt by Delta diversions affects spawning adults, larvae, and early juveniles. Older juveniles and prespawning adults generally inhabit areas downstream of the Delta. Salvage at both the Central Valley Project and State Water Project fish protection facilities has varied greatly between years. Salvage represents entrainment, but the number of fish salvaged is often much lower than total number entrained because fish, particularly those smaller than about 20-30 mm, pass through the fish screens at the salvage facilities and, therefore, are not salvaged.

With the exception of 1986, a wet year, the annual salvage of longfin smelt at the Central Valley Project and State Water Project pumps was much higher during 1984-1990 than during 1979-1983. The decline in abundance in 1984 may be attributable to increased entrainment by the Central Valley Project and State Water Project pumps and other diversions, but reduced Delta outflow, discussed previously, may be a more important factor affecting abundance.

Entrainment of adult longfin smelt has a potentially greater adverse effect on the population than entrainment of larvae and young juveniles because unless the adults have already spawned, their reproductive value is much greater than that of younger fish. Adult smelt are entrained at the State Water Project and Central Valley Project pumping facilities primarily during November-February. The number of adults entrained is low relative to the number of juveniles entrained.

Longfin smelt larvae have been captured in the southern Delta near the Central Valley Project and State Water Project export facilities (Spaar 1990, 1993; Wang 1991). Larval smelt are too small to be salvaged at the State Water Project and Central Valley Project fish protection facilities. Based on the high salvage rates of young-of-year juveniles in some years, it can be assumed that many thousands of longfin smelt larvae were also entrained, especially during February through April.

During years of high flows, most longfin smelt adults spawn in the western Delta, and their larvae are generally transported out of the Delta and therefore are unlikely to be entrained in Delta diversions in large numbers. During the 1987-1992 drought and other low flow years, however, outflows were low and exports were high. Adults, larvae, and juveniles remained in the Delta, as indicated by salvage at the Central Valley Project and State Water Project fish protection facilities. Most juveniles were entrained during April-June and averaged 30-45mm long, with length correlated with the month of entrainment. Thus, longfin smelt suffer not only loss of larval dispersal and rearing habitat in a drought, but also from higher rates of entrainment.

Adult, juvenile, and larvae longfin smelt are vulnerable to entrainment in diversions other than exports at the Central Valley Project and State Water Project pumps, including diversions to PG&E's power generating plants, industrial diversions, agricultural diversions, and others. However, entrainment of longfin smelt in these diversions has not been extensively evaluated.

Other Factors - Other factors that may affect survival of longfin smelt include food limitation and presence of toxic materials and introduced species. Abundance of *Neomysis* and other zooplankton prey (e.g., rotifers) of longfin smelt have declined in recent years (Obrebski et al. 1992). It is not known what effect the decline in prey abundance has had on longfin smelt; however, food limitation may be important because year-class strength of many fish populations, particularly species with planktonic larvae, may be strongly influenced by feeding conditions during the larval life stage (Lasker 1981).

Agricultural chemicals (including pesticides and herbicides), heavy metals, petroleum-based products, and other waste materials toxic to aquatic organisms enter the Estuary through nonpoint runoff, agricultural drainage, and municipal and industrial discharges. The effects of toxic substances have not been tested on longfin smelt, but recent bioassays indicate that water in the Sacramento River is periodically toxic to larvae of the fathead minnow, a standard EPA test organism (Stevens et al. 1990). The short life span of longfin smelt and relatively low position in the food chain probably reduce the accumulation of toxic materials in their tissues and make them less susceptible to injury than species that live longer (NHI 1992).

Many exotic species have invaded the Estuary in recent years. These species may compete with or prey on longfin smelt. No single invasion of exotic species parallels the decline the longfin smelt closely enough to suggest that competition from or predation by the species

Fish

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[1] The entrapment zone, also referred to by a variety of other discriptive terms, such as the "mixing zone," the "null zone," and and the "zone of maximum turbidity," is the area within an estuary where the freshwater from a stream meets with the salt water of the ocean.

[2] "X2" is the geographic location, measured in kilometers above the Golden Gate, of the entrapment zone.

was a primary cause of the longfin smelt's recent decline. The effects of multiple-species invasion, which have occurred in the Estuary, are extremely difficult to assess. The effects of exotic species invasions on longfin smelt is likely not large since Delta outflow explains over 60% of the variation in abundance (Baxter, pers. comm.).

Trophic Levels

Longfin smelt are secondary consumers.

Proximal Species

Predators: Brown pelican, river otter, striped bass, centrarchids.
Prey: Zooplankton (cladocerans), opossum shrimp (*Neomysis mercedis*), crustaceans (copepods).

Good Habitat

Longfin smelt are typically pelagic and use the larger sloughs and rivers of the Delta and Bay. The optimal salinity habitat for non-spawning adults is 2 to 20 ppt. Optimal salinity habitat for spawning adults is 0 to 2 ppt. Optimum habitat for spawning includes submergent vegetation that can be used as a substrate for the adhesive eggs. High quality habitat is also defined as having low levels of exposure to entrainment into water export facilities and agricultural or managed wetland diversions. Adjacent runoff of agricultural pesticides is minimal or does not occur in good habitat areas.

Juvenile longfin use the open water, shallow shoal areas of San Pablo and Suisun bays after being transported downstream from spawning areas in the Delta. An average X2 location in upper Suisun Bay defines good habitat conditions for longfin smelt. Adjacent tidal wetlands are important to supporting the nutrient cycling and carbon input functions which in turn support the prey species upon which longfin feed.

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Jacksmelt

Atherinopsis californiensis

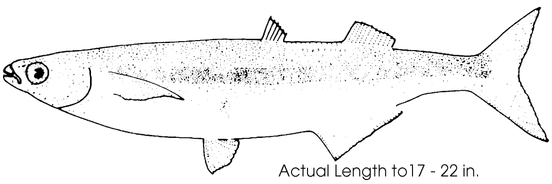
Michael K. Saiki

General Information

Although jacksmelt (Family: Atherinidae) is not an important commercial fish, it nevertheless constitutes the largest portion of "smelt" captures in California (Emmett et al. 1991). This species is also commonly caught by recreational anglers fishing from piers (Frey 1971). In an ecological sense, jacksmelt occupy an important niche in trophic pathways of nearshore coastal, bay, and estuarine ecosystems (Clark 1929, Allen and DeMartini 1983, CDFG 1987).

Reproduction

Emmett et al. (1991) describes the sexual and reproductive characteristics of jacksmelt as gonochoristic (its gender is determined by developmental rather than hereditary mechanisms) and iteroparous (it has the capacity to survive and spawn beyond one or multiple spawning seasons). Spawning occurs several times during a spawning season (Clark 1929). The eggs are demersal and adhesive, and can often be found on vegetation in shallow nearshore coastal habitats and in estuaries and bays (Clark 1929, Wang 1986).



CDFG

Actual Length to17 - 22 in.

Adults move inshore and into bays and estuaries to spawn during late winter and early spring (Clark 1929, Wang 1986). In San Francisco Bay, spawning occurs from October to early August (Wang 1986). Spawning in San Pablo Bay reportedly occurs from September to April (Ganssle 1966). Eggs are laid on substrates/vegetation (e.g., *Zostera* spp., *Gracilaria* spp., hydroids) in which they become entangled (Frey 1971, Wang 1986). Embryonic development is indirect and external, and if given a suitable environment, the yellowish-orange eggs hatch within seven days (Wang 1986). The fecundity of jacksmelt is not yet documented, but probably exceeds 2,000 eggs per female (Emmett et al. 1991). Unfertilized jacksmelt eggs are spherical in shape and 0.9-2.2 mm in diameter (Clark 1929); fertilized eggs are 1.9-2.5 mm in diameter (Wang 1986).

Growth and Development

After hatching, larvae remain on the bottom for a moment and then actively swim near the surface (Wang 1986). Larvae vary in size from 7.5 to 8.6 mm immediately after hatching, to about 25 mm long prior to the juvenile transformation (Clark 1929, Wang 1986). At eight days posthatch, they average 10.5-11.7 mm in length whereas at 24 days posthatch, they average 17.6-20.3 mm in length (Middaugh et al. 1990). Juveniles can attain 110 mm during their first year, and 180-190 mm after two years (Clark 1929). All individuals mature by their third year, but some may grow quickly and mature in their second year (Clark 1929). Adult jacksmelt have been reported to attain a length of 780 mm and an age of 11 years (Miller and Lea 1972, Frey 1971) but, more typically, the maximum size is 200 mm total length, and the maximum age is 9-10 years (Clark 1929).

Food and Feeding

The jacksmelt is omnivorous (Bane and Bane 1971, Ruagh 1976). Larvae live on their yolk-sac for about 48 hours after hatching when it is fully absorbed (Middaugh et al. 1990). Major food items for jacksmelt include algae (*Ulothrix* spp., *Melosira moniliformis*, *Enteromorpha* spp., and other filamentous algae), benthic diatoms, crustaceans (mysids, copepods, decapod larvae), and detritus (Bane and Bane 1971, Ruagh 1976). In addition, stomach analyses of juvenile jacksmelt show that amphipods are a common food item, indicating that juveniles may feed on the bottom (Wang 1986).

Distribution

Jacksmelt occur from Santa Maria Bay, Baja California, northward to Yaquina Bay, Oregon (Miller and Lea 1972, Eschmeyer et al. 1983). However, this species is uncommon north of Coos Bay, Oregon (Emmett et al. 1991).

Prior to or after the spawning season, adult jacksmelt typically occur in coastal waters near shore (Baxter 1960). Ruagh (1976) mentioned that jacksmelt are usually caught within 5 km of shore where they often school with topsmelt (*Atherinops affinis*).

Locally, jacksmelt have been reported to spawn in San Francisco Bay (Wang 1986) and San Pablo Bay (Ganssle 1966, Wang 1986). Juveniles are also present in San Francisco Bay (Baxter 1960, Aplin 1967), San Pablo Bay (Ganssle 1966), Carquinez Strait (Messersmith 1966), and occasionally in Suisun Bay (Wang 1986, Herbold et al. 1992, Jones and Stokes Assoc. 1979) and Napa marsh (Jones and Stokes Assoc. 1979). The amount of freshwater inflow seemingly affects the local distribution of jacksmelt. During years of low freshwater inflow, jacksmelt occur as far upstream as Carquinez Strait and San Pablo Bay, but during high-flow years they are seemingly restricted to Central San Francisco Bay and South San Francisco Bay (CDFG 1987).

Population Status and Influencing Factors

Presently, jacksmelt are particularly abundant in Tomales, Central San Francisco, South San Francisco, and San Pablo bays (Emmett et al. 1991). Midwater trawl samples performed in South San Francisco Bay between 1980-1988 showed that jacksmelt were the second most common species caught, behind northern anchovy (Herbold et al. 1992). Furthermore, jacksmelt were more abundant and occurred more frequently than topsmelt in the South Bay (Herbold et al. 1992). In San Pablo and Central San Francisco bays, Herbold et al. (1992) reported that jacksmelt were the third most common species caught. Midwater trawl samples performed in the Carquinez Strait between 1961-1962 found over 9% of the total catch consisted of jacksmelt (Messersmith 1966). Herbold et al. (1992) noted that during 1980-1988 jacksmelt numbers seemed to vary widely in the Central Bay and are seemingly unpredictable from year to year, whereas numbers in the South Bay show little variation from year to year.

Although specific studies relating fish abundance to environmental variables were not found during our search of the literature, jacksmelt may be vulnerable to pollution and habitat modifications because they depend on embayments and estuaries for spawning.

Trophic Levels

Omnivorous (primary and higher order consumers).

Proximal Species

Predators: Yellowtail (*Seriola lalandei*), sharks and other piscivorous fishes, piscivorous birds (e.g., brown pelicans and gulls).
Prey: Small crustaceans, algae.
Habitat: Kelp (cover for juveniles and adults); algae, hudroids, and eelgrass (spawning substrate).
Parasites: Nematodes sometimes found living in flesh.

Good Habitat

Bays and estuaries provide important spawning habitat for jacksmelt. In general, the preferred spawning areas are situated in shallow nearshore habitats containing submerged vegetation (Wang 1986). Water quality variables suitable for embryo development are as follows: temperature, 10-12° C; and salinity, polyhaline and as low as 5 ppt (Wang 1986). Schools of larvae occur near the water surface over a variety of substrates, but mostly sandy and muddy bottoms and in the kelp canopy (Frey 1971). Optimum larval and juvenile survival and growth appears to be at salinities of 10-20 ppt, indicating that larvae may prefer mesohaline environments (Middaugh and Shenker 1988, Middaugh et al. 1990). Juveniles and adults prefer sandy bottoms in murky water at depths of 1.5-15 m below the surface (Feder et al. 1974). Furthermore, they seem to use open waters in San Francisco Bay and sloughs in and near Suisun Marsh and Napa Marsh (Jones and Stokes Assoc. 1979). Jacksmelt are apparently more sensitive than topsmelt to fluctuations in salinity and temperature (Emmett et al. 1991).

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Topsmelt

Atherinops affinis

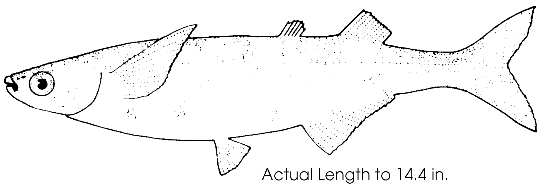
Michael K. Saiki

General Information

On the West Coast, topsmelt (Family: Atherinidae) are represented by five recognized subspecies of which only one, the San Francisco topsmelt *(Atherinops affinis affinis*), inhabits San Francisco Bay (Wang 1986). Topsmelt are a small but tasty food fish taken from piers by recreational anglers (Emmett et al. 1991). However, commercial fishing for topsmelt is limited, with the species comprising only about 15-25% of the total "smelt" catch (Bane and Bane 1971, Frey 1971). Ecologically, topsmelt are an important prey item for many piscivorous birds and fishes (Feder et al. 1974).

Reproduction

According to Emmett et al. (1991), the topsmelt is gonochoristic (its gender is determined by developmental rather than hereditary mechanisms) and iteroparous (it has the capacity to survive and spawn beyond one or multiple spawning seasons). Adults move into shallow sloughs and mud flats in late spring and summer to spawn (Wang 1986). In San Francisco Bay, spawning occurs from April to October, with peaks in May and June (Wang 1986). Although eggs are deposited singly, the thick chorion bearing 2-8 filaments becomes entangled in aquatic vegetation, resulting in the formation of large clusters of eggs (Wang 1986). Topsmelt seemingly spawn in batches, laying eggs more than once during a spawning season (Fronk 1969, Wang 1986). The fecundity of topsmelt ranges from 200 eggs/fish for females measuring 110-120 mm in length to about 1,000 eggs/fish for females measuring 160 mm or more in length (Fronk 1969). Hatching time varies from 35 days at 13°C to less than 9 days at 27°C (Hubbs 1969).


Actual Length to 14.4 in.

CDFG

Growth and Development

Topsmelt eggs are spherical in shape and approximately 1.5-1.7 mm in diameter (Wang 1986). Between nine and 35 days after fertilization, eggs hatch into planktonic larvae that measure 4.3-4.9 mm total length (TL) and 0.0011 grams wet weight (Emmett et al. 1991) or 5.1-5.4 mm standard length (SL) (Middaugh et al. 1990). Larvae measure 9.5-10.0 mm after the yolk-sac is absorbed, and begin to develop juvenile characteristics when approximately 18.5 mm long (Wang 1986). Juveniles may vary in length from 18.5 to 120.0 mm (Schultz 1933, Fronk 1969). Topsmelt mature in their second or third year, depending on subspecies, and may live six to nine years (Schultz 1933, Feder et al. 1974). Adults can attain as much as 120 mm in length for the southernmost subspecies (*A. affinis littoralis*) and as much as 370 mm in length for the northernmost subspecies (*A. affinis oregonia*) (Schultz 1933, Fronk 1969, Eschmeyer et al. 1983). In general, northern varieties grow larger than southern subspecies (Schultz 1933).

Food and Feeding

The topsmelt is characterized by an omnivorous diet (Quast 1968, Horn and Allen 1985). Topsmelt from bay and estuarine habitats consume mostly plant material (diatoms, filamentous algae, and detritus), whereas those from ocean habitats feed mainly on planktonic crustaceans (gammarid and caprellid amphipods, mysids, ostracods, copepods, and crustacean larvae) (Moyle 1976, Quast 1968, Fronk 1969). Juveniles and adults forage mostly during daylight near the surface in deep water or on the bottom in shallow water (Hobson et al. 1981).

Distribution

Topsmelt can occur from the Gulf of California northward to Vancouver Island, but are usually rare north of Tillamook Bay, Oregon (Miller and Lea 1972, Hart 1973, Eschmeyer et al. 1983). The five subspecies are *A. affinis oregonia* (occurs from Oregon to Humboldt Bay, California), *A. affinis affinis* (occurs in San Francisco Bay and surrounding waters to Monterey, California), *A. affinis littoralis* (occurs from Monterey to San Diego Bay, California), *A. affinis cedroscensis* (the kelp topsmelt), and *A. affinis insularium* (the "island topsmelt," occurs around the Santa Barbara Islands, California) (Schultz 1933, Feder et al. 1974).

In San Francisco Bay, spawning has been observed in the South Bay near the Aquatic Park in Berkeley and at the Dumbarton Bridge (Wang 1986). Small schools of larvae often occur near the surface of both shallow water and open water, and are particularly abundant in tidal basins (e.g., Aquatic Park in Berkeley; Lake Merritt in Oakland) and the sluggish waters of the South Bay (e.g., Robert Crown Memorial Park; Hunters Point; San Mateo Bridge; Dumbarton Bridge) (Wang 1986). Juvenile topsmelt generally move into open waters of the bay or into coastal kelp beds. Some juveniles may occur in Suisun Bay during summer and early fall as the salt wedge moves to the upper reaches of the Estuary (Wang 1986). In general, topsmelt seem to be much less common outside of the South Bay.

Population Status and Influencing Factors

Field studies indicate that topsmelt are among the most abundant fish species occurring in shallow-water sloughs of South San Francisco Bay (Jones and Stokes Assoc. 1979, Woods 1981, Herbold et al. 1992). Herald and Simpson (1955) reported that topsmelt were commonly caught in a fixed fish-collecting device located at the Pacific Gas and Electric Company power plant in South San Francisco Bay. Furthermore, Wild (1969) reported that topsmelt was the most abundant species of fish sampled at the mouth of Plummer Creek (located in South San Francisco Bay). Midwater trawls fished at several locations in South San Francisco Bay during 1980-1988 also yielded numerous topsmelt (Herbold et al. 1992). South Bay topsmelt increased in abundance during two of the recent drought years, but otherwise did not show consistent year-to-year patterns (Herbold et al. 1992).

Several factors may directly influence the abundance of topsmelt: salinity, water temperature, freshwater inflows, entrainment on intake screens at power plants and water diversions, and availability of spawning substrate. In Newport Bay, California, topsmelt abundance was significantly correlated with water temperature and salinity (Allen 1982). By comparison, no relationship was found between abundance indices and river flow in San Francisco Bay (CDFG 1987). Although this species is commonly impinged on intake screens of power plants and water diversions, this source of mortality may not be significant for bay populations (San Diego Gas and Electric 1980). In the Tijuana Estuary of southern California, abundance of topsmelt eggs and larvae was positively correlated with algal mats (Nordby 1982). In other words, topsmelt eggs and larvae were seemingly more abundant in areas with dense algal growth. Because this species uses algal mats and shallow-water eelgrass beds for spawning, destruction or removal of these types of vegetation may adversely affect topsmelt abundance.

Trophic Levels

Topsmelt are omnivorous (primary and higher order consumers).

Proximal Species

Predators: Many piscivorous birds and fishes.

Prey: Diatoms (major); diatoms, chironomid midge larvae, and amphipods (minor).
Habitat: Eel grass and micro algae (spawning substrate); kelp beds (adult and juvenile cover).
Cohabitors: Schools with shiner perch and jacksmelt.

Good Habitat

In general, topsmelt can tolerate a relatively broad range of environmental conditions during the time that they inhabit San Francisco Bay. However, for successful spawning to occur, they require submerged vegetation for egg attachment, water temperatures of 10-25°C, and salinities of less than 72 ppt (Schultz 1933, Carpelan 1955, Fronk 1969). By comparison, larvae must be able to school near the surface in shallow open-water areas, particularly tidal basins (Wang 1986). Young-of-the-year topsmelt are common in middle to low salinity portions of the Estuary (Wang 1986). Although juveniles can tolerate salinities varying from 2 ppt to 80 ppt, growth and survival are reduced at salinities above 30 ppt (Middaugh and Shenker 1988). In addition, juveniles and adults are seemingly eurythermal, but temperatures of 26-27° C or higher may cause stress (Carpelan 1955, Ehrlich et al. 1979). Within San Francisco Bay, topsmelt utilize mudflats for breeding, spawning, and as nursery areas for young. Subtidal areas with sandy bottoms are relied on heavily as nursery and foraging areas. Intertidal streambeds are major foraging areas (Jones and Stokes Assoc. 1979). Recent studies indicate that embryonic and larval stages of topsmelt are sensitive to the effects of pollution (Singer et al. 1990, Anderson et al. 1991, Goodman et al. 1991, Hemmer et al. 1991). Thus, habitats used by topsmelt for spawning and rearing must not be exposed to appreciable amounts of pollution.

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Threespine Stickleback

Gasterosteus aculeatus

Robert A. Leidy

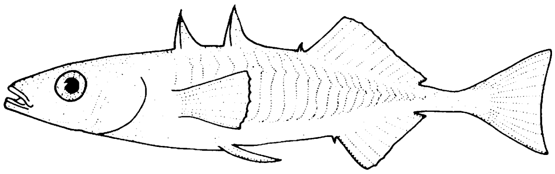
General Information

The threespine stickleback (Family: Gasterosteidae) is a small laterally-compressed fish with three spines on the dorsum and from 1 to 35 bony plates on the sides (Moyle 1976). Largely as a matter of taxonomic convenience, Miller and Hubbs (1969) suggested that there are two forms: *G. a. aculeatus* for the fully-plated, anadromous form; and *G. a. microcephalus* for the partially-plated freshwater/resident form. The threespine stickleback is a polymorphic species and as such, populations within the San Francisco Estuary and its tributary streams support resident/freshwater and anadromous/saltwater forms, as well as mixtures of the two forms that presumably interbreed (Moyle, pers. comm.). The threespine stickleback has no commercial value, but has important scientific value, especially to evolutionary biologists.

Reproduction, Growth and Development

The following discussion is taken largely from Moyle (1976) unless otherwise referenced. Threespine sticklebacks typically complete their life cycle within one year although some individuals may live two to three years. Individuals from freshwater populations typically do not exceed 60 mm total length (TL), while anadromous forms may exceed 80 mm TL. Adult females are usually larger than adult males.

Anadromous forms migrate into freshwater breeding areas as water temperatures increase during April through July, although some stickleback populations may remain in estuarine environments to spawn if suitable habitat is present (Moyle 1976, Wang 1986).



Actual Length to 4 in.

CDFG

Anadromous forms typically spawn earlier than freshwater populations. Spawning typically occurs at 15° to 18° C (Vrat 1949, Wang 1986). Males begin to display bright green and red breeding coloration as they move away from schools to set up breeding territories and construct nests.

Nests are excavated in the substrate as shallow pits. The pits are then covered with algae or other plant fragments and formed into a tunnel that is held together by a sticky renal secretion (Greenbank and Nelson 1959). Females are then courted by males into the nest where the female may lay between 50 and 300 eggs in several spawnings. Eggs are spherical and average 1.5-1.7 mm in diameter (Wang 1986). A pair can spawn up to six times within a 10-15 day period (Wang 1986). Following egg laying, the male drives away the female, fertilizes the eggs, and then begins to incubate the eggs while defending the nest from other sticklebacks and predators. The male is known to circulate water over the eggs by fanning his pectoral fins and to clean the eggs with his mouth. Immediately prior to hatching the male tears apart the nest and breaks apart the egg clusters which is thought to increase the survival of hatching young (Wang 1986). Length at hatching is between 4.2 and 5.5 mm TL (Vrat 1949, Kuntz and Radcliffe 1917).

Stickleback eggs hatch in six to eight days at temperatures of between 18° to 20° C (Breder and Rosen 1966). The fry remain in the nest for several days where they continue to be guarded by the male. Fry eventually form schools of similar-size sticklebacks or other species, usually in shallow water habitats containing dense vegetation (Wang 1986).

Juveniles are most abundant in late summer, followed by drastic declines in abundance in the fall and winter (Wang 1986). It is unknown whether populations of juveniles within the San Francisco Estuary make extensive migrations into open water/subtidal habitats within the Estuary. Moyle (1976) states that freshwater and anadromous populations range from complete ecological separation to complete interbreeding.

Food and Feeding

Threespine sticklebacks are visual feeders primarily on small benthic organisms or organisms living on submerged, rooted, or floating macrophytes such as insect larvae, chironomid midge larva, and ostracods (Hynes 1950, Beukema 1963, Hagen 1967). Anadromous forms feed mostly on free-swimming crustaceans (Barraclough and Fulton 1967, 1978; Barraclough et al. 1968). In a study of threespine stickleback diet in San Pablo Creek, a tributary to San Pablo Bay, Snyder (1984) found the diet consisted of approximately 42% insects (mainly chironomid larvae), 28% crustacea (mainly ostracods), and 10% earthworms (Lumbricidae). Fish eggs and plant material accounted for approximately 9% of the diet (Snyder 1984).

Distribution

Threespine stickleback are native to the coastal waters of Mediterranean Europe, north to Russia, and east to Japan and Korea (Moyle 1976). In North America, threespine stickleback populations occur on the East coast south to Chesapeake Bay, and on the West coast south from Alaska to Baja California. In California, populations are found below barriers such as dams and falls in coastal streams, including the San Francisco Estuary and its tributary streams, and in the Central Valley (Moyle 1976).

Within the San Francisco Estuary, threespine stickleback are widely distributed and often locally abundant in fresh-, brackish-, and saltwater intertidal upper marsh and riverine tidal marsh habitats (Leidy 1984; Leidy, unpub. data; Cathy Hieb, unpub. data). Leidy (1984) recorded threespine stickleback in 43% of 457 samples of Estuary streams between elevation 0 to 123 m.

Threespine stickleback are also abundant in large areas of formerly tidal salt and brackish marsh that have been converted to salt ponds in the South Bay and San Pablo Bay (Lonzarich 1989, Herbold et al. 1992). Carpelan (1957) recorded threespine stickleback as one of the most numerous fish in the Alviso salt ponds in the South Bay. Apparently, threespine stickleback persist in these ponds, particularly near the mouth of the Napa River, until salinities become too high (i.e., salinities between 40 to 50 ppt) (Herbold et al. 1992). There are approximately 9,059 acres of salt ponds in the Napa-Solono area of the North Bay and 27,497 acres in the South Bay that may be considered available for use by threespine stickleback on a seasonal basis (Meiorin et al. 1991).

Population Status and Influencing Factors

The current status of threespine stickleback within the San Francisco Estuary may be regarded as secure. Threespine stickleback populations currently are widespread and locally abundant in suitable habitats within the San Francisco Estuary. Because sticklebacks can readily disperse through estuarine and marine environments they are able to regularly recolonize habitats from which they may been extirpated. Important factors negatively influencing population numbers likely include excess siltation and turbidity, increased water temperatures by the removal of riparian vegetation through stream channelization, pollution, loss of nesting, feeding, and cover habitat by the removal of aquatic macrophytes, the construction of barriers such as dams or drop structures, and the introduction of exotic piscivorous fish.

Trophic Levels

Larvae are primary consumers. Juveniles and adults are primary and higher order consumers.

Proximal Species

Major Predators: Kingfisher, egrets, herons, and other wading birds.
Other Predators: Adult salmonids and other large freshwater, estuarine, and marine piscivorous fish terrestrial and aquatic snakes.
Major Prey: Aquatic insects and crustacea, earthworms, fish eggs and vegetation.
Habitat/cover: Riparian, submerged, floating, and emergent wetland and aquatic vegetation.

Good Habitat

Freshwater populations of threespine stickleback prefer clear, cool backwater and pool habitats containing submerged, floating, or emergent vegetation, with sand or small-sized gravel substrates (Moyle 1976, Leidy 1984). This species is typically uncommon in silted pools with moderate to high turbidities (Leidy 1984). Marine and estuarine populations are pelagic, although they tend to remain to close to the shore (Moyle 1976). Threespine stickleback is uncommon where water temperatures regularly exceed 24° C (Moyle 1976).

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Personal Communications

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Brown Rockfish

Sebastes auriculatus

Kurt F. Kline

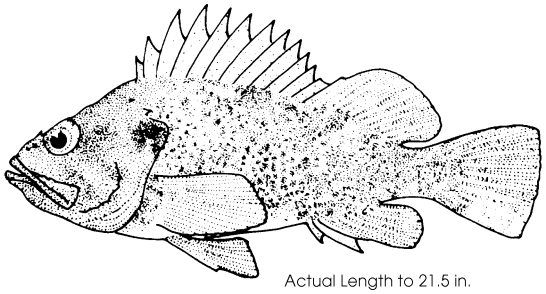
General Information

The brown rockfish (*Sebastes auriculatus*) is a member of the family Scorpaenidae, one of the largest fish families in the western Pacific. The family is dominated by the rockfishes (*Sebastes spp*.), a genus which is represented by over 50 species on the northwest Pacific coast.

The brown rockfish is the most common rockfish in San Francisco Bay (Alpin 1967, Wang 1986), and the Bay appears to be an important nursery area for juveniles (Kendall and Lenarz 1986, Baxter 1999). Brown rockfish are the most common rockfish caught by sport anglers in the Bay (W. Van Buskirk, pers. comm) and the third most frequently caught rockfish in the San Francisco region (Karpov et al. 1995). Most brown rockfish are caught by anglers fishing from partyboats, skiffs, piers, and the shoreline (Miller and Gotshall 1965, Karpov et al. 1995). It is also a minor, but important, component of the nearshore commercial fishery; in the San Francisco area, the majority of brown rockfish are caught by hook and line for the live or whole fresh fish markets. Since the early 1990s, the brown rockfish has been the most common species sold in the live in San Francisco markets (C. Ryan, pers. comm.).

Reproduction

All rockfishes, including the brown rockfish, are viviparous. Fertilization is internal and the larvae develop in the egg capsule within the ovarian cavity. The larvae hatch within the ovary and are released with little yolk remaining and ready to feed. The embryos develop in 40-50 days after fertilization and the larvae hatch about 1 week before extrusion (Kendall and Lenarz 1986). Brown rockfish larvae are 4.7-6.7 mm at hatching (Delacy et al. 1964) and pelagic for several months. Although brown rockfish fecundity is not known, *Sebastes* females typically produce 100,000 to 1,000,000 eggs per brood (Kendall and Lenarz 1986). Brown rockfish may have multiple broods within one year, with parturition from December-January and May-July in Central California (Wyllie-Echeverria 1987).



CDFG

Actual Length to 21.5 in.

Although gravid brown rockfish have been collected in San Francisco Bay, most parturition is believed to occur in coastal waters (Kendall and Lenarz 1986, Wang 1986). In San Francisco Bay, mature females were observed in winter and spring and larvae have been collected in winter and spring (Wang 1986).

Growth and Development

Brown rockfish juveniles are pelagic until 20-30 mm, whereas older juveniles settle out of the water column and are strongly association with some type of physical structure (Turner et al. 1969, Kendall and Lenarz 1986). Pelagic juveniles have been collected in nearshore coastal waters from April through June, while benthic juveniles are common in nearshore coastal waters and the Bay (Kendall and Lenarz 1986). In San Francisco Bay, age-0 juveniles were usually first collected from April to July and were common through summer and fall (Wang 1986, Baxter 1999).

Juvenile brown rockfish apparently spend several years in a very restricted home range in the Bay and gradually move to deeper waters and nearshore. Juvenile brown rockfish tagged in the Bay have been recaptured more than 80 km away in nearshore coastal waters (Kendall and Lenarz 1986).

Both male and female brown rockfish reach maturity as early as age 3 (260 mm TL); half reach maturity at age 5 (310 mm TL); and all are mature at age 10 (380 mm TL) (Wyllie-Echeverria 1987). Both sexes grow at similar rates and reach a maximum size of about 550 mm TL (Miller and Lea 1972). In southern California, the oldest male was 18 years, the oldest female 20 years (Love and Johnson 1998).

Food and Feeding

In San Francisco Bay, smaller juvenile brown rockfish (<130 mm TL) prey primarily upon small crustaceans, including amphipods, copepods, caridean shrimp, and *Cancer* crabs. Larger fish (130-310 mm TL) prey upon larger crustaceans (caridean shrimp, *Cancer* crabs, *Upogebia*) and fish (Ryan 1986).

Distribution

The brown rockfish ranges from Hipolito Bay, Baja California, to southeast Alaska (Miller and Lea 1972). It most often solitary, but may be found in small aggregations (Love and Johnson 1998). In the ocean, it is most common in shallow rocky reefs (5-20 m), but also found over sand flats near eelgrass and in kelp beds while in bays and estuaries it is found near piers and over rubble (Feder et al. 1974, Matthews 1990, Love and Johnson 1998).

In San Francisco Bay the brown rockfish is found primarily in Central San Francisco Bay, to a lesser degree in South San Francisco and San Pablo bays, and occasionally in Carquinez Strait and western Suisun Bay (Ganssle 1966, Messersmith 1966, Wang 1986, Baxter 1999).

Suitable habitat and salinity are the primary factors influencing distribution of brown rockfish in the Bay. Benthic juveniles and adults are strongly associated with structure, including rocky reefs, piers and jetties, breakwaters, and riprap. In the Bay, most brown rockfish were collected at salinities > 20l (median 28.3l , 90th percentile 31.8l, 10th percentile 21.5l, Baxter 1999, CDFG, unpubl. data).

Population Status and Influencing Factors

There is a modest brown rockfish population in the San Francisco Bay region. San Francisco Bay is a nursery area for brown rockfish, and most juveniles immigrate to the Bay from the nearshore coastal area soon after settlement. It is not clear if resident adult brown rockfish spawn successfully in the Bay. Juveniles rear in the Bay for several years, and the population is comprised of several year classes. But there is no reliable index or measure of year class strength in the Bay, as brown rockfish are strongly associated with structure, and are undoubtedly undersampled by trawls or other towed nets typically used by research studies.

Trophic Levels

Secondary carnivore. Feeds primarily on crustaceans and fishes.

Proximal Species

Prey: Crustaceans (caridean shrimp, *Cancer* crabs, *Upogebia*, amphipods, copepods), polychaetes, fishes, herring eggs.
Predators: Larger predatory fishes, including striped bass.

Good Habitat

Structure, including piers and rocky shores, in the higher salinity regions of the Bay

Acknowledgments

Some of the material in this report was summarized from the brown rockfish chapter in IEP Technical Report 63, which is referenced below (Baxter 1999).

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Personal Communications

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Pacific Staghorn Sculpin

Leptocottus armatus armatus

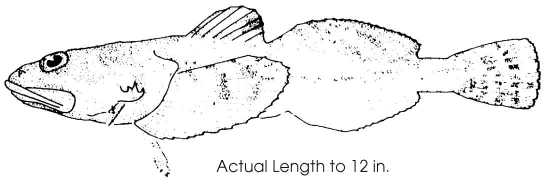
Robert N. Tasto

General Information

The Pacific staghorn sculpin (Family: Cottidae) is found from Kodiak Island, Alaska to San Quintin Bay, Baja, California (Miller and Lea 1972). It is the only true euryhaline species among the California cottids (CDFG 1987), and appears to move freely between fresh and saltwater environments (Moyle 1976). It is regarded as a nuisance species by many sportfishermen, but has shown some limited value as bait for gamefish (particularly striped bass) in the Estuary. Bolin (1944) recorded its maximum depth of capture offshore coastal California at 300 feet. It is a target species of the National Status and Trends Program (Emmett et al. 1991), as it is considered an indicator of stress in the estuarine environment, and may spend its entire life in Pacific coast estuaries.

Reproduction

Pacific staghorn sculpin may reach sexual maturity in their first year, and sex ratios within a population appear to favor females slightly (Boothe 1967, Tasto 1975). In northern California, spawning begins in October (Tomales Bay) or November (San Francisco Bay), peaks in January-February, and ends in March (Jones 1962, Boothe 1967). In southern California (Anaheim Bay), spawning does not begin until December, but also peaks in January-February and ends around mid-March (Tasto 1975). Fertilization is external. Staghorn sculpin eggs are adhesive and laid in shallow subtidal and intertidal waters. Fecundity averages 5,000 eggs per female (Jones 1962), and ranges from 2,000 to 11,000 eggs per female (Moyle 1976). Eggs range from 1.36 to 1.50 mm in diameter and hatch in 9 to 14 days at 15.5°C (Emmett et al. 1991).



CDFG

Actual Length to 12 in.

Growth and Development

At hatching, Pacific staghorn sculpin larvae range from 3.9 to 4.8 mm total length (TL) (Jones 1962). Metamorphosis to the juvenile begins after about 2 months, when the larvae are 15 to 20 mm standard length (SL) (Emmett et al. 1991). The juvenile size range is approximately 20 to 120 mm TL (Jones 1962), and there appears to be considerable overlap in the length distribution of 0+ and 1+ fish, particularly in the summer and fall (CDFG 1987). The staghorn sculpin reaches maturity at about 120 mm TL its first year, and can grow to over 200 mm TL (3 years old) in California (Jones 1962). In southern California, growth was determined to be curvilinear (Tasto 1975). The largest specimen recorded was about 30 cm (Barnhart 1936).

Food and Feeding

Pacific staghorn sculpin larvae are planktivorous (Emmett et al. 1991). The juvenile and adult forms are, however, demersal predators, particularly over intertidal and shallow subtidal mudflats, and have been shown to feed on a variety of non-burrowing benthic organisms (Jones 1962, Boothe 1967, Tasto 1975). Feeding behavior of the staghorn sculpin is thought to be continuous, although there appears to be a preference for feeding at night (Tasto 1975). The principal food items for staghorn sculpin within San Francisco Bay were found to be bay shrimp (*Crangon* spp.), bay goby (*Lepidogobius lepidus*), mud crab (*Hemigrapsus oregonensis*), callianassid shrimp (i.e., *Upogebia*), and a variety of amphipods, isopods, and polychaetes (Boothe 1967). Elkhorn Slough studies showed predation on epifaunal crustaceans and infaunal and epifaunal worms (Barry et al. 1996). In Anaheim Bay, major food items were similar to Elkhorn Slough and San Francisco Bay, including callianasiid shrimp (i.e., *Callinassa sp.),* mud crab, and arrow goby (*Clevelandia ios*) (Tasto 1975). Jones (1962) found that in Tomales Bay, staghorn sculpin fed heavily upon *Upogebia* and *Crangon* shrimp. In Grays Harbor, Washington, the staghorn sculpin's diet consisted of amphipods, crangonid shrimp, small fish, *Upogebia* sp., juvenile Dungeness crab, and polychaetes (Armstrong et al. 1995). Several studies indicate that the staghorn sculpin

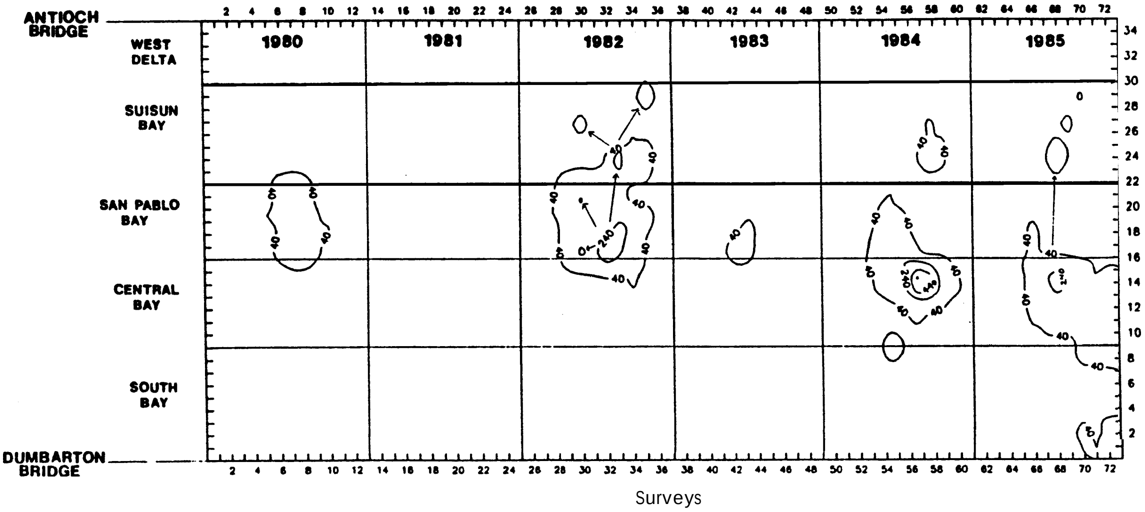


Figure 2.5 Spatial and Temporal Distribution of Young-of-the-Year Pacific Staghorn Sculpin (CDFG 1987)

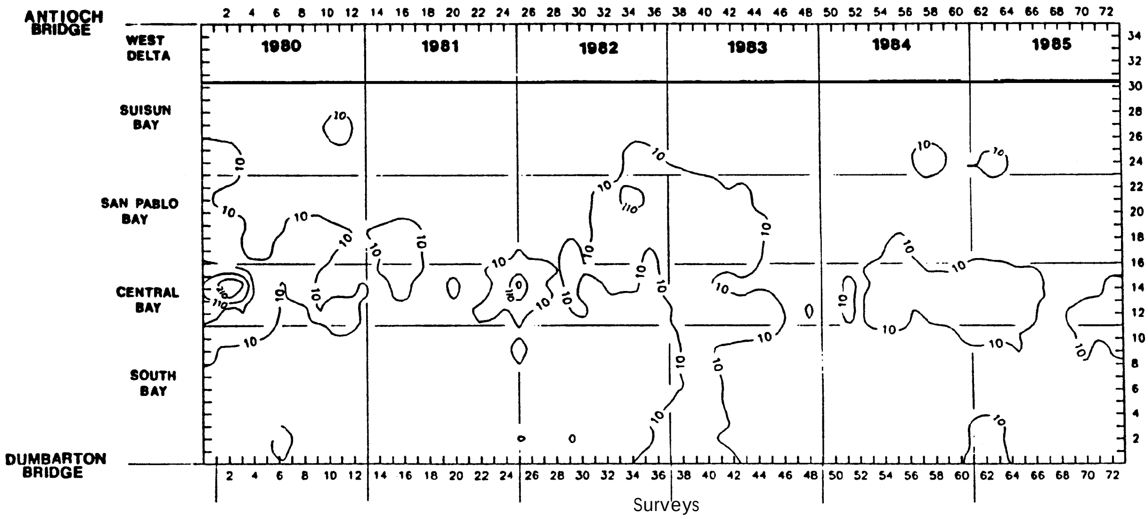


Figure 2.6 Spatial and Temporal Distribution of Adult Pacific Staghorn Sculpin (CDFG 1987)

is an important prey item for aquatic birds, particularly the great blue heron (Tasto 1975, Bayer 1985, Emmett et al. 1991).

Distribution

Pacific staghorn sculpin have been collected in all four subregions of the Bay. Larval abundance was determined to be highest from December through March, peaking in February, in various parts of the Estuary south of the Carquinez Bridge (CDFG 1987). Small juveniles are often found intertidally; catch patterns suggest that, during their first year, these early post larval forms move gradually from shallow inshore areas to deeper Bay waters (CDFG 1987, Emmett et al. 1991). In studies conducted in Yaquina Bay, Oregon, young-of-the-year first appeared in December, and were collected through April (Bayer 1985). Juveniles and adults are most frequently captured in central Bay and San Pablo Bay, and are more abundant in the channels in winter, and on the shoals in spring and summer (**Figures 2.5** and **2.6**). Adults experience their widest distribution during high Delta outflow, and it appears that a portion of the adult population moves out of the Estuary by late spring of their second year (CDFG 1987). In Elkhorn Slough (Monterey County), staghorn sculpin were highest in abundance, and frequently the dominant species, at sampling stations furthest inland, near sources of fresh water (Yoklavich et al. 1991). A tidal marsh population studied in Anaheim Bay, a relatively small embayment in southern California with little freshwater input, was composed almost entirely of juveniles (Tasto 1975). Pacific staghorn sculpin can also be found a mile or two up coastal streams in association with exclusively freshwater species (Moyle 1976).

Population Status and Influencing Factors

Multiple gear catch statistics from 1980-85 showed that Pacific staghorn sculpin was the most abundant of all the sculpins caught in the Estuary, and approximately 4% of all fishes caught by otter trawl and beach seine (CDFG 1987). The highest abundance of larvae noted in this study occurred during years of low Delta outflows, yet juvenile and adult numbers showed no quantifiable relationship to magnitude of flows (CDFG 1987). Larval success is thought to be the determining factor in overall recruitment to local populations (Emmett et al. 1991).

Trophic Levels

Larvae are first and second order consumers (Emmett et al. 1991). Adults and juveniles are higher order consumers.

Proximal Species

Predators: Diving ducks, great blue heron, western grebe, Caspian tern, loons, cormorants, gulls, marine mammals.
Prey: *Crangon* shrimp (principal prey item), bay goby (prey of large adults), mud crab, callianassid shrimp, amphipods (juvenile prey item, dominant in fresh water).
Competitor: Starry flounder.

Good Habitat

Success of local staghorn sculpin populations depends upon the quality and quantity of suitable habitat. Newly settled juveniles use intertidal and shallow subtidal mudflats for protection and feeding (Tasto 1975), although older juveniles and adults are said to prefer more sandy substrates and somewhat deeper waters (Bayer 1981, Emmett et al. 1991). Pacific staghorn sculpin are known to bury themselves in soft substrates, and have been found buried in mudflats after the tide has retreated (Tasto 1975, Bayer 1985). Staghorn sculpin have also been found associated with eelgrass (Bayer 1981).

Water quality factors are equally important for successful populations. Demersal eggs hatch most successfully at 26 ppt and larvae survive best at 10 to 17 ppt (Jones 1962). Greatest catches of larvae were in surface salinities of 18 to 30 ppt (CDFG 1987). The juvenile stage appears to be the most euryhaline, with the maturing and adult forms most likely to be found in the higher salinity waters (CDFG 1987, Emmett et al. 1991). Laboratory experiments have shown that adult *L. armatus* can survive 67.5 ppt at 12°C, but gradually lose their tolerance of high salinities as temperatures rise to 25°C (Morris 1960). Since larval development is planktonic, it does not appear that, under normal conditions in the San Francisco Estuary, either temperature or salinity are very limiting to distribution.

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Prickly Sculpin

Cottus asper

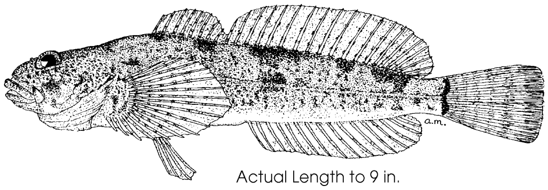
Bruce Herbold

General Information

Sculpins (Family: Cottidae) are specialized for living on the bottom, generally hiding in the nooks and crannies among rocks or rooted vegetation. Their large, flattened heads and proportionally small bodies, their fan-shaped pectoral fins, and their lack of an air bladder allow sculpins to hold their position even in wave-swept coasts or high-velocity mountain streams. The use of such habitats, combined with their secretive habits and cryptic coloration, make sculpins difficult to see by predators, prey, or inquisitive fish biologists. The large mouth relative to body size permits sculpins to consume prey almost as large as themselves. Sculpins are found in the northern Pacific Ocean and New Zealand. Most members of the family are marine but a number of species (most in the genus *Cottus*) occur in the fresh waters of North America.

Reproduction

Sculpins generally spawn in the late winter or early spring, although some upstream populations seem to delay spawning into the early summer (Wang 1986). Male sculpins prepare for spawning by moving downstream and establishing a nest site where they clean off some kind of overhanging structure such as a flat rock, tule root, or beer can (Kresja 1965, Moyle 1976). Females then enter the spawning area and, after a nocturnal courtship, attach their eggs to the prepared overhanging structure. Females produce between 280 and 11,000 eggs (Patten 1971), but one male may court many females and end up with a nest containing up to 30,000 eggs (Kresja 1965). Males stay in the nest protecting the eggs and circulating water around them until they hatch. Hatching rates appear to improve in saltier water (Millikan 1968). After hatching, the larvae become planktonic and are carried further downstream. Young sculpins (15-30 mm SL, Broadway and Moyle 1978) settle to the bottom and begin a general upstream movement (McLarney 1968, Mason and Machidori 1976).



Moyle 1976

Actual Length to 9 in.

The amount of movement associated with spawning appears to vary tremendously among sculpin populations (Wang 1986). Earlier observers suggested that substantial downstream movements were only found in coastal populations, not in the Central Valley (Kresja 1967). However, very high densities of newly hatched prickly sculpins have been reported from the Delta and Suisun Bay (Turner 1966, Wang 1986), as well as in upstream sites (Wang 1986) which has led to the conclusion that the Central Valley contains both ‘migratory’ and ‘non-migratory’ populations. Recent studies suggest that the same may be true in coastal streams, such as the Eel River, where young prickly sculpins were found 100 km above the river mouth (Brown et al. 1995). Regardless of the degree to which they move for spawning, mainstem rivers appear to be an important habitat for most prickly sculpin populations. Young prickly sculpins are often found in saline water at the tributary mouths in spring months (Leidy pers. comm.).

Growth and Development

Fry at hatching average six mm total length. Newly emerged fry swim soon after hatching and appear to drift downstream as plankton for three to five weeks. This early developmental pattern leads to high concentrations in the slower waters of the Delta (Turner 1966). Young fish assume a bottom-feeding existence at sizes of 20 to 30 mm, at which time they appear to begin moving upstream (McLarney 1968).

Food and Feeding

Sculpins have a reputation amongst anglers as predators on salmonid eggs and fry (Munro and Clements 1937, Shapovalov and Taft 1954, Reed 1967) which is probably undeserved (Moyle 1976, 1977). Diet studies generally show that sculpins prey principally on invertebrates, with younger prickly sculpins eating planktonic crustaceans and older fish eating larger, benthic animals and small fish (Moyle 1976). In Suisun Marsh their diet is predominately benthic amphipods of the genus *Gammarus* (Herbold 1987).

Distribution

Prickly sculpins are found in fresh to brackish water from the Kenai Peninsula in Alaska to the Ventura River in southern California. In California’s Central Valley, they can be found in the lower reaches of most foothill streams. Prickly sculpins often overlap in distribution with the similar riffle sculpin (*Cottus gulosus*) which is found more in upper elevations. Neither is found in the upper Pit River drainage. Their range includes tidal habitats of brackish salinity, such as Suisun Marsh. Prickly sculpins are found from headwaters to the mouths of many of the small tributaries that flow into San Francisco Bay, (including Alameda Creek, Walnut Creek, Corte Madera Creek, Coyote Creek and the Petaluma River; Leidy 1984).

Habitats

Like freshwater sculpins generally, prickly sculpins use very diverse habitats from small headwater streams to coastal estuaries, and are widely distributed from Alaska to southern California (Moyle 1976). Whatever the habitat, prickly sculpins usually are found under some sort of cover: rocks in streams, vegetation in pools and marshes, or simply at depth in lakes and reservoirs (Moyle 1976, Brown et al. 1995).

Population Status and Influencing Factors

Many of the most recent, successful invading species of the Estuary have the potential to affect prickly sculpins. In 1986, the Asiatic clam *(Potamocorbula amurensis*) began a rapid and thorough domination of the benthic community. Although the decline in abundance of other benthic species has been well-documented, there is no information on the impact of these changes on the diet, distribution, or abundance of prickly sculpin. Also in the mid-1980s, the Estuary was invaded by the shimofuri goby *(Tridentiger bifasciatus*) which lives in the same kinds of habitats and microhabitats as prickly sculpin. However, the very small mouth of the goby reduces the likelihood of interspecific competition. Since 1996, mitten crabs (*Eriochier sinensis*) have become extremely abundant and are voracious and indiscriminate predators on benthic organisms. Mitten crabs undergo an annual upstream migration to spawn that results in a large overlap with the range of prickly sculpins. In the Eel River of northern California, it appears likely that the introduction of predatory pikeminnows (*Ptychocheilus grandis*) has resulted in a substantial change in sculpin behavior when compared to the similar Smith River (Brown and Moyle 1991, Brown et al. 1995, White and Harvey in press). In the tributary creeks of the San Francisco Bay drainage, prickly sculpins are often associated with native species and are usually absent in areas where large non-native predatory fish are found (Leidy 1984). No work has been done to document interactions of prickly sculpin with the vastly changed benthic community of the Central Valley.

Habitat changes and degradations of water quality are associated with a restricted range of prickly sculpins in the San Joaquin River watershed (Brown 1998). Sculpins are part of an assemblage of native species that are characteristic of smaller San Joaquin tributaries that have suffered little change in habitat structure or water quality. Unfortunately, the close associations of land use practices, habitat alteration and water quality degradation in the rest of the watershed make it impossible to identify the effects of individual environmental variables on sculpin biology.

As in the San Joaquin River, prickly sculpins in Suisun Marsh tend to be found most often in association with other native fishes and in less disturbed habitats (Herbold 1987). However, the actual physical parameters of low dissolved solids and high gradient that characterize usual sculpin sites in the San Joaquin River, are absent in Suisun Marsh. This suggests that the impacts of land use and disturbance on the distribution and abundance of prickly sculpins are not simple and that the parameters that reflect disturbance in one area may not be causally connected to the parameter of importance to sculpins in that area.

California's immense water projects appear to have had little effect on prickly sculpins. Construction of dams has isolated populations and prevented the downstream movements exhibited elsewhere, but populations have remained large in the warmwater reservoir behind Friant Dam. Prickly sculpins are also found in stream habitats upstream of impassable dams on a number of other Central Valley streams. Water export from the Delta has resulted in the establishment of new populations of prickly sculpins within the facilities of the state and federal projects, as well as within aquatic habitats in southern California outside the historic range of prickly sculpin (Wang 1986). The impacts of these introductions on the native species in southern California streams have been little studied.

Trophic Levels

Prickly sculpins are secondary and tertiary consumers.

Proximal Species

Predators: Centrarchids and pikeminnows.
Prey: Planktonic crustacea (for young); benthic invertebrates, particularly gammarid amphipods; *neomysis*; juvenile fish.
Habitat: Emergent aquatic vegetation (root masses).

Good Habitat

In contrast to staghorn sculpins (*Leptocottus armatus*), prickly sculpins larger than 20 mm are usually found in association with some kind of complex, physical cover. In upstream sites, cover consists of interstices in cobble, root wads and woody debris and even discarded soda cans and tires. In downstream sites, cover usually consists of root wads of emergent aquatic vegetation. Although more tolerant of salinity than most other California freshwater fish, sculpins are seldom found in salinities greater than 10 ppt.

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Personal Communications

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Striped Bass

Morone saxatilis

Ted R. Sommer

General Information

Striped bass (Family: Percichthyidae) were introduced into the Estuary in 1879, leading to a successful commercial fishery within 10 years (Herbold et al. 1992). The commercial fishery for striped bass was banned in 1935 following a substantial decline in abundance which appears to have begun at the turn of the century. The species are presently the principal sport fish caught in San Francisco Bay and is estimated to bring approximately $45 million per year into local economies in the Estuary.

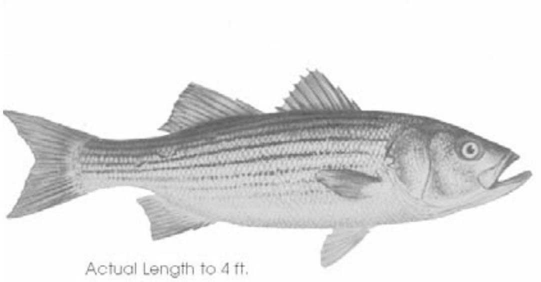
Reproduction

Striped bass are present in the San Francisco Estuary throughout the year (Moyle 1976). They generally congregate in San Pablo and Suisun Bays in autumn and move into the Delta and Sacramento River system on their spawning migration during winter and early spring. The timing and location of spawning depends on temperature, flow and salinity, but typically peaks in May and early June. The annual spawning distribution appears to shift between the Sacramento and San Joaquin rivers and the Delta.

Striped bass spawn in freshwater, with optimum spawning at salinities of less than 1 ppt (Moyle 1976). The species has exceptionally high fecundity—females commonly broadcast from 0.5 to 4.5 million semi-buoyant eggs into the water column. The drifting eggs hatch in the current in about 2 days. Eggs and newly-hatched larvae are carried downstream to the Delta and Suisun Bay. Larvae show peak abundance at the upstream edge of the entrapment zone, located at a salinity of approximately 2 ppt.

Growth and Development

Striped bass grow to about 38 mm by late July or August (Moyle 1976). They typically reach 23 to 35 cm FL by their second year, 38 to 39 cm fork length (FL; the measure to the bottom of the fork of the tail fin) on their third year, and 48 to 50 cm in their fourth year. Growth of older adults is 1 to 3 cm annually. Most females mature at four to six years, but many are mature by the end of their third year. Males typically mature at two to three years old. Although striped bass apparently have the potential to live in excess of 30 years, most adults are three to seven years old.



Food and Feeding

Striped bass are gregarious pelagic predators (Moyle 1976). They begin feeding at a length of 5-6 mm on several invertebrates including cladocerans and copepods. Copepods generally dominate the diet of 7 to 11 mm larvae, but the opposum shrimp, *Neomysis*, become a more important food source in larger individuals. Young-of-the-year feed mostly on opossum shrimp, but amphipods, copepods, and threadfin shad are important alternative prey items. Fish gradually become a more important food source in juvenile bass (13 to 35 cm FL). Subadult and adult bass (age 2+) are primarily piscivorous, although they are highly opportunistic depending on prey availability.

Distribution

In contrast to the coastal Atlantic populations of striped bass, most of the local population spend their lives in the San Francisco Estuary. However, recent tagging studies suggest that striped bass are spending more time in Suisun Bay, the Delta, and surrounding freshwater areas (Sweetnam 1990). The current distribution of the species includes San Francisco Bay, San Pablo Bay, Suisun Bay, the Delta, tributaries of the Sacramento River and the Pacific Ocean (Herbold et al. 1992).

Population Status and Influencing Factors

Adult abundance has declined over the past 30 years, from over 1.5 million in the late 1960s to about 0.5 million in recent years (CDFG 1992). The decline was most dramatic between the beginning and the end of the 1970s, prompting the initiation of a hatchery stocking program to supplement natural production (Harris and Kohlhorst 1996). Stocking was conducted from 1981 through 1991—hatchery fish presently comprise a substantial percentage (e.g., 35% of the 1990 year class) of the adult population.

Year class abundance is assumed to depend on the environmental conditions experienced by the eggs and young fish (CDFG 1987, 1992). However, a steady decline in the survival rate of yearlings stocked into the Estuary suggests that habitat conditions for older fish also play an important role (Harris and Kohlhorst 1996). Abundance of young bass is strongly correlated with

Delta outflow and entrapment zone position, although in recent years this relationship has deteriorated. For example, in 1995 striped bass production was exceptionally poor despite wet conditions that increased the abundance of several other outflow-dependent species. Entrainment at diversions is known to be substantial, and there is statistical evidence that these losses affect abundance. Nonetheless, losses at the projects during the 1980s were at least partially mitigated using hatchery fish, yet the population decline has continued. The reduction in several invertebrate prey species has also been dramatic, particularly since the introduction of the Asian clam *Potamocorbula*. The decline in survival of stocked fish strongly suggests that competition for food has had an effect on the population. Other potentially important factors include toxic substances, exotic species and illegal fishing.

Trophic Levels

Striped bass are secondary and higher order consumers.

Proximal Species

Major Prey Items: Zooplankton (cladocerans and copepods), terrestrial insects, opossum shrimp (*Neomysis mercedis*), splittail, salmon, threadfin shad, American shad.

Good Habitat

Striped bass are able to tolerate a wide range of environmental conditions, illustrated by their ability to move regularly between salt- and fresh-water (Moyle 1976). Optimal temperatures for spawning appear to be from 15.6° to 20.0° C. Low oxygen (4 ppm) and high turbidity are also tolerated. Large rivers or tidal channels with moderate water velocities are required to keep the eggs and larvae suspended in the water column. Young-of-the-year striped bass show highest abundance in the entrapment zone, the region where fresh- and salt-water mix.

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White Croaker

Genyonemus lineatus

Kurt F. Kline

General Information

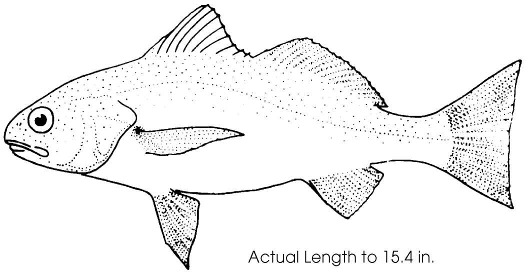
The white croaker (Family: Sciaenidae) is found in small schools (Skogsberg 1939) and ranges from Magdalena Bay, Baja California, to Mayne Bay, Vancouver Island, British Columbia (Baxter, 1980, Hart 1973, Miller and Lea 1972). It is abundant in San Francisco Bay, and supports both commercial and sport fisheries in nearshore coastal waters, and a sport fishery in the Bay.

Reproduction

Approximately 50% of all white croakers are mature after their first year and all are mature by their fourth year (Love et al. 1984). Along the coast, spawning appears to take place in water from eight to 36 meters deep (Love et al. 1984). In San Francisco Bay spawning occurs from September through May (Wang 1986), with most yolk-sac larvae (YSL) collected from November through March (CDFG, unpub. data). Females batch spawn 18-24 times per season, with a batch consisting of 800-37,200 eggs (Love et al. 1984).

Growth and Development

White croaker eggs are pelagic, spherical and transparent. Under laboratory conditions (~20°C), eggs hatched in 52 hours. The newly hatched YSL are poorly devel-


Actual Length to 15.4 in.

CDFG

oped, but by the sixth day the yolk-sac is absorbed, the swim bladder is inflated and feeding begins (Watson 1982).

Throughout their life, white croaker growth is fairly constant (Love et al. 1984). They may live to 12 years (Love et al. 1984) and reach a total length (TL) of 41.1 cm (Miller and Lea 1972).

Distribution

Along the coast, the greatest densities of larvae are found near the bottom between 15 and 20 meters. The smallest juveniles are common from 3 to 6 meters, and move to deeper water as they grow. Most adults are found in waters less than 30 meters, although white croakers have been recorded to 183 meters (Love et al. 1984).

Within San Francisco Bay, most of the pelagic eggs and YSL are found in Central Bay (Wang 1986; CDFG, unpub. data). As the larvae develop to the post yolk-sac stage, they move toward the bottom. Tidal currents probably transported white croaker larvae to South and San Pablo bays. High outflow events during the winter, which increases the gravitational currents, may increase the transport of larvae to San Pablo Bay (Fleming, pers. comm.). By September, most of the young-of-the-year (YOY) migrate to Central Bay and by winter, emigrate from the Bay (Fleming 1999)

Within the Bay, YOY white croaker are found at lower salinities and higher temperatures than the one year and older fish (1+), reflecting the broader distribution of YOY. The movements of older YOY and 1+ white croaker out of the Bay during the late fall and winter may be temperature related.

Population Status and Influencing Factors

The California Department of Fish and Game's Bay Study has generated annual abundance indices for white croaker since 1980. The abundance of YOY white croaker has fluctuated greatly over the past 19 years (**Figure 2.7**). Highest abundance indices of YOY were in 1980, 1986, 1992, 1993, and 1994. White croaker 1+ indices peaked between 1988 and 1991.

From 1981 to 1986, white croaker 1+ catches were dominated by the 1980 year class and from 1987 to 1993, they were dominated by the large 1986 year class. However, the relative size of a year class as YOY is not indicative of the future abundance of 1+ fish in the Bay. For example, the 1986 year class apparently contributed to the subsequent 1+ indices more than either the 1980 or the 1993 year classes. The drought from 1987-1992 may have caused greater use of the Bay by the 1986 year class than either 1980 or 1993 year classes.

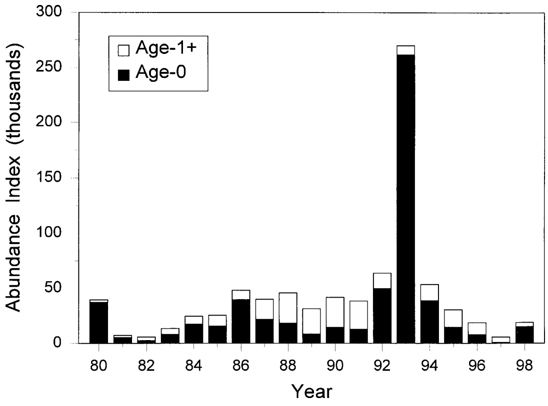


Figure 2.7 Annual Abundance Indices of White Croaker (Hieb 1999)

Examination of the annual indices shows no relationship between the number of mature fish and YOY, while the length frequency data shows that single year classes tend to dominate subsequent years' 1+ catch and the monthly catch per unit effort (CPUE) shows seasonal migration patterns within and out of the Bay. From these data, one could draw the following conclusions: 1) the white croaker "population" within the Bay is an extension of the nearshore coastal population; 2) factors that influence the nearshore population of white croaker are independent of the Bay; and 3) factors that influence the Bay "population" appear to be the salinity, temperature and, perhaps most importantly, the size and distribution of the nearshore population.

Trophic Levels

Secondary consumers.

Proximal Species

Prey: Northern anchovies, *Cancer* spp., shrimp spp., polychaetes.

Good Habitat

White croaker are associated with soft substrates (Love et al. 1984). In the Bay, white croaker are primarily found in areas with the most marine-like (salinity and temperature) conditions.

Acknowledgments

Some of the materials in this report are summarized from the white croaker chapter of IEP Technical Report 63 (Flemming 1999).

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Shiner Perch

Cymatogaster aggregata

Michael F. McGowan

General Information

The shiner perch (Family: Embiotocidae) is a small but abundant species common to the intertidal and subtidal zones of bays, estuaries, and the nearshore regions of California. They are commonly caught by anglers around rocks, and pilings, from shore and docks, and just about any fishing area. They are also used as live bait in the San Francisco fisheries for striped bass and California halibut.

Reproduction

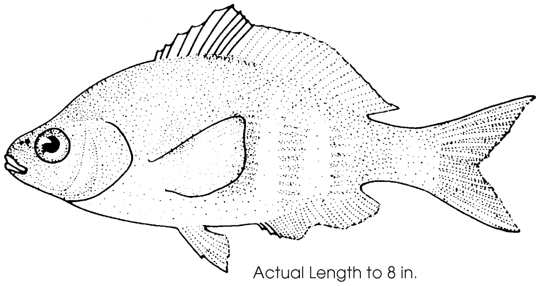
The shiner perch, like other members of the family Embiotocidae, is a live-bearer. Mating is accompanied by elaborate courtship behavior and occurs primarily in the spring and summer in California (Shaw 1971). Females give birth during April and May (Odenweller 1975) in California. Fecundity ranges from 5-36 young per female, depending on size (Emmett et al. 1991).

Growth and Development

At birth, the fully developed young are 34.0-43.7 mm long (Wang 1986). Juveniles become adults at 5 cm in length. Growth is rapid the first year but slows subsequently (Odenweller 1975). Most females mature their first year. They may live 8 years and reach 20 cm long. Males mature soon after birth and rarely grow beyond 13 cm.

Food and Feeding

Embryos receive nutrition and gas exchange through ovarian placenta tissues and fluids. Juveniles and adults feed on plankton and benthos depending on availability. Prey items include copepods, isopods, amphipods, mussels, barnacle appendages, mysids, crab larvae, and other small invertebrates or protruding parts of invertebrates (Emmett et al. 1991).



Actual Length to 8 in.

CDFG

Distribution

The shiner perch occurs near shore and in bays and estuaries from Baja California to Alaska commonly associated with aquatic vegetation. Juveniles prefer intertidal and shallow subtidal habitats in bays and estuaries (Moyle 1976). In winter they may move out of estuaries to nearshore areas and have been found as deep as 70 m (Hart 1973). In Elkhorn Slough, where they are a numerically dominant component of the fish fauna, they were classified as partial residents (Yoklavich et al. 1991).

Population Status and Influencing Factors

The availability and quality of estuarine areas for giving birth and rearing young may limit populations. Key factors are water temperature, not excessively hot (Odenweller 1975), and seagrass beds for shelter and feeding. San Francisco Bay shiner perch catches in trawl surveys declined in 1983, perhaps due to high outflow (and resulting low salinity) that year (Herbold et al. 1992). Because it uses nearshore areas, the shiner perch may have high body burdens of pesticides and other compounds (Earnest and Benville 1971), but population effects of chronic pollution have not been documented.

Trophic Levels

Shiner perch are secondary and higher level consumers. Plant matter found in some stomach analysis studies may be due to feeding on invertebrates that occur on the aquatic vegetation.

Proximal Species

Predators: Sturgeon spp., salmon spp., striped bass, California halibut, cormorant spp., great blue heron, bald eagle.

Prey: Copepods, isopods, amphipods, mussels, barnacle appendages, mysids, crab larvae, and other small invertebrates or protruding parts of invertebrates.

Good Habitat

The shiner perch appears to favor aquatic vegetation if present, but is also found over shallow sand and mud bottoms. They prefer salinities greater than 8-10 ppt and were reported in water temperatures ranging from 4 to 21°C (Emmett et al. 1991). In San Francisco Bay, they are widespread but are most abundant downstream of the Carquinez Strait. Herbold et al. (1992) considered them a euryhaline species. Eelgrass beds may be important feeding areas because shiner perch use them more at night than during the day (Bayer 1979).

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Tule Perch

Hysterocarpus traskii

Robert A. Leidy

General Information

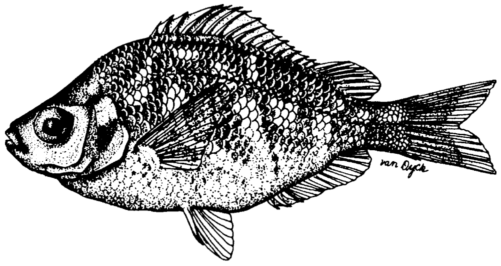
Tule perch are the only viviparous freshwater fish native to California and the only freshwater member of the surfperch family (Embiotocidae)(Baltz and Moyle 1982). They are deep-bodied, spiny-rayed fish found in lakes, rivers, streams, and estuaries in habitats characterized by complex cover, especially well developed beds of aquatic macrophytes (Moyle 1976). There are three recognized subspecies of tule perch, *H. t. pomo* from the Russian River drainage, *H. t. lagunae* from Clear lake, and *H. t. traskii* from the Sacramento-San Joaquin drainage, which includes populations found in the San Francisco Estuary (Hopkirk 1973, Baltz and Moyle 1981 and 1982). Because of their small size, tule perch have no commercial and limited sport value.

Reproduction

Tule perch breed during July through September, but fertilization of the eggs is delayed within the female until January (Bundy 1970, Bryant 1977). Embryos develop within the females ovarian compartments and are born as juveniles in May or June, at a length of between 30-40 mm standard length (SL) (Bryant 1977). The number of fish produced per female is positively correlated with the size of the female fish and ranges between 22 and 93 (Bundy 1970, Bryant 1977).

Growth and Development

Juveniles begin schooling immediately following birth within aquatic vegetation, submerged logs, or boulders (Wang 1986). It is not known whether juveniles move into tributaries following birth, but it is interesting to note that several streams feeding into Suisun Marsh and San Pablo Bay contain large numbers of juvenile tule perch (Leidy, pers. observ.). Juveniles grow rapidly and individuals in the Sacramento-San Joaquin Delta may reach 80 to 100 mm SL following the first year of growth (Moyle 1976). Maximum size for tule perch is approximately 160 mm SL, although a single individual measuring 175 mm SL was collected in Napa Slough, Napa County (Leidy, unpub. data). Tule perch rarely live longer than five years (Moyle 1976).



Moyle 1976

Actual Length to 6 in.

Food and Feeding

Within the Sacramento-San Joaquin Delta and upper Estuary, tule perch feed primarily on mysid shrimp, small amphipods, midge larvae (Chironomidae), and clams (Cook 1964, Turner 1966). Hopkirk (1962) recorded that tule perch collected in brackish water habitats near the mouth of the Napa River fed mostly on small-sized brachyuran crabs, while juvenile fish feed predominantly on midge larvae and pupae. Tule perch are also known to feed on zooplankton, aquatic insects, and a variety of benthic and plant-dwelling invertebrates in lakes and rivers (Moyle 1976, Wang 1986).

Distribution

Tule perch are native to low-elevation valley waters of the Central Valley, the Sacramento-San Joaquin Delta, including Suisun Marsh and several streams tributary to the San Francisco Estuary, Clear Lake, and the Russian, Salinas, and Pajaro Rivers (Moyle 1976). Within the San Francisco Estuary tule perch have been recorded from Suisun Marsh (Herbold et al. 1992), including Montezuma Slough, Suisun Bay (Ganssle 1966), Carquinez Strait (Messersmith 1966), the Napa River and its marshes (Moyle 1976; Leidy 1984; Leidy, unpub. data), and Sonoma, Alameda, and Coyote creeks (Leidy 1984). Tule perch may be considered locally abundant in lower estuarine and riverine intertidal marsh and pelagic habitats of Suisun Marsh and several of its tributary streams, the Napa and Sonoma Creek marshes, and portions of San Pablo Bay (Leidy, unpub. data). Tule perch no longer occur in the Pajaro and Salinas rivers, and are rare in Alameda and Coyote creeks (Leidy, unpub. data).

Population Status and Influencing Factors

While the historical range of tule perch within the San Francisco Estuary has been reduced, tule perch are still locally abundant in Suisun Marsh and the Napa River and Sonoma Creek and its tidal marshes. Important factors negatively influencing population numbers likely include excess siltation and turbidity, reduced freshwater flows, pollution, removal of riparian vegetation and aquatic macrophytes through stream channelization and other flood control measures, and the resultant loss of nesting, feeding, and cover habitat, and possibly the introduction of exotic centrarchids (Moyle et al.1995). Moyle et al. (1995) identified introduced fish predators, such as smallmouth bass (*Micropterus dolomieui*), pond and dam construction, and reduced flows and poor water quality as threats to the Russian River subspecies of the tule perch. These are likely threats to the other two subspecies of tule perch as well. Interestingly, otter trawl data collected in Suisun Marsh shows a significant decline in tule perch numbers during 1983-84, a year of extremely high outflow (Herbold et al. 1992).

Trophic Levels

Juveniles and adults are primary and higher order consumers.

Proximal Species

Juvenile predators: Other large freshwater and estuarine piscivorous fish, egrets, herons and other wading birds.
Prey: Aquatic and terrestrial insects, zooplankton, mysid shrimp, amphipods, clams, brachyuran crabs, midge larvae and pupae.

Good Habitat

Tule perch may be found in a variety of habitats from the slow-moving, turbid channels of the Delta, marshes between the mouths of Sonoma Creek and the Napa River, to relatively clear, fast-flowing rivers and streams (Moyle 1976; Leidy, unpub. data). In tidal riverine marshes, tule perch prefer slow-moving backwater and slough habitats with structurally-complex beds of floating or emergent aquatic macrophytes, overhanging banks and/or submerged woody debris. These areas serve as important feeding and breeding habitats, as well as protective rearing areas (Moyle 1976). Structurally-complex cover appears to be essential for near-term females and juveniles as refugia from predators (Moyle et al. 1995).

Although Moyle (1976) states that tule perch seldom venture into brackish water, they are present in the pelagic zone of tidal riverine and intertidal estuarine environments, such as the Napa River marshes and Suisun Marsh (Leidy, unpub. data). This suggests that some populations of tule perch may be able to tolerate brackish water conditions, or at least utilize these areas when freshwater outflows dilute surface water. In Suisun Marsh tule perch are most frequently collected in the small, heavily vegetated, dead-end sloughs where introduced centrarchids are uncommon (Moyle et al. 1985).

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Arrow Goby

Clevelandia ios

Kathryn A. Hieb

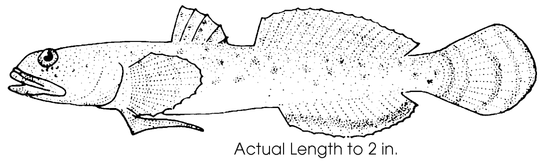
General Information

The arrow goby (Family: Gobiidae) is probably the most abundant native goby in San Francisco Bay. It ranges from the Gulf of California to Vancouver Island, British Columbia (Miller and Lea 1972) and is common to intertidal mudflats and shallow subtidal areas of bays, estuaries, and coastal lagoons. It is often commensal with burrowing invertebrates. The arrow goby grows to a maximum size of 45 to 50 mm total length (TL). This small fish is an important component of the intertidal food web, as it is a common prey item for a variety of birds and fishes. It has no sport or commercial value.

Reproduction

In Elkhorn Slough, ripe females were collected from December through August, but were most common from March through June (Prasad 1948). The reproductive period occurs approximately one to two months earlier in southern California—in Mission Bay, ripe females were collected from September through June, with peak abundance from November through April (Brothers 1975), while in Anaheim Bay, ripe females were collected from December through September, with peak abundance from February through June (Macdonald 1972). Ovary development is asynchronous, as ovaries are found in various stages of maturation during the spawning season (Macdonald 1972, Brothers 1975). This indicates that each female may spawn several times during the spawning season. Fecundity ranges from 800 to 1,200 eggs per female, with clutch size ranging from 150 to 350 eggs (Brothers 1975) or from 750 to 1,000 eggs (Prasad 1948).

Some disagreement exists in the literature on the deposition of the eggs and parental care. The eggs are either deposited on surfaces with no additional parental investment (Prasad 1948, Macdonald 1972) or deposited on the wall of burrows constructed by the male and guarded by the male until hatching (Brothers 1975). In Mission Bay, all males collected in January and February were brooding clutches of eggs in burrows. Typical of most gobies, the fertilized eggs are club-shaped, with an attachment thread at one pole. Hatching occurs in 10 to 12 days and the newly hatched larvae are pelagic (Prasad 1948, Brothers 1975).



Actual Length to 2 in.

CDFG

Growth and Development

Newly hatched larvae range from 2.75-3.25 mm TL (Prasad 1948). Juvenile arrow gobies settle from the plankton at approximately 8 mm standard length (SL) and are found in burrows when they are 10-14 mm SL (Macdonald 1972). The arrow goby matures at one year and a length of 30 to 40 mm SL in Anaheim and Mission bays (Macdonald 1972, Brothers 1975); in Elkhorn Slough females begin to mature at 29 mm SL and all are mature at 34 mm SL (Prasad 1948). In southern California, most arrow gobies die after spawning, with a few living to two years (Macdonald 1972, Brothers 1975). In Elkhorn Slough, arrow gobies commonly live two to three years (Prasad 1948). Fish from Elkhorn Slough apparently spawn later, grow slower, mature later, and reach a larger size than fish from southern California populations (Brothers 1975).

Food and Feeding

The arrow goby preys on a variety of small invertebrates. In Mission Bay, the major prey items (percent occurrence) of juveniles and adults are harpacticoid copepods (88%), ostracods (58%), tanacians (32%), gammarid amphipods (19%), mollusc siphon tips (11%), caprellids (8%), nematodes (7%), and polychaetes (7%) (Brothers 1975). In Anaheim Bay, the most important prey items are harpacticoid copepods, nematodes, oligochaetes, ostracods, and cylcopoid copepods (Macdonald 1972). Larvae prey primarily upon the calanoid copepod *Acartia tonsa* (Macdonald 1975).

The arrow goby is preyed upon by a variety of demersal fishes, including Pacific staghorn sculpin (MacGinitie and MacGinitie 1949, Brothers 1975, Tasto 1975), California halibut (Haaker 1975, Drawbridge 1990), and diamond turbot (Lane 1975). MacGinitie and MacGinitie (1949) presumed probing shorebirds, including willets, godwits, and curlews would capture arrow gobies while exploring burrows at low tides. Arrow gobies have been found in the stomachs of greater yellowlegs and dowitchers (Reeder 1951).

Distribution

The arrow goby is common on mudflats inhabited by its invertebrate commensal hosts (Brothers 1975), with densities up to $20/m^2$ in Anaheim Bay (Macdonald 1972). It apparently utilizes invertebrate burrows as a refuge from predators and as a temporary shelter during low tides. The arrow goby primarily inhabits burrows of the ghost shrimp (*Callianassa californiensis*), the fat innkeeper worm (*Urechis caupo*), the mud shrimp (*Upogebia spp.*), and various bivalves (Prasad 1948, Brothers 1975). Males also construct burrows for reproduction (Brothers 1975). At low tides the arrow goby is also common in remnant pools of water on the mudflats (Prasad 1948).

In San Francisco Bay, larval arrow gobies are most abundant in South and San Pablo bays, with few collected upstream of Carquinez Strait in years with low freshwater outflow (Wang 1986, CDFG 1987). Juveniles and adults are common in shallow subtidal and intertidal areas of South, Central, and San Pablo bays and have occasionally been collected in Suisun Bay (CDFG 1987). The arrow goby is also common in some tidal marsh habitats from South Bay to lower San Pablo Bay. It was the second most common species collected in otter trawl samples from Hayward Regional Shoreline Marsh channel sites (Woods 1981). The arrow goby was common in weir samples collected in Plummer Creek (South Bay near Newark), although gobies were not speciated in this study, so their relative abundance is unknown (Wild 1969). In a survey of Castro Creek, Corte Madera Creek, and Gallinas Creek marshes, the arrow goby was relatively common in otter trawl samples from creek channels and mudflats adjacent to the marshes, but rare in gill nets and not collected by minnow traps set in the marsh channels (CH$_2$M Hill 1982). A few arrow gobies were collected in Petaluma River marshes, Napa-Sonoma Marsh, but none in Suisun Marsh (CDFG, unpub. data; ANATEC Laboratories 1981; CH$_2$M Hill 1996; Matern et al. 1996).

Arrow goby larvae have been collected year-round in San Francisco Bay, with peak larval abundance from April through July (CDFG 1987). Peak abundance in beach seine samples from the Bay is from March though August; these catches include recently settled juveniles and adults (CDFG 1987). In southern California, most juveniles settle in the spring (February through May in Mission Bay, February through June in Anaheim Bay), although juveniles have been collected all but one or two months in the fall (Macdonald 1972, Brothers 1975).

Juvenile and adult arrow gobies are euryhaline and have been reported to tolerate salinities ranging from freshwater to greater than seawater (Carter 1965, as cited in Emmett et al. 1991). In San Francisco Bay, arrow goby juveniles and adults have been collected from a wide range of salinities (0.9-33.9‰), with 90% collected from 11.7 to 32.4‰ (5th and 95th percentiles, respectively, CDFG 1987 and unpub. data). The arrow goby is also reported to be eurythermal; in aquaria, gobies withstood temperatures from 4-26°C, but were "distressed" at temperatures above 22°C (Prasad 1948). In San Francisco Bay, arrow gobies were collected from 7.5 to 30.5°C, with 90% collected between 16.9 and 24.3°C (5th and 95th percentiles, respectively, CDFG 1987 and unpub. data).

Population Status and Influencing Factors

Because the arrow goby is most common in intertidal and shallow subtidal habitats, it is more effectively sampled by seines than trawls. In a beach seine survey of San Francisco Bay conducted by California Department of Fish and Game in the 1980s, the arrow goby comprised approximately 4% of the catch, ranking eigth of all fishes collected. In contrast, it comprised only 0.04% of the fishes collected by the otter trawl (Orsi 1999). As the beach seine survey has been discontinued, there is no long-term monitoring program in the Bay that effectively samples the arrow goby, and its current status is difficult to assess. From 1981 to 1986, the arrow goby beach seine annual "abundance index" varied almost 10-fold, with the highest indices in 1981 and 1986 (**Figure 2.8**).

Brothers (1975) hypothesized that arrow goby abundance and distribution could be controlled by the abundance and distribution of the commensal invertebrates, especially the ghost shrimp. Because the arrow goby is an annual species, devoting a large proportion of its resources to reproduction ("r-strategist"), it would be expected to undergo large population fluctuations.

Trophic Level

Arrow goby larvae, juveniles, and adults are secondary consumers, preying primarily on small benthic and epibenthic invertebrates.

Proximal Species

Predators: Pacific staghorn sculpin, California halibut, diamond turbot.

Prey: Harpacticoid copepods, ostracods, tanacians, gammarid amphipods, mollusk siphon tips, nematodes, oligochaetes.

Commensal Hosts: Burrowing invertebrates. Bat rays and leopard sharks impact the abundance and distribution of burrowing invertebrates.

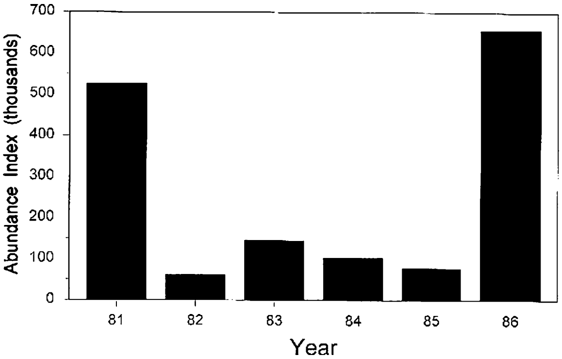


Figure 2.8 Annual Abundance Indices of Arrow Goby from San Francisco Bay, Beach Seine (CDFG, unpublished data)

Good Habitat

Good habitat for the arrow goby is shallow subtidal and intertidal mudflats inhabited by the commensal invertebrate hosts. All habitats in tidal marshes may not suitable, as the arrow goby has been collected from larger channels and adjacent mudflats, but not from smaller order channels.

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Bay Goby

Lepidogobius lepidus

Kathryn A. Hieb

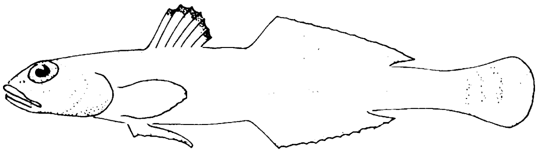
General Information

The bay goby (Family: Gobiidae) ranges from Baja California to Vancouver Island, British Columbia (Miller and Lea 1976). It is common to bays and estuaries and often commensal with burrowing invertebrates on intertidal mudflats (Grossman 1979a). Because it often occupies burrows, the bay goby is not effectively sampled by trawls and seines and its relative abundance is undoubtedly greater than indicated by most surveys. It is the most abundant native goby in larval surveys of San Francisco, Humboldt, and Yaquina bays. The bay goby grows to approximately 100 mm total length (TL) and has no commercial or sport value.

Reproduction

Females with yolk filled eggs were collected from September through March, with the peak of reproductive activity from January through March in Morro Bay (Grossman 1979b). Gonadal development is asynchronous, typical of species that spawn several times a season and have a protracted spawning period. As for many other species of gobies from temperate waters, it is assumed the eggs are laid in burrows constructed by either the males or commensal invertebrate hosts and are guarded by the male until hatching (Wang 1986). Eggs are club shaped with an adhesive thread at one pole for attachment to the burrow wall or substrate.

In San Francisco Bay, larvae were collected throughout the year, with peak abundance from June to October (CDFG 1987). The period of peak abundance is similar in other Pacific Coast estuaries—peak larval abundance is from April to September in Yaquina Bay, Oregon (Pearcy and Myers 1974) and larvae were collected from April to September in Humboldt Bay (Eldridge and Bryan 1972). In San Francisco Bay, most larvae were collected in Central Bay and northern South Bay, with relatively few collected upstream of San Pablo Bay (CDFG 1987).



Actual Length to 4 in.

CDFG

Growth and Development

Bay goby larvae are approximately 2.5-3.0 mm TL at hatching (Wang 1986). The larvae are planktonic for three to four months (Grossman 1979b) and settle to the bottom as juveniles at approximately 25 mm TL (Wang 1986). Although the bay goby is reported to grow to about 87 mm TL (Miller and Lea 1976), specimens as large as 108 mm TL have been collected in San Francisco Bay (CDFG, unpub. data). Some bay gobies reach sexual maturity by the end of their first year and by the end of their second year all are mature (Grossman 1979b). Bay gobies reportedly live up to 7+ years (Grossman 1979b), although based upon length frequency data from San Francisco Bay (CDFG 1987, Fleming 1999), their life span may be as short as one to two years.

Food and Feeding

The bay goby is an opportunistic predator and major prey items include polychaetes, harpacticoid copepods, gammarid amphipods, and bivalves (Grossman et al. 1980). Although larger fish ($\geq$50 mm SL) and smaller fish (<50 mm SL) consume similar prey items, larger fish include more mollusks, polychaetes, and other larger prey items in their diet.

Predators of the bay goby include the California halibut (Drawbridge 1990) and the Pacific staghorn sculpin (Boothe 1967). It is assumed that other demersal piscivorous fish prey upon bay gobies.

Distribution

In San Francisco Bay, the bay goby is common from South to San Pablo bays, and is occasionally collected in Carquinez Strait and lower Suisun Bay. Densities of young-of-the-year (YOY) bay gobies are usually highest in South or San Pablo bays while densities of older fish are usually highest in Central Bay (CDFG 1987, Fleming 1999). From 1980 to 1995, the bay goby was the most common goby and the second most common fish collected by an otter trawl survey of San Francisco Bay, comprising 14.3% of all fishes collected (Orsi 1999). Although mean densities of YOY fish were higher at shoal stations than channel stations all months, older fish appear to move from the shoals to the channels in the late summer and fall (CDFG 1987 and unpub. data).

Surprisingly, the bay goby was not common in a beach seine survey conducted by CDFG in San Francisco Bay from 1980-1987; it was the fourth most common goby and comprised only 0.06% of all fishes collected by this net (Orsi 1999). These data indicate that the bay goby may not be common in the very shallow subtidal and intertidal areas of San Francisco Bay, although Grossman (1979a) concluded it to be one of the numerically dominant fish species of Morro Bay lower intertidal mudflats. The bay goby inhabits burrows of the blue mud shrimp (*Upogebia pugettensis*) and the innkeeper worm (*Urechis caupo*) and siphon holes of the geoduck clam (*Panope generosa*) in Morro Bay (Grossman 1979a). As for several other species of gobies common to San Francisco Bay, including arrow goby and longjaw mudsucker, the bay goby probably utilizes burrows as a refuge from predators and to avoid desiccation at low tides.

Few bay gobies have been collected in San Francisco Bay tidal marshes. One bay goby was reported from Gallinas Marsh and one from Corte Madera Marsh (CH_2M Hill 1982). Both fish were collected by gill nets, which were used to sample the larger channels. In contrast, the bay goby was the most common species collected in otter trawl samples from Corte Madera Creek channel, adjacent to Corte Madera Marsh. No bay gobies have been collected by other San Francisco Bay tidal marsh studies (Wild 1969; Woods 1981; ANATEC Laboratories1981; CH_2 MHill 1996; CDFG, unpub. data) or by a study of fishes of Elkhorn Slough tidal marshes (Barry 1983).

Bay goby YOY are most abundant in otter trawl samples from February through June, which is a one or two months after peak abundance period for smaller juveniles from the ichthyoplankton net (CDFG 1987 and unpub. data). In several years, multiple cohorts of YOY fish have been collected; this was especially noticeable in four of the six years of the 1987-1992 drought (CDFG, unpub. data). Peak abundance of older fish is usually from May through September, which corresponds with the peak period of larval abundance in San Francisco Bay.

The bay goby has been collected primarily from polyhaline salinities in San Francisco Bay, with YOY fish collected at lower salinities than older fish (**Table 2.6**). YOY were also collected at slightly lower temperatures than older fish (**Table 2.6**). These differences in salinity and temperature by age class are reflected by the distribution of YOY somewhat further upstream than older fish and by the peak abundance of YOY in the winter and spring and older fish in summer and fall.

Table 2.6 Bay Goby Salinity and Temperature Statistics: 1980-92 (CDFG unpublished data)

Age Class	Mean	5th percentile	Median	95th percentile
Salinity (ppt):				
YOY	27.3	14.9	29.2	31.7
1+ and older	28.1	17.1	29.7	32.4
Temperature (°C):				
YOY	15.4	11.3	15.2	18.8
1+ and older	16.0	12.4	16.3	18.9

Population Status and Influencing Factors

Although trawls are usually considered ineffective for gobies, the bay goby is a very common fish in San Francisco Bay otter trawl surveys. As such, the abundance indices derived from trawl data may be good indicators of population trends. California Department of Fish and Game otter trawl data from 1980-1998 is the longest data set available for the Bay. The indices from 1988 to 1997 were generally higher than the pre-1988 indices (**Figure 2.9**). The relatively stable salinities year-round during the 1987-92 drought may have resulted in increased nursery habitat for this species (Hieb and Baxter 1993). The multiple cohorts of YOY collected these years, which indicate successful recruitment over a period of several months, in part support this hypothesis. Additionally, high winter outflow events may carry larvae or pelagic juveniles from the Bay.

Abundance of predators, as California halibut and Pacific staghorn sculpin, could influence the bay goby population. Additionally, factors controlling the abundance of the commensal burrowing invertebrate hosts may effect the bay goby population. This would include the abundance and distribution of intertidal and subtidal mudflat invertebrate predators, such as the bat ray and leopard shark.

Trophic Level

Secondary consumer.

Proximal Species

Predators: California halibut, Pacific staghorn sculpin.
Prey: Polychaetes, gammarid amphipods, harpacticoid copepods, bivalves.

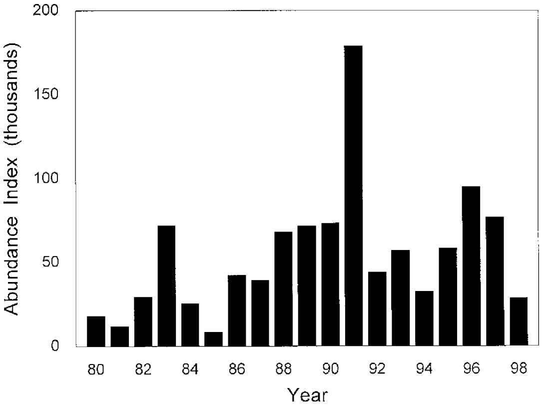


Figure 2.9 Annual Abundance Indices of All Sizes of Bay Goby, Otter Trawl (CDFG unpublished data)

Commensal Hosts: Blue mud shrimp, inn-keeper worm, geoduck clam. Bat ray and leopard shark impact the abundance of commensal hosts.

Good Habitat

Good habitat for the bay goby is shallow subtidal areas with mud or a mud/sand mixture and possibly intertidal mudflats. The presence of burrowing invertebrates, which may serve as commensal hosts, would be beneficial. There is no evidence that this species utilizes tidal marshes in San Francisco Bay or elsewhere in its range.

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Longjaw Mudsucker

Gillichthys mirabilis

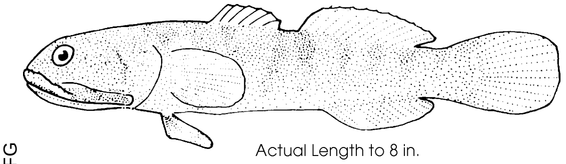
Kathryn A. Hieb

General Information

The longjaw mudsucker (Family: Gobiidae) is the largest goby native to San Francisco Bay, reaching a size of 200 mm total length (TL). It ranges from Baja California to Tomales Bay (Miller and Lea 1972) and was successfully introduced to the Salton Sea in 1930 (Walker et al. 1961). The longjaw mudsucker is a common resident of mudflats and sloughs in estuaries and coastal streams. It is also common in salt ponds, as it can tolerate a wide range of salinities. As the tide ebbs, the longjaw mudsucker retreats to burrows or buries in the mud rather than migrate to deeper water. Due to their ability to live out of water and in freshwater for several days, mudsuckers or "mud puppies" are a sought after bait-fish; however, in recent years, the San Francisco Bay area bait fishery has targeted the yellowfin goby, a large introduced species that is very common in many shallow water habitats.

Reproduction

Male longjaw mudsuckers construct burrows for breeding, which they aggressively guard until the eggs hatch. A single female lays 4,000 to 9,000 eggs, depending on size (Weisel 1947). In southern California, spawning occurs from January through July, with peak activity apparently from February through April (Weisel 1947). In South Bay salt ponds, the spawning period is also protracted, occurring from November through June, with peak activity in February and March (Lonzarich 1989). Gonadal regression occurs from July to September, when temperatures in the salt ponds reach their maximum (de Vlaming 1972). Females were reported to spawn more than once per season in South Bay salt ponds (de Vlaming 1972) and two and possibly three times per season in the Salton Sea (Walker et al. 1961), with an interval of 40 to 50 days between spawnings (Barlow 1963). Ovarian development and spawning are asynchronous, which is typical of species that spawn more than once per season and have a protracted spawning season (de Vlaming 1972).



Actual Length to 8 in.

CDFG

The eggs are club shaped, 2.8-3.4 mm long, with an adhesive thread at one pole that attaches to the burrow wall. Hatching occurs in 10 to 12 days at 18°C (Weisel 1947). Larvae have been collected year-round in the Bay, with peak abundance in May and June (CDFG, unpub. data); in South Bay salt ponds, larvae were collected at salinities up to 70‰ (Lonzarich 1989).

Growth and Development

In South Bay salt ponds, longjaw mudsuckers grow to 80-100 mm standard length (SL) by the end of year one and 120-140 mm SL by the end of year two (Lonzarich 1989). Few live more than one year and none more than two years; both sexes mature at age one (Barlow 1963, Lonzarich 1989). In the Salton Sea, longjaw mudsuckers hatched in the early spring reach 60-80 mm SL by fall and 80-120 mm SL by the next spring (Walker et al. 1961).

Food and Feeding

In Elkhorn Slough, California, the longjaw mudsucker preys primarily on gammarid amphipods, especially *Orchestia traskiana*, *Eogammarus confervicolus*, *Corophium* spp., and polychaetes (Barry 1983). Dipterans, harpacticoid copepods, and grapsid crabs (primarily *Hemigrapsus oregonensis*) are also important food items. In South San Francisco Bay salt ponds, longjaw mudsucker diet varies by salinity—in the lower salinity (20-40‰) ponds, they consume primarily polychaetes and amphipods while in the higher salinity (to 84‰) ponds they consume primarily brine shrimp and waterboatmen (Lonzarich 1989). Copepods are an important prey item in the winter, when brine shrimp are unavailable.

Distribution

In San Francisco Bay, the longjaw mudsucker has been collected in South, Central, San Pablo, and Suisun bays, although it is not common upstream of Carquinez Strait. It is the least common goby collected in trawl surveys of open water habitats and larger channels, but usually the most common goby collected in smaller marsh channels. For example, it was not collected in trawls near Castro Creek, Corte Madera Creek, and Gallinas Creek marshes, but was the most abundant goby and third most abundant species collected in minnow traps set in the marsh channels (CH$_2$M Hill 1982). Similarly, in a study of a restored marsh near Hayward, it was not common in trawls of the larger channels, but the only goby and most common species collected in minnow traps set on the mudflats (Woods 1981). It was also the second most common species collected in first and second order channels of tidal marshes in lower Petaluma River (CDFG, unpub. data). This distribution has also been reported from Elkhorn Slough, where the longjaw mudsucker was not an important component of the otter trawl samples from deeper (>1.5 m) channels, but was the third most abundant species and most common goby in beach seine and channel net samples from shallower (<1.5 m) channels (Barry 1983).

The longjaw mudsucker is also common in salt ponds in San Francisco Bay. It was the most common goby and the second most common fish collected in South Bay salt ponds (Carpelan 1957, Lonzarich 1989). Lonzarich (1989) reported highest catches in the summer and fall.

Although longjaw mudsucker can tolerate a wide range of salinities, they are usually absent from fresh or slightly brackish water (Barlow 1963). They have been collected from salinities as high as 82.5‰ in the upper Gulf of California (Barlow 1963), and as high as 84‰ in South Bay salt ponds (Lonzarich 1989).

Although longjaw mudsuckers have been collected at temperatures as high as 33°C (Carpelan 1957), in laboratory thermal selection studies, they preferred temperatures from 9-23°C and strongly avoided temperatures greater than 23°C (de Vlaming 1971). In another laboratory study, Courtois (1973) concluded that the longjaw mudsucker was best adapted to temperatures between 20 and 30°C.

In intertidal areas, the longjaw mudsucker often remains in the mud or burrows at low tide and is subject to fluctuating oxygen concentrations. The jaw membranes are richly vascularized and serve as an accessory respiratory apparatus (Weisel 1947). Additionally, the longjaw mudsucker will respire aerially at low (<2.0 mg/L) oxygen concentrations; they gulp air at the water surface and hold the bubbles in their large buccopharyngeal cavity (Todd and Ebeling 1966).

Population Status and Influencing Factors

There is no survey which routinely samples the longjaw mudsucker or its preferred habitat in San Francisco Bay, so the current status of the population cannot be assessed. With the introduction and establishment of the yellowfin goby in the 1960s, the longjaw mudsucker is no longer as sought after for bait. However, the introduction of the yellowfin goby may have had a negative impact on the longjaw mudsucker, as there is substantial overlap in the habitats of the two species.

Trophic Levels

The longjaw mudsucker is a secondary consumer.

Proximal Species

Predators: Bait fishers and possibly great blue herons, egrets, and larger shorebirds.

Prey: Gammarid amphipods, polychaetes, dipterans, copepods, *Hemigrapsus oregonensis*, waterboatmen, brine shrimp.

Good Habitat

The intertidal area of tidal marsh channels is the typical habitat of the longjaw mudsucker. Because this species can tolerate a wide range of environmental conditions, "good habitat" is probably defined by the complexity of these sloughs. More complex channels, with undercut banks and pools of water at low tide, would offer more protection from predators than sloughs with little incision and ponded water. These more complex channels are typical of mature marshes vs. recently "restored" marshes.

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California Halibut

Paralichthys californicus

Michael K. Saiki

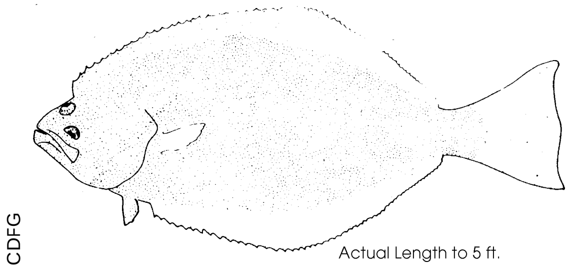
General Information

The California halibut (Family: Bothidae) is a large marine flatfish that is sought after in the market place because of its large size and excellent taste (Frey 1971). Commercial fishing for California halibut was historically centered in the Baja California-Los Angeles area, but has recently shifted northward to the Santa Barbara region (Barsky 1990). It is harvested by gill net, trammel net, and trawl nets (Schultze 1986). California commercial fishermen landed an average of 534 tons per year from 1983 to 1987, and received $0.64-$1.59/kg in 1987 (CDFG 1988). California halibut is also highly prized by recreational anglers and is caught primarily from piers and boats using hook, line, and live bait. Over 916,000 California halibut were caught by anglers in 1985 (USDC 1986).

Reproduction

Emmett et al. (1991) described the California halibut as being gonochoristic (its gender is determined by developmental rather than hereditary mechanisms) and iteroparous (it has the capacity to survive and spawn beyond one or multiple spawning seasons). It is a broadcast spawner whose eggs are fertilized externally (Emmett et al. 1991).

The eggs of California halibut are pelagic (Allen 1988). In a laboratory tank with water depth of 2-3 m, California halibut spawned while swimming near the water surface (Allen 1990). Adults typically move into shallow (6-20 m deep) coastal waters in early spring and usually spawn over sandy substrates (Ginsburg 1952, Frey 1971, Feder et al. 1974, Haaker 1975). Spawning occurs from February through August, peaking in May with a great number of mature fish (Frey 1971, Feder et al. 1974, Wang 1986). Spawning most often occurs when water temperatures are 15.0-16.5°C, and day lengths are greater than or equal to 10.5 hours (Caddell et al. 1990). However, abundant eggs and larvae have also been reported from nearshore coastal waters during winter-spring when surface temperatures are 13-15°C, and even during summer when surface waters occasionally reach 22°C (Lavenberg et al. 1986, Petersen et al. 1986).



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Actual Length to 5 ft.

During the spawning season, small (55.9-61.0 cm long) California halibut produce approximately 300,000 eggs every 7 days, whereas large (>114.3 cm long) halibut produce about 1 million eggs per day (Emmett et al. 1991).

Growth and Development

California halibut eggs are spherical in shape and 0.74-0.84 mm in diameter (Ahlstrom et al. 1984). Eggs hatch approximately two days after fertilization at 16°C (Emmett et al. 1991). Newly hatched larvae of California halibut measure about 2.0 mm total length (TL) (Ahlstrom and Moser 1975, Ahlstrom et al. 1984). The larval yolk sac is depleted about six days after hatching (Gadomski and Petersen 1988).

Metamorphosis occurs at a length of 7.5-9.4 mm (Ahlstrom et al. 1984) when the pelagic, bilaterally symmetrical larvae become benthic, asymmetrical juveniles. Along with other physical changes, the most visible part of this process is a change in pigmentation patterns and the migration of one eye across the top of the head to its final resting place close to the other eye (Moyle and Cech 1988).

Temperature has a major effect on survival of eggs and larvae of the California halibut. Successful hatching occurred at 12°, 16°, and 20°C, but death occurred prior to embryo formation at 8° and 24°C (Gadomski and Caddell 1991). At 17 days posthatch, all larvae died at 12°C, whereas survival varied from 23% to 46% at 16°, 20°, and 24°C. The survival of older larval stages of California halibut progressively increased as incubation temperatures rose from 16°C to 28°C. Temperature also affected the settlement rate of juveniles that had just completed metamorphosis.

Although juveniles are reported to vary in length from 8 mm to 430 mm (Emmett et al. 1991), males can mature at 200-300 mm standard length (SL) when 2-3 years old whereas females can mature at 380-430 mm SL when 4-5 years old (Fitch 1965, Fitch and Lavenberg

1971, Haaker 1975). California halibut may reach a maximum length of 1,520 mm and a maximum weight of 33 kg (Eschmeyer et al. 1983), with certain individuals living for as long as 30 years (Frey 1971).

Food and Feeding

California halibut feed initially on small invertebrates, but later switch almost exclusively to feeding on fish (Haaker 1975). Although the diet of larvae has not been examined, they probably feed on tiny planktonic organisms (Allen 1990). Small juveniles in three southern California embayments fed mostly on harpacticoid copepods and gammaridean amphipods, with some polychaetes, mysids, small fish, and crab megalopae also being taken (Haaker 1975, Allen 1988). In Anaheim Bay, California, large juveniles and small adults ate bay shrimp, topsmelt, California killifish, and gobies, whereas subadults and adults more than 23.0 cm SL consumed mostly northern anchovy, croaker, and other larger fishes (Haaker 1975). Other forage taxa in the diets included ostracods and acteonid snails. In Tomales Bay, adult California halibut (65.4-83.3 cm SL) fed on Pacific saury, Pacific herring, sanddabs, white sea perch, and California market squid (Bane and Bane 1971). The California halibut is an ambush predator (Haaker 1975). During foraging it lies partially buried on the sandy bottom and waits until its prey is close enough to seize.

Distribution

The geographic distribution of California halibut extends from the Quillayute River, Washington, southward to Magdalena Bay, Baja California (Ginsburg 1952, Miller and Lea 1972, Eschmeyer et al. 1983). However, it is common only in bays and estuaries south of Tomales Bay, California, and reaches peak abundance in estuaries south of Point Conception (Emmett et al. 1991). Recently, large numbers of mostly female California halibut were caught by recreational anglers in Humboldt Bay, with some caught as far north as Crescent City and southern Oregon (R. Baxter, pers. comm.). A survey of carcasses suggested that the females had not developed mature eggs.

Larvae of California halibut occur primarily in the upper 30 m of coastal waters, where they apparently settle or migrate from the 0-10 m stratum to the 10-20 m stratum at night (Moser and Watson 1990). Conversely, larvae over shallow water (13 m bottom depth) tend to move downward during the day (Barnett et al. 1984). Juveniles settle in shallow water on the open coast, but are more abundant in bays (Allen 1988, Moser and Watson 1990). Juveniles remain in bays for about two years until they emigrate to the coast where they settle at water depths less than 100 m, with greatest abundance at depths less than 30 m (Miller and Lea 1972, Allen 1982). Larger juveniles (greater than 20 mm in length) may move from open coastal areas to resettle in bays (Kramer 1990).

Adults move inshore during spring and summer, and offshore during winter (Ginsburg 1952, Haaker 1975). Although the inshore movements are associated with spawning, they may also be influenced by seasonal patterns in forage fish abundance. For example, during spring and summer, California grunion *(Leuresthes tenuis*) are abundant near the surf zone (Feder et al. 1974), whereas northern anchovy *(Engraulis mordax)* are abundant in bays and estuaries (Tupen 1990).

California halibut are occasionally found in Central and South San Francisco Bay (Alpin 1967, Pearson 1989) and San Pablo Bay (Ganssle 1966). Recently, eggs of a description similar to those of California halibut were collected in San Francisco Bay; however, their identity was not verified (Wang 1986). Both larval and juvenile California halibut have been captured in San Francisco and San Pablo bays (Wang 1986).

Population Status and Influencing Factors

Catch records indicate that the abundance of California halibut within its historic range was high in the late 1960s, declined in the 1970s, and increased in the 1980s. The intense El Niño in 1982-83 coincided with higher abundance and landings of halibut (Jow 1990). Overall, however, California halibut populations seem to be undergoing a long-term decline. This decline may be related to large-scale changes in the marine environment, overfishing, alterations and destruction of estuarine habitat, or a shift in location of population centers (Plummer et al. 1983). Pollution has been shown to reduce hatching success, reduce size of larvae at hatching, produce morphological and anatomical abnormalities, and reduce feeding and growth rates (MBC Applied Environmental Sciences 1987). By comparison, thermal effluents from California coastal power plants do not seemingly inhibit growth and may be advantageous to California halibut (Innis 1990).

Early records indicate that California halibut were uncommon in San Francisco Bay. Alpin (1967) sampled the Central Bay with bottom trawls during 1963-1966 and reported catching only three California halibut (two in the spring and one in June). Ganssle (1966) reported catching only two adult California halibut (May 1963, 1964) while fishing bottom trawls in San Pablo Bay. Recently, consistent high salinities probably have contributed to increased abundance of California halibut in the bay. Moreover, recent data suggest that successful year classes in 1983, 1987, and 1990 have contributed to increased abundance in the bay (CDWR 1991). These were years with warm water ocean events, and it is hypothesized that California halibut abundance in the San Francisco Bay increased because of increased local spawning, higher survival of larvae, or migration of juveniles from more southern coastal areas with warmer ocean waters (Hieb and Baxter 1994).

Abundance indices (determined from trawl samples) for California halibut in San Francisco Bay increased from 1989 to 1992 (Hieb and Baxter 1994). The 1992 index was the highest since the study began in 1980. Also, most halibut collected in San Francisco Bay are age two and older, whereas other flatfishes are caught primarily as young-of-the-year. Nevertheless, California halibut abundance indices are still very low relative to other common species of flatfish in the Bay (Hieb and Baxter 1994).

In an attempt to increase California halibut numbers, natural production has been augmented by hatchery production (Crooke and Taucher 1988). Although this effort could increase future recruitment, negative effects of the hatchery program include a possible reduction in genetic variability within natural populations and the high cost producing fish (Hobbs et al.1990).

Trophic Levels

Larvae, juveniles, and adults are carnivorous (secondary and higher order consumers).

Proximal Species

Predators: Thornback (important predator on settling juveniles), California sea lions (predator on large juveniles and adults), northern sea lions, Pacific angel shark, Pacific electric, bottlenose dolphin.

Prey:
Plankton—major prey item for larvae.
Harpacticoid copepods, gammaridean amphipods—major prey item for young juveniles.
Polychaetes, mysids, and crab—minor prey item for young juveniles.
Mysids—major prey item for juveniles.
Gobies—prey item for juveniles and adults.
Bay shrimp, ghost shrimp—prey item for older juveniles.
Topsmelt, California killifish—prey item for older juveniles and adults.
Northern anchovy—major prey item for adults.
White croakers, hornyhead turbot—prey item for large adults.
Octopus, squid, California grunion—prey item for adults.

Parasites: Trematodes, cestodes, and nematodes (endoparasites); copepods and isopods (ectoparasite).

Competitors: Speckled sanddab (potentially important).

Good Habitat

Good spawning habitat for California halibut is limited to inshore waters or bays and estuaries in moderately shallow water where temperatures approximate 13-15°C, although successful spawning may also occur at temperatures approaching 22°C (Gadomski and Caddell 1991). Favorable characteristics for bays and estuaries that serve as nursery areas include productive habitats with abundant food supplies and shallow areas that allow juveniles to avoid predators, including adult halibut (Plummer et al. 1983). Juveniles and adults prefer sandy bottoms and water temperatures between 10-25°C, with a preference for 20.8°C (Ehrlich et al. 1979). Juveniles are relatively tolerant of reduced dissolved oxygen and increased water temperatures (Waggoner and Feldmeth 1971). Higher water temperatures induces faster growth rates and decreases the time to settlement for most young-of-the-year halibut (Gadomski et al.1990). Eggs, larvae, and adults are found in euhaline waters, but juveniles often occur in oligohaline to euhaline conditions (Haaker 1975).

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Starry Flounder

Platichthys stellatus

Kurt F. Kline

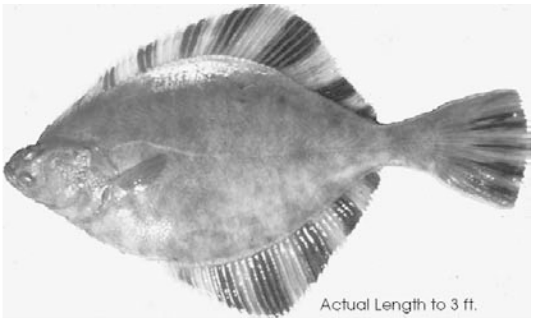
General Information

The starry flounder is in the family Pleuronectidae, or right-eyed flounders. Pleuronectids are generally found in temperate marine environments, with only a few species found in the tropics or sub-tropics. There are 22 species found along the coast of California. The starry flounder is one of the few pleuronectids commonly found in brackish and freshwater (Orcutt 1950, Haertel and Osterberg 1967). While placed in the Pleuronectidae, the starry flounder is commonly right or left-eyed. However, it is quite distinguishable from other flatfishes due to the alternating dark gray and orange-yellow bands on the dorsal, anal, and caudal fins.

Many of the pleuronectids support commercial and sport fisheries. The starry flounder is a minor sport species in San Francisco Bay and most fish are taken from boats when fishing for California halibut, sturgeon, or striped bass. It common in the commercial fishery, but as a by-catch to targeted species such as petrale sole and California halibut. In recent years, nearshore gear restrictions have resulted in a decrease in starry flounder landings, as this species is most common within a few miles of shore (Haugen 1992).

Reproduction

Spawning occurs in winter in shallow coastal areas near the mouths of rivers and sloughs (Orcutt 1950, Wang 1986, Baxter 1999). Some researchers have suggested that spawning may occur within San Francisco Bay



(Radtke 1966, Moyle 1976); however, neither ripe female starry flounder nor mature flounder eggs or pre-flexion larvae were collected from San Francisco Bay in the early 1980s (B. Spies, pers. comm., Wang 1986).

Growth and Development

Eggs and larvae are pelagic and found mostly in the upper water column (Orcutt 1950, Wang 1986). Starry flounder larvae are approximately 2 mm long at hatching and settle to the bottom about two months after hatching, at approximately 7 mm standard length (SL) (Policansky and Sieswerda 1979, Policansky 1982). Larvae depend upon favorable ocean currents to keep them near their estuarine nursery areas before settlement. Transforming larvae and juveniles migrate from the coast to brackish or freshwater nursery areas, where they rear for 1 or more years (Haertel and Osterberg 1967, Wang 1986, Hieb and Baxter 1993). As they grow, juvenile starry flounder move to higher salinity, but appear to remain in estuaries through at least their second year of life (Haertel and Osterberg 1967, Hieb and Baxter 1993).

Most males mature by the end of their second year of life (220-276 mm SL), while females mature at 3 or 4 (239-405 mm SL) (Orcutt 1950). During the late fall and winter, mature starry flounder probably migrate to shallow coastal waters to spawn (Orcutt 1950). After spawning, some adult starry flounder return to the Bay for feeding, and are most common in the Bay from late spring through early fall (Ganssle 1966). They reach a maximum length of 915 mm (Miller and Lea 1972)

Food and Feeding

In Monterey Bay and Elkhorn Slough, the smallest starry flounder (10-99 mm SL) fed primarily on copepods and amphipods. Larger juveniles (100-199 mm SL) fed on larger amphipods, polychaetes, and bivalves (especially siphon tips). Fish >199 SL mm fed on whole crabs and bivalves, sand dollars, brittle stars, and occasionally fish (Orcutt 1950). In San Francisco Bay, a large portion of the diet of starry flounders > 199 mm was bivalves (primarily *Mya*, *Ischadium*, *Tapes*, *Solen*, *Mytilus*, and *Gemma*), polychaetes, and crustaceans (especially *Upogebia*, *Cancer magister*, *C. gracilis*, and *Hemigraphsus oregonensis*) (CDFG, unpubl. data).

Distribution

Starry flounder range from Santa Barbara, California northward to arctic Alaska, then southwesterly to the Sea of Japan (Miller and Lea 1972). Adult starry flounder inhabit shallow coastal marine water, whereas juveniles rear in bays and estuaries (Orcutt 1950, Moyle 1976, Wang 1986). Emmett et al. (1991) state that juvenile starry flounder are found almost exclusively in estuaries.

In San Francisco Bay, there is a shift in distribution with growth. Age-0 fish are found more commonly in fresh to brackish water (Suisun Bay, Suisun Marsh, and the delta), while age-1 and older juveniles are more commonly associated with brackish to marine waters (Suisun and San Pablo bays). Throughout their time in the San Francisco Bay, juvenile starry flounder are commonly found in shallow water, including shoals, intertidal areas, and tidal marshes (Woods 1981, Moyle et al 1986, Baxter 1999, CDFG, unpubl. data).

Population Status and Influencing Factors

There is evidence of a long-term decline in the San Francisco Bay starry flounder population from the Commercial Passenger Fishing Vessel log book data. Both catch/hour (CPUE) and total catch of starry flounder declined in the mid-1970s from a peak in the late 1960s and early 1970s (CDFG 1992). This decline in CPUE and catch continued at least through the early 1990s. Additionally, juvenile starry flounder abundance indices from San Francisco Bay steadily declined from the early to the late 1980s (**Figure 2.10**). Abundance remained very low through 1994 and increased somewhat from 1995-99. Outflow related mechanisms have been proposed to control recruitment of age-0 starry flounder to the Bay (CDFG 1992, Hieb and Baxter 1993). The increase in the abundance of age-0 fish from 1995 to 1999 supports this hypothesis.

Hydrologic factors and other environmental conditions in San Pablo and Suisun bays are important in determining the distribution of juvenile starry flounder. The San Francisco Estuary is close to the southern limit of the distribution for starry flounder and long-term

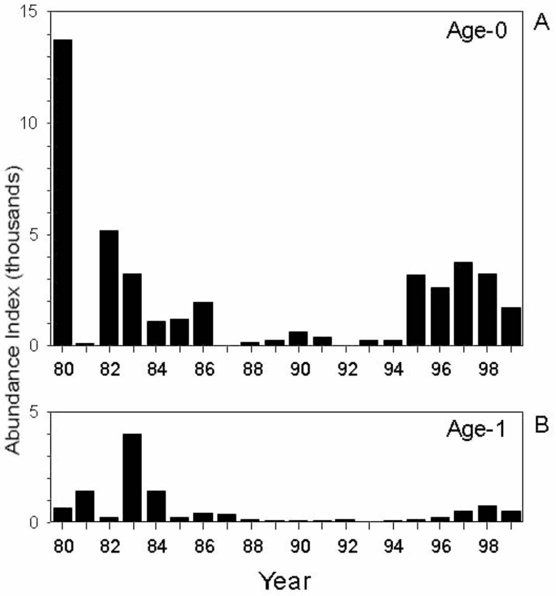


Figure 2.10 Annual Abundance Indices of Starry Flounder: A. Age-0, May-October; B. Age-1, February-October (CDFG Otter Trawl data)

changes in the oceanic environment (particularly temperature) may also affect recruitment. Ocean temperatures have been above average for the region for much of the 1980s and 1990s and it is possible that adult populations moved northward into cooler waters. Temperature can also influence spawning and early development, as increased temperatures may result in decreased hatching success and larval survival.

Trophic Levels

Primary to secondary carnivore. Feeds primarily on large benthic invertebrates and rarely on fish.

Proximal Species

Prey: Benthic invertebrates including bivalves, polychaetes, and crustaceans.

Good Habitat

Suitable habitat includes shallow to deep subtidal mud and sand flats. Juvenile rearing occurs in the shallow areas of Suisun and San Pablo bays. Open deeper waters with higher salinity are generally more acceptable for adults.

Acknowledgments

Some of the materials in this report are summarized from the Plueronectiformes chapter of IEP Technical Report 63 which is referenced below (Baxter 1999).

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