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THE ECOLOGY OF SAN FRANCISCO BAY TIDAL MARSHES: A Community Profile

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THE ECOLOGY OF SAN FRANCISCO BAY TIDAL MARSHES: A COMMUNITY PROFILE

by

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CONVERSION FACTORS

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (mt)	2205.0	pounds
metric tons (mt)	1.102	short tons
kilocalories (kcal)	3.968	BTU
Celsius degrees	1.8(C°) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
acres	0.4047	hectares
square miles (mi^2)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
BTU	0.2520	kilocalories
Fahrenheit degrees	0.5556(F° - 32)	Celsius degrees

PREFACE

This description of the tidal marshes of San Francisco Bay is part of a series of profiles concerning coastal habitats of the United States. Its purpose is to describe the structure and functioning of salt and brackish tidal marshes in San Francisco Bay. Cowardin et al. (1979) classify this habitat as occurring in the Californian province, estuarine system, intertidal subsystem, emergent wetland class and persistent subclass. Water regimes vary from regularly flooded to irregularly flooded, and water chemistry is brackish to euhaline. In addition, some discussion of diked habitats is included.

The profile provides a useful reference to the scientific information on the plant and animal inhabitants of bay tidal marshes. No one habitat can be considered typical of tidal marshes due to the estuarine salinity gradient in San Francisco Bay. A distinction is made, however, between salt marshes dominated by Pacific cordgrass (*Spartina foliosa*) and pickleweed (*Salicornia virginica*) and brackish marshes dominated by bulrushes (*Scirpus* spp) and cattails (*Typha* spp). Greater emphasis in this profile has been placed on salt marshes because of the larger body of available information. Where scientific information is lacking, an effort has been made to indicate needed research or to propose hypotheses based on similar systems.

The information in the profile will be useful to environmental managers, resource planners, estuarine ecologists, marine science students, and interested laymen who wish to learn about the myriad of organisms inhabiting tidal marshes and their interrelationships. The format, style, and level of presentation should make this report adaptable to a diversity of needs, from preparation of environmental assessment reports to supplementary reading material in college marine science courses.

The profile includes a description of the general location and setting (Chapter 1), a summary of the geologic circumstances which are responsible for the formation of the bay and its tidal marshes (Chapter 2), and an account of the human impacts on historic and present-day marshes (Chapter 3). A detailed description of the tidal marsh community includes information on physical attributes (Chapter 4), plant species and their distribution (Chapter 5), and animal inhabitants (Chapter 6). A synthesis of community interactions and processes is presented (Chapter 7) and concluding remarks focus on management issues for the preservation of remaining tidal marshes and habitat guidelines for marsh restoration (Chapter 8).

Any questions or comments about or requests for this publication should be directed to:

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ACKNOWLEDGMENTS

A review of this nature relies on work by researchers in many diverse fields. I cannot truly do justice to their detailed studies. I hope the short summaries presented accurately reflect their work and conclusions. The majority of the review is based on published work, however, many researchers shared unpublished manuscripts and personal observations. In addition, students in my classes and at other California State University campuses provided an important source of data and observations. The review has been influenced by my research on San Francisco Bay marshes sponsored by the US Fish and Wildlife Service, the San Francisco Foundation, and San Francisco State University. The preparation of this profile has been sponsored by the Environmental Resources Branch of the Office of the Chief of Engineers in association with the San Francisco District, Army Corps of Engineers, and the US Fish and Wildlife Service.

I am especially appreciative of the close scrutiny of earlier drafts of the manuscript given by: James Buchholz (Tiburon Center for Environmental Studies); Raymond Krone (UC, Davis); H.Thomas Harvey (Harvey and Stanley Assoc.); Keith Macdonald (Keith Macdonald and Assoc.); Margaret Race (Stanford University); James Schooley (California State University, Hayward); Nancy Wakeman (Bay Conservation and Development Commission); and Joy Zedler (San Diego State University). The efforts of the reviewers steered me from ambiguous or incorrect statements; however, I retain responsibility for any remaining inaccuracies. In addition, I appreciate the comments provided by various agency staff including: T. E. Harvey and R. Lowe (San Francisco Bay National Wildlife Refuge); Margaret Kohl and Karen Miller (US Fish and Wildlife Service, Sacramento); Penny Herring, Wiley Kitchens, and Kate Lyster (National Coastal Ecosystem Team); and Roderick Chisholm, Lars Forsman, Scott Miner, and Jody Batlin (US Army COE, San Francisco District). Steven Balling (UC, Berkeley), Dale Hopkins (San Francisco State University), and Margaret Race provided valuable pre-publication reprints for my use.

Molly Martindale ably assisted me in the compilation of literature, preparation of figures, and typing of portions of the manuscript. Barbara Nabors formatted and typed the tables. Douglas Spicher and Leonard Compagno generously provided photographs for inclusion in the profile.

This work could not have been completed without the support and understanding given to me by my family: Margaret, Michael, and Alexander. Thank you for putting up with many long hours of preparation and writing.

CHAPTER 1

INTRODUCTION

San Francisco Bay sits at the terminus of a great drainage system: the Sacramento-San Joaquin basin which covers 40% of the land area of California (Figure 1). Approximately 20 billion cubic meters of freshwater flow into the bay annually and mix with saltwater which has passed through the Golden Gate from the Pacific. The largest contiguous tidal marsh system on the Pacific Coast of North America was created over the last 10,000 years by the tidal submergence of the bay margins coupled with sediments deposited by the rivers. At the time of European man's arrival, the tidal marshes of San Francisco Bay and the Sacramento-San Joaquin Delta covered over 2200 km^2 more than twice as much area as the open water of the bay and delta combined (Atwater et al. 1979). The colonization and eventual development of the bay and delta led to the destruction of 95% of this habitat leaving only 125 km^2 of tidal marsh. This represents only 10% of the current open water area. It will never be known what effects such a tremendous reversal in relative areas of marsh and open water have had on the bay ecosystem.

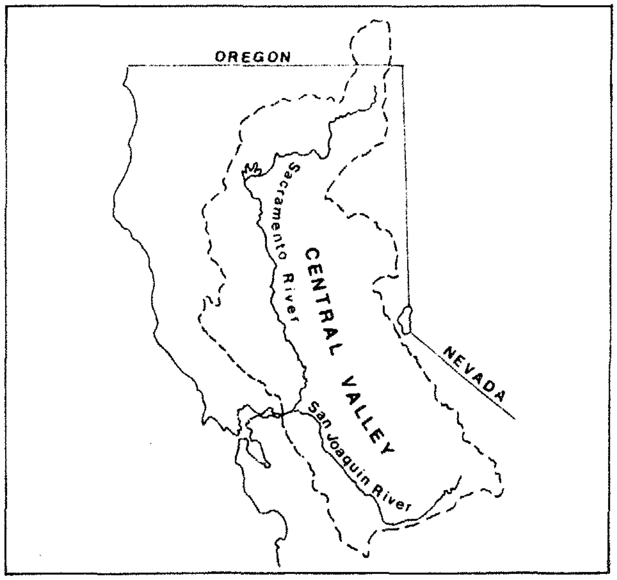

FIGURE 1. Sacramento-San Joaquin River drainage system and location of San Francisco Bay.

San Francisco Bay is a continuum of habitats from deep channel bottoms to shallow marsh pools. The community structure varies from those adjacent to the Pacific to those bordering the freshwater Sacramento-San Joaquin Delta. Broad definitions of wetlands include all these habitats (Cowardin et al. 1979). More restricted definitions require that wetlands have both saturated sediments and vegetation adapted to saturated conditions (Calif. Coastal Comm. 1981, US Army Corps of Engineers 1977). Wetland, in this sense, is more applicable to the community described herein. This profile will focus on the vegetated habitat between approximately mean low water and extreme high water, the area commonly referred to as a tidal marsh. However, because marshes are dissected with internal circulation channels and generally grade imperceptibly to unvegetated mudflats, some discussion must focus on these areas as well. As we shall see, precise boundaries are difficult to establish.

Some areas can retain wetland characteristics even when removed from tidal action. The term diked wetland can refer to lagoons, vegetated marshes, and salt ponds (Bay Conservation and Development Commission 1982). Much less is known about the ecology of these systems than their tidally influenced counterparts and they will be mentioned here only in their relationship to tidal marshes. Tidal freshwater wetlands are also not discussed in this profile. Basic differences in species composition warrant their inclusion in a separate profile.

Lack of quantitative information has greatly hampered our ability to understand the role of tidal marsh organisms in the overall functioning of the bay. Historic surveys concentrated on the organisms of potential commercial significance and ignored the wetlands except for purposes of mapping navigable waters and determining land grants and ownership (Hedgpeth 1979, Briscoe 1979). Only recently, studies have departed from the ecological assumptions derived from Atlantic and Gulf coast wetlands and provided new information necessary to understand wetland functioning in San Francisco Bay.

The geographic extent of this community profile includes the saline and brackish water wetlands of San Francisco, San Pablo, and Suisun Bays (Figure 2). Frequently these basins are collectively referred to as the San Francisco Bay estuary. The term estuary implies a region where salt and freshwater mix. All of the marshes considered here are influenced by saline conditions at some time during the year. The Sacramento-San Joaquin Delta is eastward of Suisun Bay and only during extremely dry years does saline water intrude. It is generally considered tidal freshwater habitat. For brevity, the term south bay will be used to refer to marshes south of the city of San Francisco and north bay for areas to the north of Richmond. The central bay between Richmond, Oakland, and San Francisco has limited marsh habitat but will be sometimes referred to in relation to more oceanic conditions. San Francisco Bay is used to refer to the entire estuary.

It is the purpose of this community profile to review the research conducted in San Francisco Bay tidal marshes and provide greater insight to their unique attributes. The information provided herein is both a compilation and an analysis. Unfortunately, there are large gaps in our knowledge of San Francisco Bay tidal marshes making it difficult to develop even qualitative models on their functioning and the interrelationships of species. This is a modest beginning with the hope that some stimulus is provided for further work.

The completion of this profile comes at an opportune time in the history of San Francisco Bay. Legislative and regulatory actions are striving to preserve existing wetlands and require the restoration of former marshes. The Bay Conservation and Development Commission (BCDC) which is charged with the protection of bay tidal marshes has sought to develop methods to better manage these natural resources through the Suisun Marsh Protection Plan (BCDC 1976) and the Diked Wetlands Study (BCDC 1982). Yet, management can only be as effective as the data and research on which it is based. Hazardous wastes, water diversion, and sewage effluents are the results of urbanization and development which place new pressures on the natural environment. Understanding their influence on tidal wetlands requires further research, both basic and applied.

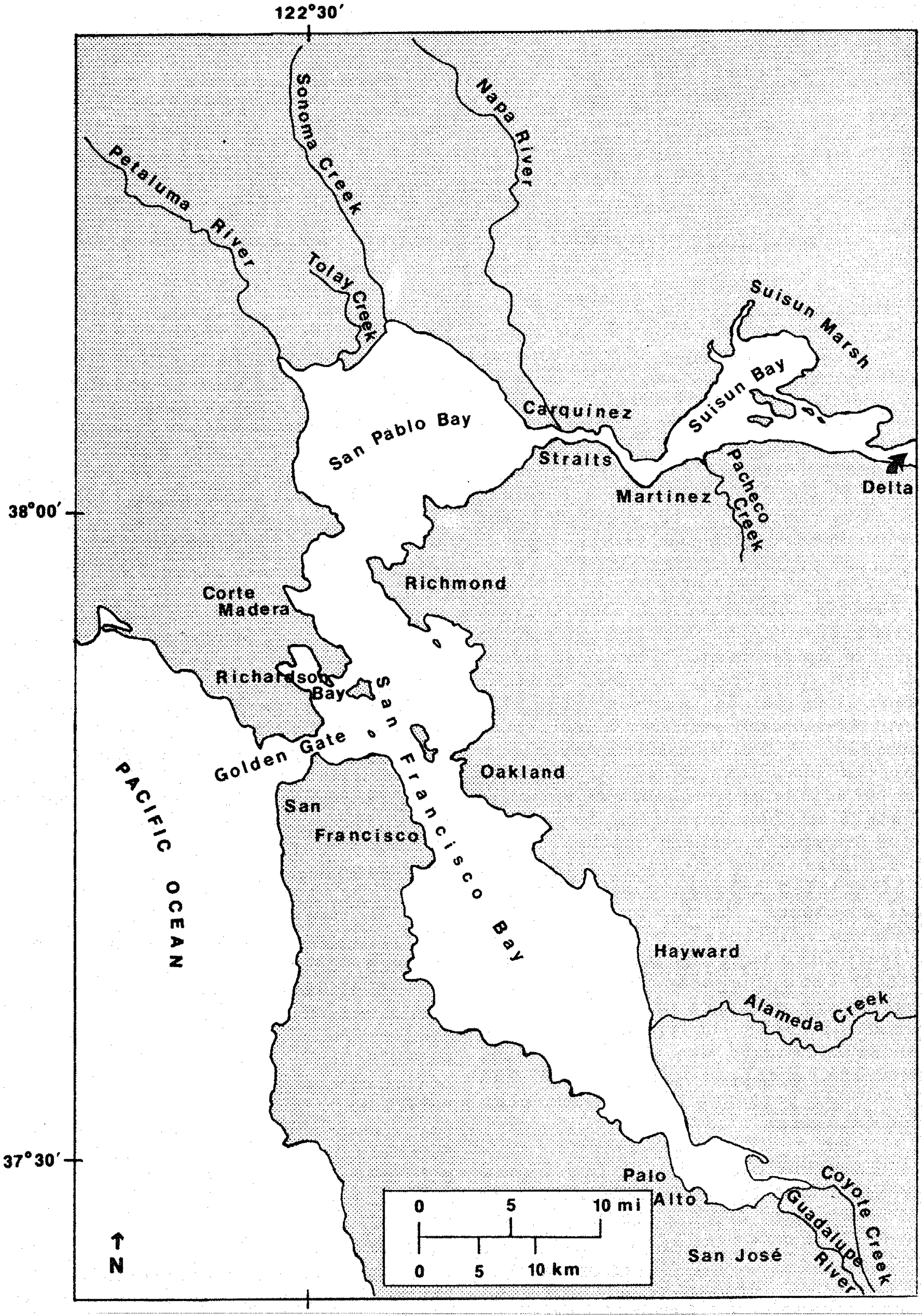

Figure 2. Geographic locations and place names for San Francisco Bay and vicinity.

CHAPTER 2

PREHISTORIC DEVELOPMENT OF TIDAL MARSHES IN SAN FRANCISCO BAY

San Francisco Bay, like most estuaries, is a relatively recent geomorphological feature. Although its origins can be traced to the early Pliocene, about 10 to 12 million years ago, the bay as we now know it has existed for less than 10,000 years (Atwater et al. 1977). The evolution of San Francisco Bay is a result of a complex interplay between tectonic processes and changing sea levels.

Located on the western edge of the North American continental plate, the San Francisco Bay region has been strongly influenced by the earth's crustal movements. The relatively rapid horizontal movement along the San Andreas Fault (10-30 m per millennium) and the slower vertical movement of the coastal ranges (0.5 m per millennium) have contributed greatly to the formation of the basin containing the waters of San Francisco Bay. The relative movements between the two lithospheric plates along the California coast have alternated between subduction and lateral movement. The former process has contributed additional rock and crustal material to the continental plate while the latter has influenced the basin morphology at the entrance of San Francisco Bay (Atwater 1979). Uplifted marine and estuarine sediments provide further evidence of the variation in the size of the basin and the previous connections with the Pacific Ocean.

The present basin was formed during the late Pliocene period (approximately 10 million years ago) after a period of acute folding and associated faulting (Louderback 1951). This period of intense deformation also influenced the drainage patterns of the great Central Valley to the east, then a large marine embayment. A structural depression in the Coastal Ranges in the vicinity of Suisun Bay eventually provided the passage for exchange between the interior valley and the Pacific. This narrow opening (0.75 km) is now called the Carquinez Straits. Borings for bridge piers that have extended to bedrock indicate that rivers entering the San Pablo Bay Basin flowed over ground that is currently 45 to 60 m below sea level and out through the Golden Gate at approximately 120 m below present sea level.

The canyons eroded by the prehistoric rivers were traversed by numerous northwest trending ridges, the highest of which now protrude above the surface as islands: Angel, Alcatraz, Yerba Buena, and Red Rock. The uplifting of the Berkeley Hills, with strongly folded sediments of the Pliocene at their summit, completed the major geologic processes contributing to the great basin now known as San Francisco Bay.

The San Francisco Bay Estuary is a drowned river valley. Evidence from borings indicate that the basin was the site of at least three ephemeral estuaries over the past 1 million years (Ross 1977, Atwater 1979). While early argument centered around the occurrence of tectonic movements by the land, Louderback (1951) recognized the significance of rising sea level due to glacial melting as responsible for the formation of these estuaries. The current period of inundation began approximately 10,000 to 11,000 years ago (Atwater et al. 1979)(Figure 3). The initial rise in sea level was rapid, advancing along the valley floor in the south basin almost 30 m/year. Depositional processes in the flooded valleys contributed alluvial sand, silt, gravel, and clay to the sediments

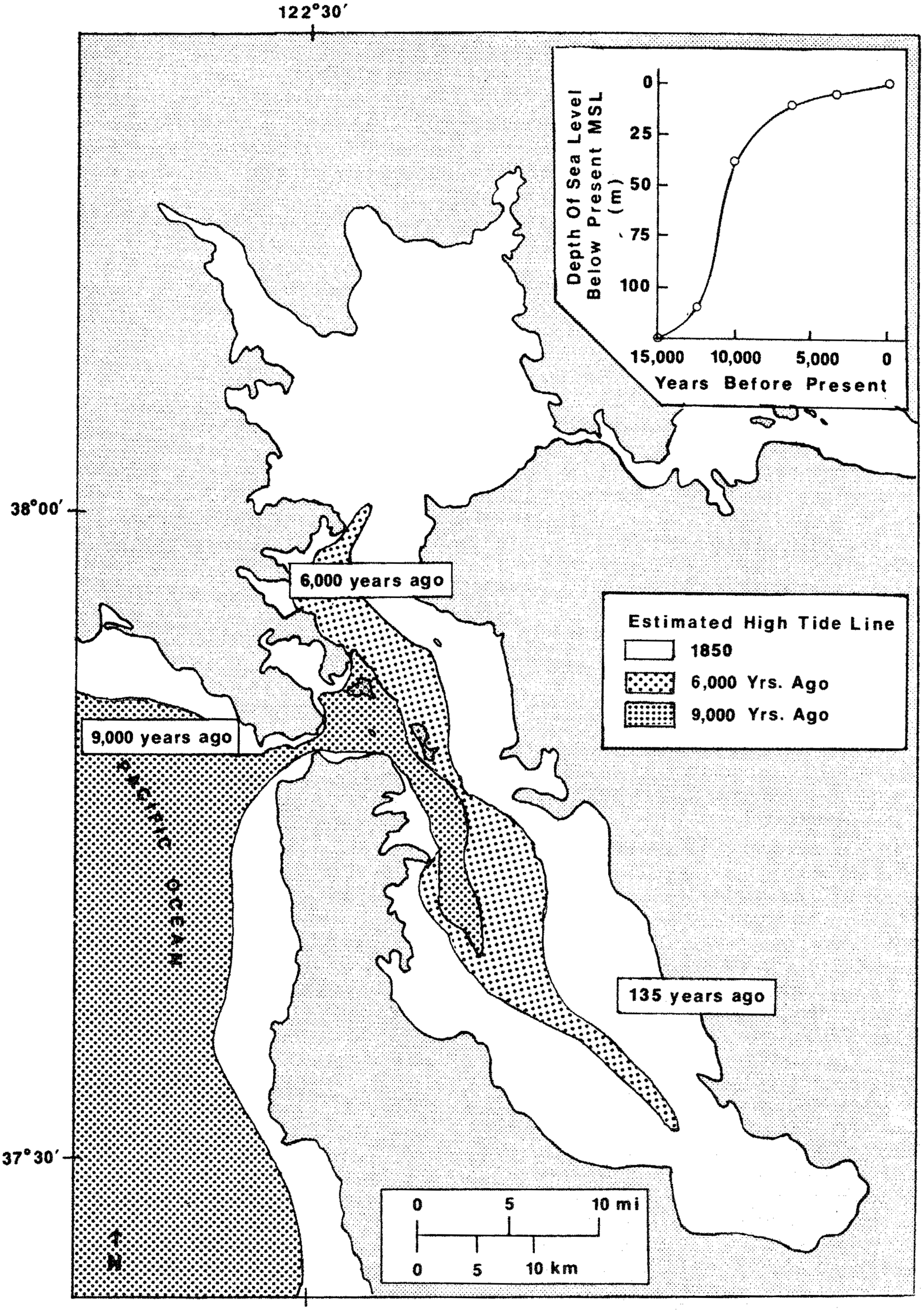

Figure 3. Estimated high tide shorelines based on rate of sea level rise in southern San Francisco Bay (Atwater et al. 1977) and current bay bathymetry (modified from Helley et al. 1979).

underlying the bay. The deposits of the latest transgression of the sea are referred to as "younger bay mud" (Treasher 1963) and range in thickness from 0 to 30 m. Radiocarbon dating from samples in the younger bay mud indicates an age of between 7,360 to 2,420 years before present (Storey *et al*. 1966).

A marked decrease in the rate of sea level rise occurred approximately 7,000 to 6,000 years ago. At this time, seawater began flowing over extensive flatland deposits in the south bay, as well as invading the Suisun Basin via the Carquinez Straits. Eventually, sedimentation rates exceeded the sea level rise of 0.1 to 0.2 cm/yr and extensive intertidal mudflats developed. During the past several thousand years, bayward growth of marshes has occurred as evidenced by the presence of characteristic subtidal deposits underlying salt marshes (Atwater *et al*. 1977). The maximum extent of tidal marshes was documented by the United States Coast and Geodetic Survey (USC&GS) between 1850 and 1897. Total acreage for marshes surrounding San Francisco, San Pablo, and Suisun Bays probably exceeded 800 km^2 (Gilbert 1917). The Sacramento-San Joaquin Delta contained an additional 1400 km^2 of tidal freshwater marshes.

Fossil evidence in sediments and the middens of aboriginal man provide the only evidence of the prehistoric nature of the bay flora and fauna. Prior to the most recent flooding of the basin, plant fossils indicate a cool, wet climate existed, with forests dominated by cedar and Douglas fir. Associated animals included camels, bison, horses, sloths, and mammoths. Freshwater marsh sediments containing possible bulrush (*Scirpus*) seeds have been found on the bedrock valley floor. The rapid rise in sea level from 11,000 to 7,000 years ago probably precluded any extensive salt or brackish marsh development. The earliest dated core sample containing fossilized salt marsh plant roots is 8,300 years old (Atwater *et al*. 1977)(Table 1). None of the roots were positively identified. Most resembled the small roots and rhizomes of the present day high marsh plants: pickleweed (*Salicornia virginica*) and saltgrass (*Distichlis spicata*). In addition, they noted a change in the diatom composition, from a dominant fresh and brackish water assemblage to one composed primarily of marine forms.

Human habitation of the San Francisco Bay area provides further evidence of prehistoric shorelines and associated flora and fauna. Many tribes occupied sites along the bay shoreline and deposited items of their food and culture into large shell mounds called middens. Gifford (1916) described 425 middens in the bay area, the largest at Ellis Landing, near Richmond. It measured 14 m x 7 m and was over 9 m deep, giving an estimated period of occupation of 3,500 years. In addition to tools and human remains, the midden contained large quantities of shells identified as mussels (*Mytilus edulis*), oysters (*Ostrea lurida*), and bent-nosed clams (*Macoma nasuta*). Archaeologists have long been interested in replacement of the native oyster (*O. lurida*), a hard substrate bivalve, by the bent-nosed clam (*M. nasuta*), a mudflat dwelling organism, in the upper levels of the middens. The middens were located initially on gravelly beds near creek discharges and are now partially submerged under bay mud. It is possible that as sea level rose, alluvial deposition of coarse particles occurred further upstream, isolating the shell mounds in a finer depositional environment.

European explorers described the beauty of the natural harbor afforded by the bay and the abundance of timber, potential farmland, and plentiful wildlife, but paid little attention to the bordering wetlands. Early paintings (Figure 4) provide some idea of the appearance of bay tidal marshes. Gilbert (1917), the first to document the tremendous changes inflicted on the bay, briefly described the typical marsh as "a plain traversed by a branching system of sloughs" and mentioned the presence of tules and cordgrass. Unfortunately, present day tidal wetlands have been greatly impacted by anthropogenic influences and we can now only infer how prehistoric marshes appeared and functioned.

Table 1. Age and description of fossil deposits from boreholes in south San Francisco Bay (adapted from Atwater *et al*. 1977). Wetland type determined by comparison to present-day root profiles. Elevation at time of deposition estimated based on analogy with present-day vertical distributions of plants and animals.

Distance from G.G. Bridge	Borehole	Depth in relation to current mean sea level (m)	Elevation at time of deposition (m)	Fossils	Wetland type at time of deposition	Date before 1950 (years)
50 km	Dumbarton Bridge-main channel	-7.9	+1.0	forams, pennate diatoms	salt	3,360
37 km	San Mateo Bridge-Hayward side	-6.6	-0.5	plant detritus, *Ostrea*	mudflat	3,930
22 km	Alameda	-11.8	+0.7	plant roots in growth positions, forams, pennate diatoms	salt marsh	6,485
10 km	north portion of south bay -main channel	-21.0	+0.7	plant roots in growth positions, forams, pennate diatoms	salt marsh	8,293
17 km	off Hunters Point, San Francisco	-37.5	+4.0	plant roots, *Scripus* seeds	freshwater	9,280

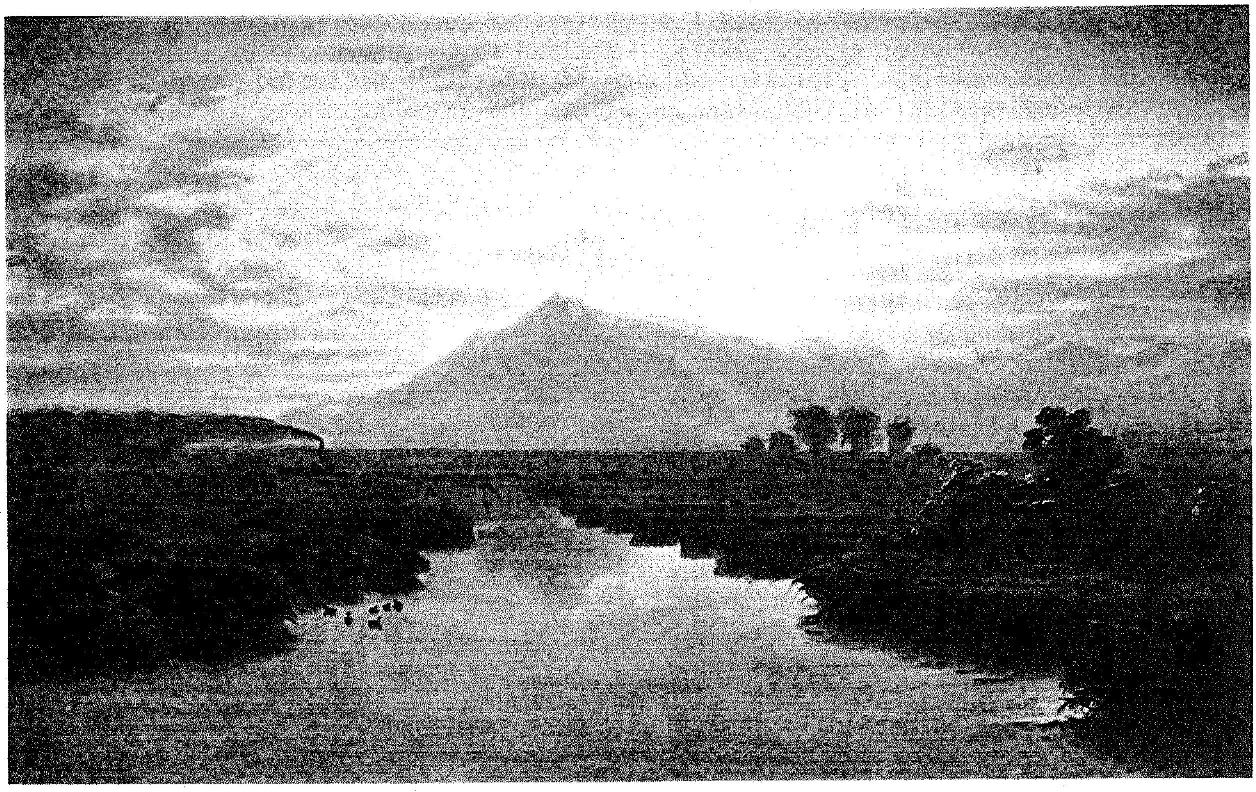

Figure 4. Napa marshes and Mount Tamalpais by William Marple, 1869 (Courtesy of California Historical Society).

CHAPTER 3

HISTORIC, PRESENT, AND FUTURE MODIFICATIONS OF TIDAL MARSHES

The recorded history of tidal marshes in San Francisco Bay spans only a brief period of time. Discovered in 1769, the bay was little explored until 50 years later when naturalists and cartographers began investigating the shorelines and inland water routes (Hedgpeth 1979). Undoubtedly, they observed extensive marshlands undisturbed by the aboriginal inhabitants except for isolated middens. The marshlands were primarily considered for their agricultural potential and abundant wildlife. The possibilities for commercial and industrial uses became more significant following the population boom brought by the Gold Rush era in the 1850's. These perceptions dictated the activities that took place in the marshes over the next 150 years, a period which witnessed an accelerating loss of tidal wetlands. Understanding the ecological processes occurring in the remaining marshes requires some background on past impacts.

3.1 EARLY HISTORIC CONDITION OF TIDAL MARSHES

The early surveys by the USC&GS during the 1850-70's provide a baseline against which marsh losses can be measured. These surveys have recently been recompiled and mapped by Nichols and Wright (1971) and show tremendous detail in the features of the wetlands including sloughs, ponds, and natural salt ponds. The maps provide sufficient detail to follow modifications in drainage patterns, morphological changes due to erosion and accretion, and encroachment of upland fills over former marshland (see Atwater et al. 1979: Fig 5). Atwater et al. (1979) determined that of the remaining tidal marsh (including the delta), only 85 km^2 represents marsh that was in existence in 1850; the rest (40 km^2) has been created through new sedimentation. Additional acreage has been added recently due to restoration activities (see Chapter 8) and the present extent of tidal marshes is mapped in Figure 5. The upland boundary of the early surveys was determined at "the dividing line between marshland and fast or upland" or approximately "the penetration of the highest tides" (Shalowitz 1964). This vague definition has caused considerable dispute over historic wetland boundaries within the courts and among land owners, surveyors, and biologists. Although it may be one measure of jurisdictional extent for federal and state agencies, many other factors must be weighed in reaching a final decision (Briscoe 1979). BCDC has used this boundary to estimate diked wetland land use (BCDC 1982).

The early impact of the European colonizers was largely in the central bay in the region of Yerba Buena (now San Francisco). The coves along the eastern edge of the pennisula provided docking facilities and were developed by the early settlers for residential and commercial uses. Military and shipbuilding activities required lumber. Landings were constructed across some marshlands to transport redwoods to the Presidio at the Golden Gate and Yerba Buena (Figure 6). Spanish and Mexican land grants included wetlands, but most landowners made little use of them.

The Gold Rush following 1849 and statehood for California in 1850 accelerated changes in the bay area.

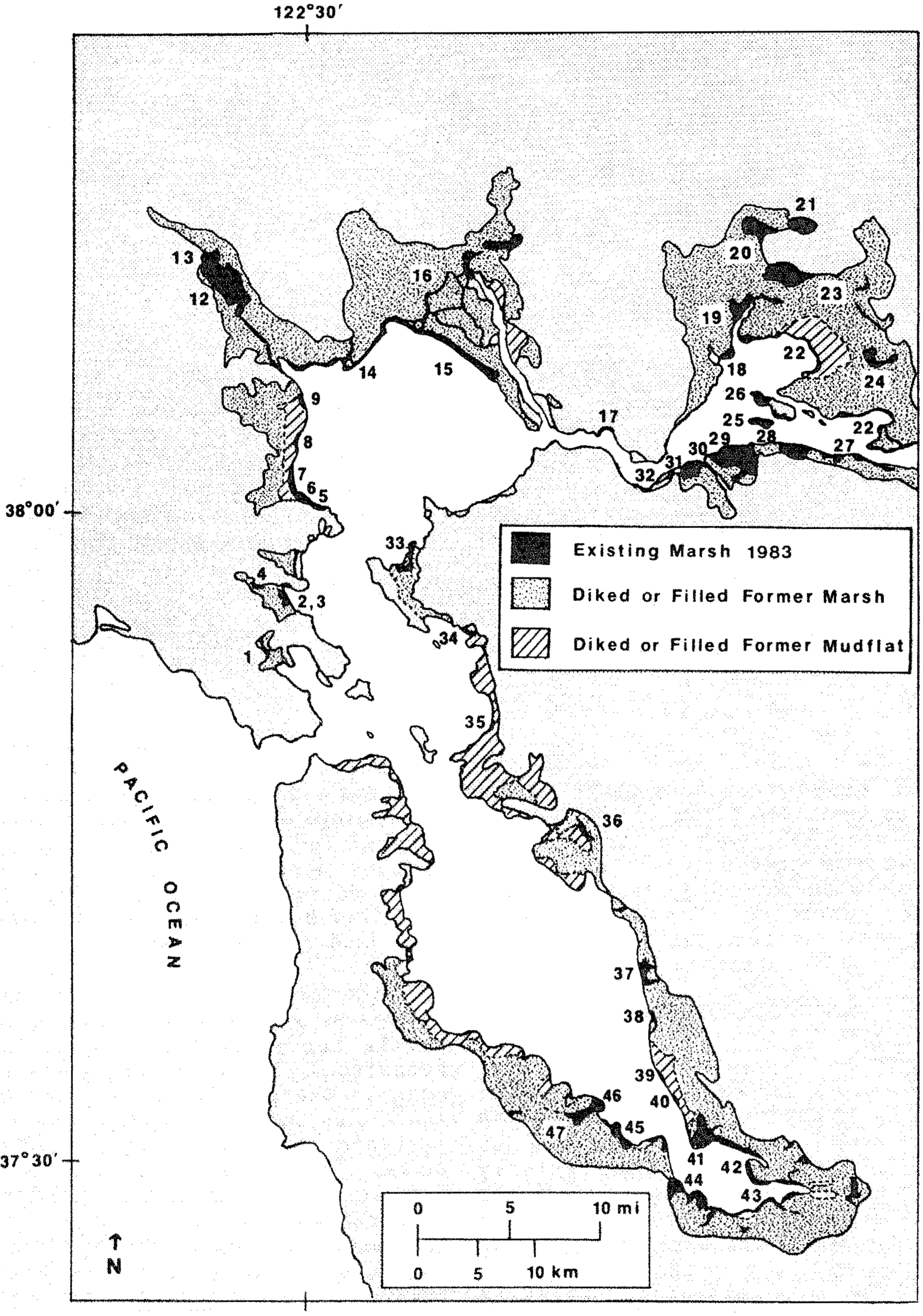

Figure 5. Historic and present extent of tidal wetlands in San Francisco, San Pablo, and Suisun Bays. The innermost line represents historic high water mark (see Figure 3). Numbers refer to tidal marshes described in Table 3. Some areas are too small to be represented on map (Modified from Atwater et al. 1979, Jones and Stokes Assoc. 1979, and BCDC 1982).

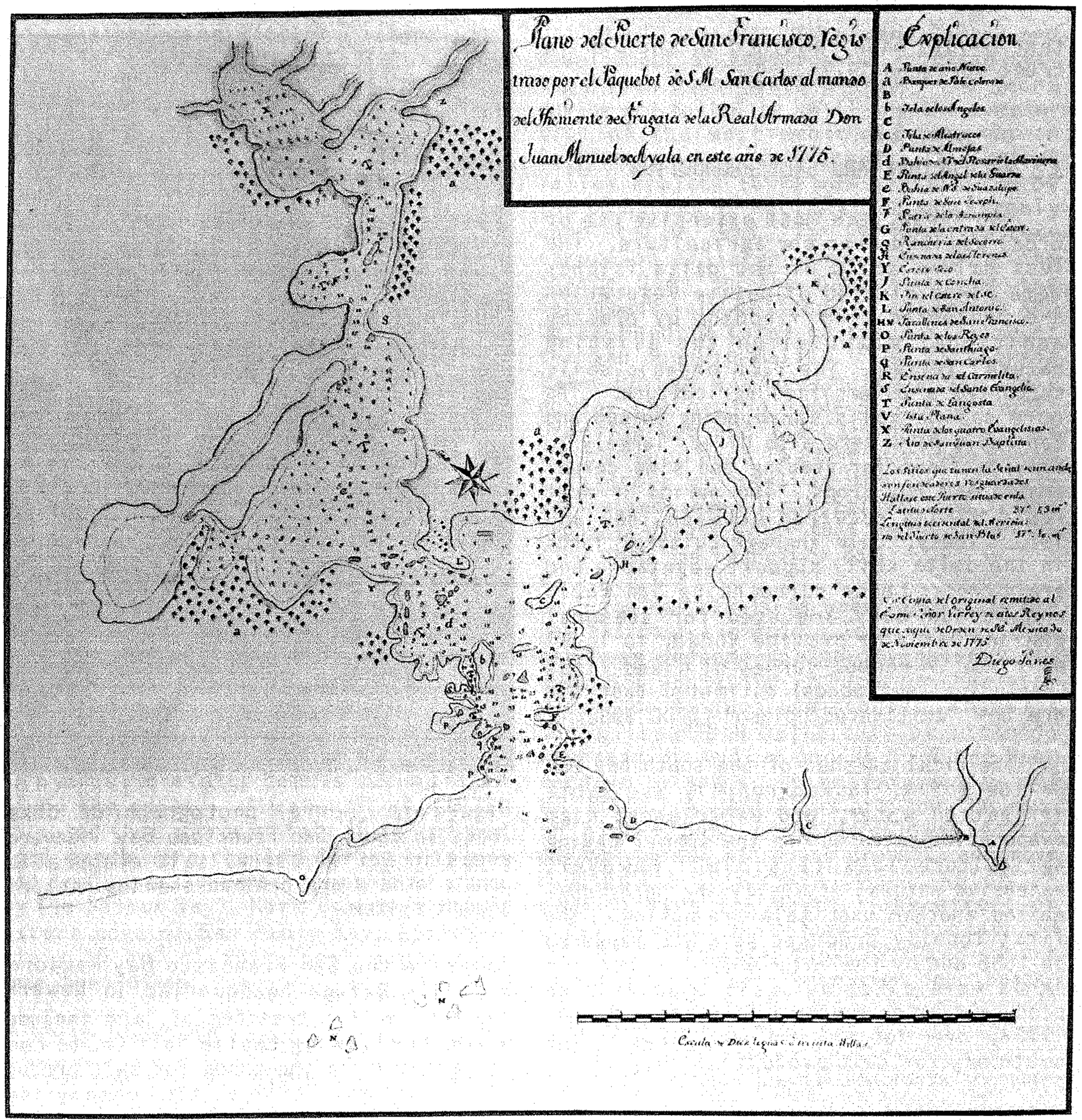

Figure 6. Map of San Francisco Bay by Don Jose Canizares, showing areas of forest cover (1776). Golden Gate at bottom of map, Suisun Bay at top. Small tree symbols indicate wood lots (Courtesy of Bancroft Museum, University of California).

Marshes, once shunned, now could be bought and sold at high profits by speculators. Lands determined as swamp-and-overflowed lands (non-tidal wetlands) were released from any future public trust and tidelands (land below the "ordinary high water mark") could be sold but subject to an easement for the public trust which was held by the state. The public trust at the time primarily dealt with uses for navigation and commerce. Land surveys were often inaccurate and frequently included tidal wetlands as upland. As a result, tidal marshes were filled in areas that should have remained in the public trust (Briscoe 1979).

3.2 AGRICULTURE AND SALT PRODUCTION

At first, the most extensive use of tidal wetlands was for agriculture. The less saline soils of the delta islands were first cleared of native vegetation and protected from flooding by placing additional material on the existing natural levees. The rich organic soils supported a diversified agriculture. The more saline soils surrounding Suisun and San Pablo Bays were also diked, largely to provide land for grazing and some cereal grains and row crops. The period of most rapid diking occurred between 1860 and 1910. Today, only the agricultural lands in the delta still support vegetable and grain crops; those surrounding San Pablo and Suisun Bays are used for seasonal grazing lands or provide fodder to local dairies. A recent survey of diked lands (excluding salt ponds) estimated that 63% are now "cultivated/upland" (BCDC 1982).

The tidal marshes of the south bay had saline soils, lacked readily available irrigation water, and experienced high evaporation rates during the summer making agriculture less feasible. However, extensive natural crystallizing ponds suggested another use: salt production. The first locally produced salt was marketed in 1856 and by the late 1800's, extensive lands were diked by small companies to produce salt in evaporation ponds. By the 1930's, over 160 km^2 had been diked in the south bay for salt production (Figure 7). Although initially undertaken by independent companies, salt production was eventually controlled by the Leslie Salt Co. through mergers and acquisitions. The company expanded its operations to the San Pablo Bay in 1952 when it purchased 45 km^2 of diked agricultural land and converted it to solar evaporation ponds. Salt produced in San Francisco Bay totals approximately 2 million tons annually, but is highly dependent on the weather conditions over the 5-7 years necessary to evaporate the bay water. USFWS recently purchased 62 km^2 of salt ponds from Leslie Salt, primarily in the south bay. The ponds along with outer tidal wetlands comprise the San Francisco Bay National Wildlife Refuge headquartered in Newark, California. The transfer of land included a clause allowing Leslie Salt Co. to continue operating the ponds for salt production until such time as the company goes out of business. USFWS may then manage the land as it sees fit.

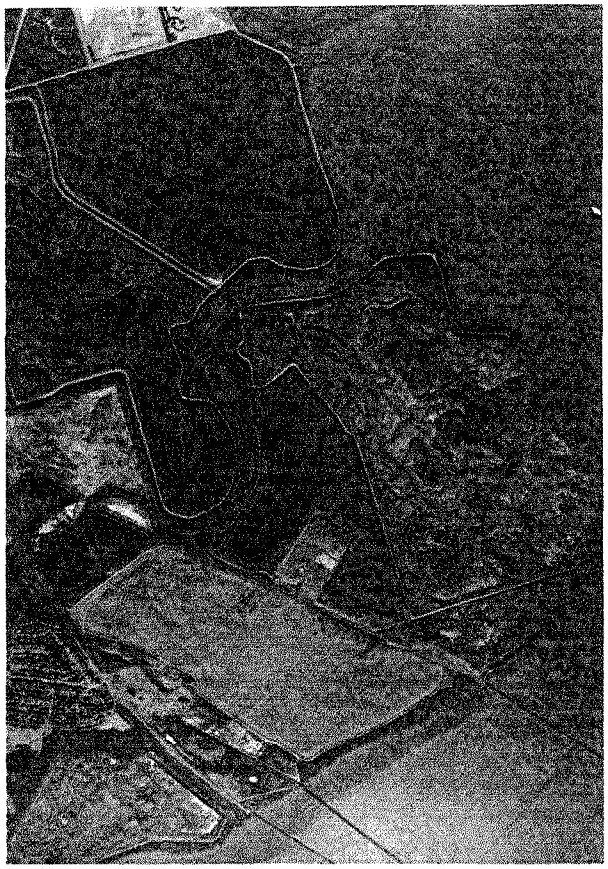

Figure 7. Aerial photograph of diked lands in south San Francisco Bay. Several areas in active use as salt evaporation ponds; others are drained showing historic slough system.

3.3 HYDRAULIC MINING DEBRIS

As tidal marshes were lost through diking, new wetlands were being created through increased sedimentation. The most dramatic changes occurred during the period of hydraulic mining for gold in the Sierra Nevada (1855-1884). Large water guns were used to wash overburden and gold-containing deposits through sluiceways. The sediments flowed into streams and rivers, smothering fish hatchery areas, interfering with navigation, and causing extensive flooding by raising the river bed above the natural levees. The fine sediments reached Suisun and San Pablo Bays causing widespread shoaling (Gilbert 1917). Court injunctions brought by farmers stopped the practice, but sediments probably continued to accumulate in the bay through the early 20th century. Smith (1965) and Krone (1979) estimated sediment accumulations during the period 1870-1950 based on bathymetry changes in each basin. Approximately 49 x 10^6 m^3 of sediment accumulated in Suisun Bay between 1870 and 1896, and 138 x 10^6 m^3 accumulated in San Pablo Bay. This compares to a net erosion in Suisun Bay of 3.6 x 10^6 m^3 in the most recent period (1923-1950) and a slight accumulation of 13.2 x 10^6 m^3 in San Pablo Bay. Thus, recent deposits amount to only 10% of that during the hydraulic mining period.

The amount deposited during the hydraulic mining period averaged 6.9 x 10^6 m^3/yr. This is the same order of magnitude as present day dredging operations (8 x 10^6 m^3/yr)(Sustar 1982). The primary difference is that dredge spoil is deposited in deep areas of the bay whereas the hydraulic mining debris accumulated around the edges. Atwater et al. (1979) estimated that approximately 75 km^2 of new tidal marsh were created during this period including large portions in Grizzly Bay (in Suisun Bay), Mare Island, and the western edge of San Pablo Bay. Approximately 35 km^2 of this "new" marsh have since been diked.

3.4 WATER DIVERSION

As rapidly as dikes were erected around wetlands and as hydraulic mining debris accumulated in the bay, freshwater sources for the bay and its marshes were being diverted. Irrigation water for agriculture and domestic water for cities justified the development of extensive water management systems during the early part of the 20th century (Kahrl 1978). Prior to 1915, San Francisco had extended its water supply to the streams of the Sierra Nevada via the Hetch Hetchy aqueduct. During the 20's and 30's, other cities and regions expanded their water supply systems through importation of upstream sources (East Bay Municipal Utility District: Mokelumne River) and development of ground water recharge systems (San Jose-Santa Clara). The years during and following WW II saw the completion of the most ambitious program in California water development. The Central Valley Project (CVP) was constructed by the US Bureau of Reclamation and largely completed in 1943. The CVP involved construction of large dams (including the Shasta Dam) on the headwaters of the Sacramento and delivery of water via the Delta-Mendota Canal to the west side of the San Joaquin Valley. The California Water Project was constructed by the state during the period 1960-70 and includes Oroville Dam and the California Aqueduct which supplies water to southern California as well as the San Joaquin Valley and several coastal valleys. Both projects divert water that would otherwise flow into San Francisco Bay.

The net result on water flow into the bay has been two-fold. Total annual flow has been reduced due to diversion, and seasonal variation in flow has been reduced due to dams and storage (Chadwick 1982). Pre-1850 delta outflow probably averaged 36 km^3/yr and by 1978 had been reduced by 44% to 20 km^3/yr (Russell et al. 1982). Summer flows are now the same or higher than historic flows (except during periods of severe drought) and have reduced the occurrence of salt water intrusion into the delta. The effect on tidal marshes has been a reduction in high winter flushing flows, reduced summer variability in salt intrusion into brackish and freshwater marshes, and an overall reduction in sediment load (Russell et al. 1982). It is likely that further water development will result in more frequent low total annual flows. Between 1922 and 1971, total annual flows less than 12 km^3 occurred only 4% of the time whereas by the year 2000 such annual flows may occur 60% of the time depending upon the level of water facility construction (Chadwick 1982).

The drastic reduction in total freshwater input will have a significant impact on salinity patterns in Suisun Bay and its marshes. The current brackish wetlands (both tidal and managed) are highly valued as wildlife habitat (BCDC 1976). Extensive water diversion and management projects are proposed to provide freshwater from sources further upstream and from wastewater discharge (California Dept. of Water Resources [DWR] 1982). Tidal wetlands not included in this project are likely to become more saline, especially in the Carquinez Straits and northern San Pablo Bay area. In addition, total sediment loading to the bay will also be reduced by as much as 64% by the year 2020 (Krone 1979). A portion of these sediments are deposited in marshes so that they maintain their elevation with respect to rising sea level, and a portion forms new shoals for plant colonization. The estimated reduction in sediment supply could result in greater erosion and loss of tidal marsh habitat.

Some of the diverted water does enter the bay as sewage effluent. Current amounts of point source discharge total 0.70 km^3/yr or about 3% of the delta outflow (Russell et al. 1982). This percentage is much less in winter and rises in the summer when delta outflow declines. Former salt marshes along Guadalupe, Alviso, Coyote, and Mud Sloughs in the south bay have been converted to brackish marshes due to year-round discharges from sewage treatment facilities (R. Lowe, pers. comm.).

In addition, total nitrogen and phosphorus loadings from treated sewage effluent amount to 21 and 10×10^3 tons/yr, respectively, as compared to that from delta outflow at 13 and 2.4×10^3 tons/yr, respectively. Since nitrogen is often cited as a limiting nutrient for marsh plant growth (Valiela and Teal 1974), the effluent may be stimulating marsh production. Although detailed experiments on nutrient uptake by bay tidal marshes have not been completed, numerous agencies have suggested or are planning projects to recycle treated effluents through wetlands (Hall 1982). An additional source of nutrients, and possibly agricultural chemicals, may arise from a plan to discharge agricultural drain water into Suisun Bay from the Central Valley. This project, the San Luis Drain, may add as much as 9.5×10^3 tons/yr of nitrogen, a 25% increase over the current total annual input.

3.5 CURRENT STATUS

The summation of all of these modifications to San Francisco Bay and its tidal marshes is an environment much different than that of 1850. Ninety-five percent of the tidal marshes have been diked or filled. Nevertheless, many of the diked areas retain some marsh characteristics (Table 2). Factors such as elevation, seasonal ponding of rainwater, amount of tidal exchange, and sediment salinities affect the type of wetland which remains and its ecological functioning. Some diked wetlands may be extremely stressed and barren while others are important habitat for rare and endangered species which have been displaced from their preferred tidal habitats. The largest diked wetland, the Suisun Marsh, is a significant waterfowl habitat within the Pacific flyway system (Skinner 1962). Numerous ecological values have been attributed to diked wetlands (eg. wildlife habitat, buffers, diversity, productivity, wastewater treatment) based on their similarities to tidal marshes (Madrone Assoc. et al. 1982). Yet, few studies other than bird observations have been conducted to compare diked with tidal marshes. Thus, little empirical evidence is available to support these assumed similarities. Such research is especially important in light of continued pressure to develop diked wetlands and to mitigate development through restoration of tidal marshes or mudflats.

The remaining tidal marshes of San Francisco, San Pablo, and Suisun Bays are scattered in isolated pockets or form linear strips along sloughs or bay-front dikes (Table 3). They range in size from a few hectares to over 1300. The largest contiguous marshes are located in Suisun Bay and along the Petaluma River. In addition, a complex mosaic of salt and brackish marshes is located along the Sonoma and Napa River systems. The central bay area is characterized by relatively small tidal wetlands bordered by dikes, steep hills, or urbanized areas. South bay has extensive tidal marshes along the outboard portions of diked saltponds as well as a few preserved or restored wetlands. Brackish marshes are

Table 2. Areas of diked lands which have retained some marsh characteristics usually on a seasonal basis only. Habitat classification based on dominant vegetation type. Area in km^2 (adapted from BCDC as adopted October 21, 1982).

County	Salt marsh	Brackish marsh	Freshwater marsh	Total
Alameda	8.29	-	1.87	10.16
Contra Costa	1.80	1.71	0.42	3.93
Marin	3.82	2.54	0.12	6.48
Napa	-	0.68	-	0.68
San Mateo	0.89	0.10	-	0.99
Santa Clara	7.62	0.68	-	8.30
Solano	1.30	0.13	-	1.43
Sonoma	1.21	-	-	1.21
Total	24.93	5.84	2.41	33.18

extending along sloughs which carry treated effluent in the extreme southern portion of the bay.

The urbanization of the bay area in the post-WWII era has encroached substantially on the remaining tidal wetlands. Cities, subdivisions, and highways have been built regardless of geologic hazards or environmetal concerns (Josselyn and Atwater 1982)(Figure 8). The most fundamental problem relates to the deformation of soft bay mud under both static (structural foundations) and accelerating (earthquakes) loads. Intertidal elevations in areas adjacent to construction sites can be increased substantially due to the displacement of bay mud and formation of mud waves (Josselyn and Atwater 1982). During earthquakes, the stability of buildings and dikes constructed on bay mud is threatened by liquefaction. Liquefaction is a phenomenon that requires saturated sand lenses between relatively impervious (clayey) strata. Buildings founded on deep bay mud suffer during earthquakes because of the mechanical properties of the deep saturated clay gel.

Another effect of urbanization, overdrafting ground water supplies, can cause subsidence of tidal wetlands as has occurred in Palo Alto (Poland 1971).

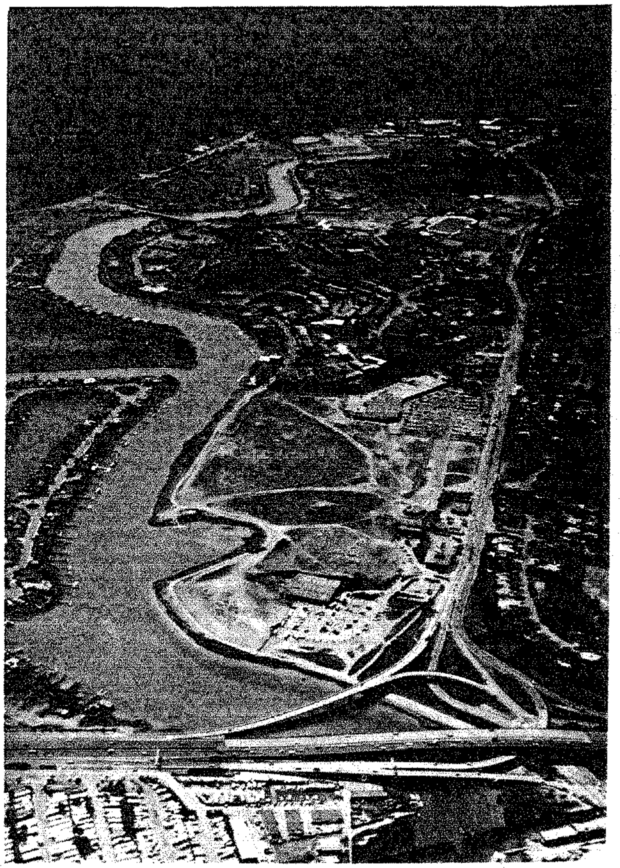

Figure 8. Aerial photograph of Corte Madera Creek showing various developments on former salt marsh.

Table 3. Listing of major tidal marshes of San Francisco, San Pablo, and Suisun Bays. Listing adapted from Shellhammer and Harvey (1982) and BCDC (1982). Other names may apply to these areas (R. Lowe, pers. comm.). Acreage from Shellhammer and Harvey (1982) indicated by a; or estimated from tidal wetland as mapped by BCDC (1982) indicated by b. Acreage only approximate and may include some diked land with restricted tidal flow. Total acreage higher than Atwater et al. (1979) due to inclusion of restored and some diked lands in table. Management authority given for major agency only; others may share in ownership/management. Private holdings or claims not indicated. DGF = Calif. Dept. Fish and Game; USFWS = U.S. Fish and Wildlife Service. References refer to studies discussed in profile.

Number	Name/County	Habitat type	Size	Management/Comments	References
1	Richardson Bay/Marin	Salt marsh/ tidal flat	23^a	Under review in Richardson Bay plan	Shellem and Josselyn (1982)
2	Muzzi Marsh/Marin	Salt marsh	55^a	DFG/Diked land restored to tidal action	Faber (1980)
3	Corte Madera Ecological Reserve/Marin	Salt marsh	39^a	DFG/Clapper and black rail habitat	Evens and Page (1983) Chan and Hulberd (1978)
4	Corte Madera Creek/ Marin	Salt marsh	25^b	Includes Creekside and Pickleweed Parks	
5	China Camp State Park/ Marin	Salt marsh	110^b	Calif. Parks and Rec.	Hopkins and Parker (in press)
6	Gallinas Creek south/ Marin	Salt marsh	46^a		
7	Gallinas Creek north/ Marin	Salt marsh	183^a	Includes McInnis County Park	
8	West San Pablo Bay/ Marin	Salt marsh	62^a	USFWS/Outboard of diked wetlands	
9	Novato Creek/Marin	Salt marsh/ slough	114^a	Clapper rail breeding population	

(Continued)

Table 3. Continued.

Number	Name/County	Habitat type	Size	Management/Comments	References
10	Black John Slough/ Marin	Salt marsh/ slough	344^a	Restoration planned for adjacent diked land	
11	Petaluma River/ Marin, Sonoma	Salt marsh	92^a	Outboard of diked agricultural land	
12	Petaluma Marsh Wildlife Area/Sonoma	Salt/brackish	812^a	DFG	Balling and Resh (1982, 1983a, b)
13	Petaluma Marsh north/ Sonoma	Salt/brackish	412^a	Estensive upper transition zone	
14	Midshipman Point/ Sonoma	Salt	27^b		Cameron (1972)
15	North San Pablo Bay/ Sonoma	Salt	540^b	USFWS	Mahall and Park (1976a, b, c)
16	North San Pablo Bay sloughs and creeks/ Sonoma, Napa	Brackish	$1,347^a$	Tidal marsh surrounded by salt ponds, diked agricultural land	Pearcy et al. (1981) Madrone Assoc. (1977)
17	Southhampton Bay/ Solano	Salt/brackish	68^a	Calif. Parks and Rec./ Invasion of cordgrass in dry years	
18	Joice Island south/ Solano	Brackish	265^a	DFG/Outboard of diked lands	
19	Joice Island north/ Solano	Brackish	$1,289^a$	DFG	
20	Suisun and Peytonia Sloughs/Solano	Brackish	612^b	DFG	Moyle et al. (1982)
21	Hill Slough/Solano	Brackish	42^b	DFG	

(Continued)

Table 3. Continued.

Number	Name/County	Habitat type	Size	Management/Comments	References
22	Grizzly and Honker Bays/Solano	Brackish	274[b]	DFG/Outboard of diked lands	
23	Montezuma and Nurse Sloughs/Solano	Brackish	219[b]		
24	Grizzly Island/Solano	Brackish	349[b]		
25	Roe Island/Solano	Brackish	102[b]	US Navy	
26	Ryer Island/Solano	Brackish	163[b]		
27	McAvoy/Contra Costa	Brackish	182[a]		
28	Port Chicago/Contra Costa	Brackish	111[a]	US Navy	
29	Avon and Hastings Sloughs/Contra Costa	Brackish	398[a]	US Navy/Portion set aside for harvest mouse	
30	Point Edith/Contra Costa	Brackish	166[a]	DFG/Used as mitigation bank	
31	Martinez/Contra Costa	Brackish	192[a]	80% Calif. Fish and Game	
32	Martinez Shoreline Park/Contra Costa	Brackish	11[b]	East Bay Regional Park	
33	San Pablo and Wildcat Creeks/Contra Costa	Salt	202[a]	Possible oil refinery/ Dump impacts	
34	Hoffman Marsh/Contra Costa	Salt	14[a]	High impact from traffic	Murray and Horne (1979)
35	Emeryville Crescent/ Alameda	Salt	51[a]	Features urban sculpture activity	

(Continued)

Table 3. Concluded.

Number	Name/County	Habitat type	Size	Management/Comments	References
36	San Leandro Bay/ Alameda	Salt	27^a	East Bay Regional Parks	
37	Hayward Shoreline/ Alamdea	Salt	100^a	East Bay Regional Parks/ Restored to tidal action 1980	Niesen and Josselyn (1981) Buchholz (1982)
38	Mount Eden and Alameda Creek/Alameda	Salt	114^a		
39	Pond 3/Alameda	Salt	44^b	Alameda Flood Control District/Restored to tidal action 1976	Mason (1976) Newcombe and Pride (1976)
40	Dumbarton Point north/ Alameda	Salt	33^b		
41	Dumbarton Point and Newark Slough/Alameda	Salt	407^b	Headquarters San Francisco Bay National Wildlife Refuge; USFWS	
42	Mowry Slough/Alameda	Salt	235^b	USFWS/Seal habitat area	Fancher (1979)
43	South San Francisco Bay sloughs/Alameda, Santa Clara	Salt/brackish	393^b	USFWS/Impacted by treated sewage effluent	
44	Mountain View, Palo Alto Bay lands/San Mateo	Salt	145^a	Education center	Applegarth (1938) Felton (1978) Lane (1969)
45	Greco Island/San Mateo	Salt	346^b	USFWS; private	
46	Bair Island/San Mateo	Salt/diked	163^a	Impoundment bird habitat	
47	Belmont Slough/San Mateo	Salt	94^b		

Pacific cordgrass (Spartina foliosa) has apparently invaded a former pickleweed (Salicornia virginica) habitat as a result of such lowered elevations (Atwater *et al.* 1979). Higher than normal sea level may also cause vegetation changes.

The proximity of industrial activity to the bay increases the likelihood for petroleum spills and hazardous waste contamination. The impacts are usually chronic; however, direct spills into tidal marshes do occur. Vector control activities, largely to reduce mosquito breeding areas, have had a direct impact on tidal and diked marshes through ditching to increase tidal circulation. Pesticides are also frequently applied to marshes. Thus, the tidal marsh community which remains can hardly be classified as pristine. It has been shaped for over 100 years by human interference and is likely to be further influenced by the urbanization of San Francisco Bay area.

CHAPTER 4

GEOPHYSICAL ATTRIBUTES OF SAN FRANCISCO BAY AND ITS TIDAL MARSHES

4.1 MACROCLIMATE

Sunny California: a climate typified by clear, summer days and mild, cool winters. The climate is classified as Mediterranean, the normal pattern consists of two seasons. The rainy season extends from late October to mid-April, a period during which 94% of the annual precipitation falls. The dry season is influenced by cool marine air along the coast and hot, dry weather inland. The two seasons vary in length and intensity each year, however, a "normal" year in the bay area has a mean monthly temperature ranging from 12° to 17°C and an annual precipitation of 48 cm (Conomos 1979). It is rare that a normal or average year occurs as weather patterns in the state follow extremes from drought to almost continuous winter rainfall. Such variation is attributed to large scale changes in the water temperature of the Pacific and is only beginning to be understood.

The proximity of the Pacific Ocean, the local topography, and the bay itself contribute to further variation in the local climate. For example, precipitation (Figure 9) is strongly affected by the coastal mountain ranges, with peak mean annual precipitation of 130 cm falling on Mt. Tamalpais in the north bay and 110 cm on the Santa Cruz Mountains in the south bay (Rantz 1971). Annual rainfall on the bay surface is much less, averaging between 35 and 50 cm. Wetlands along Corte Madera Creek receive upwards of 75 cm per year due to the proximity of Mt. Tamalpais. On the other hand, the relatively low topography around Suisun Bay has little influence on rainfall and the yearly total is less than 40 cm. The amount of rain falling within the watersheds of local creeks and rivers may affect wetlands in the immediate region of discharge. Portions of the watershed of the Napa River receive up to 100 cm of rainfall annually, and that of Coyote Creek up to 50 cm. Harvey _et al_. (1982) suggest that brackish marshes were quite common at the mouths of the Napa River, Guadalupe River, Alameda Creek, and Corte Madera Creek. Large springs along the east bay hills north of the Little Coyote Hills may have supported some fresh and brackish marshes. Many creeks and streams, however, were probably dry washes during the summer and fall and and lacked sufficent flow to support brackish marshes.

Of equal importance to the water budget of tidal wetlands is the high rate of evaporation during summer months. The annual evaporation rate averages 120 cm which yields a net bay-wide evaporative loss of 72 cm when the average annual precipitation is subtracted (Selleck _et al_. 1966). This climatic feature was responsible for the natural crystallizing ponds once present in the south bay and encouraged the extensive development of the salt production industry in south bay and along the Napa River. This industry currently occupies 140 km^2 along the bay shore, much of it within historic wetland habitat. Evaporation loss is also influenced by local weather patterns with maximum rates occurring in regions of higher insolation, air temperature, and persistent winds. Wetlands in the south bay and in Suisun Bay experience the greatest evaporative losses. The marsh vegetation itself also contributes to evaporative loss through evapotranspiration. Yearly total loss from freshwater marsh vegetation (tules (_Scirpus_) and cattails (_Typha_) is estimated at 140 cm

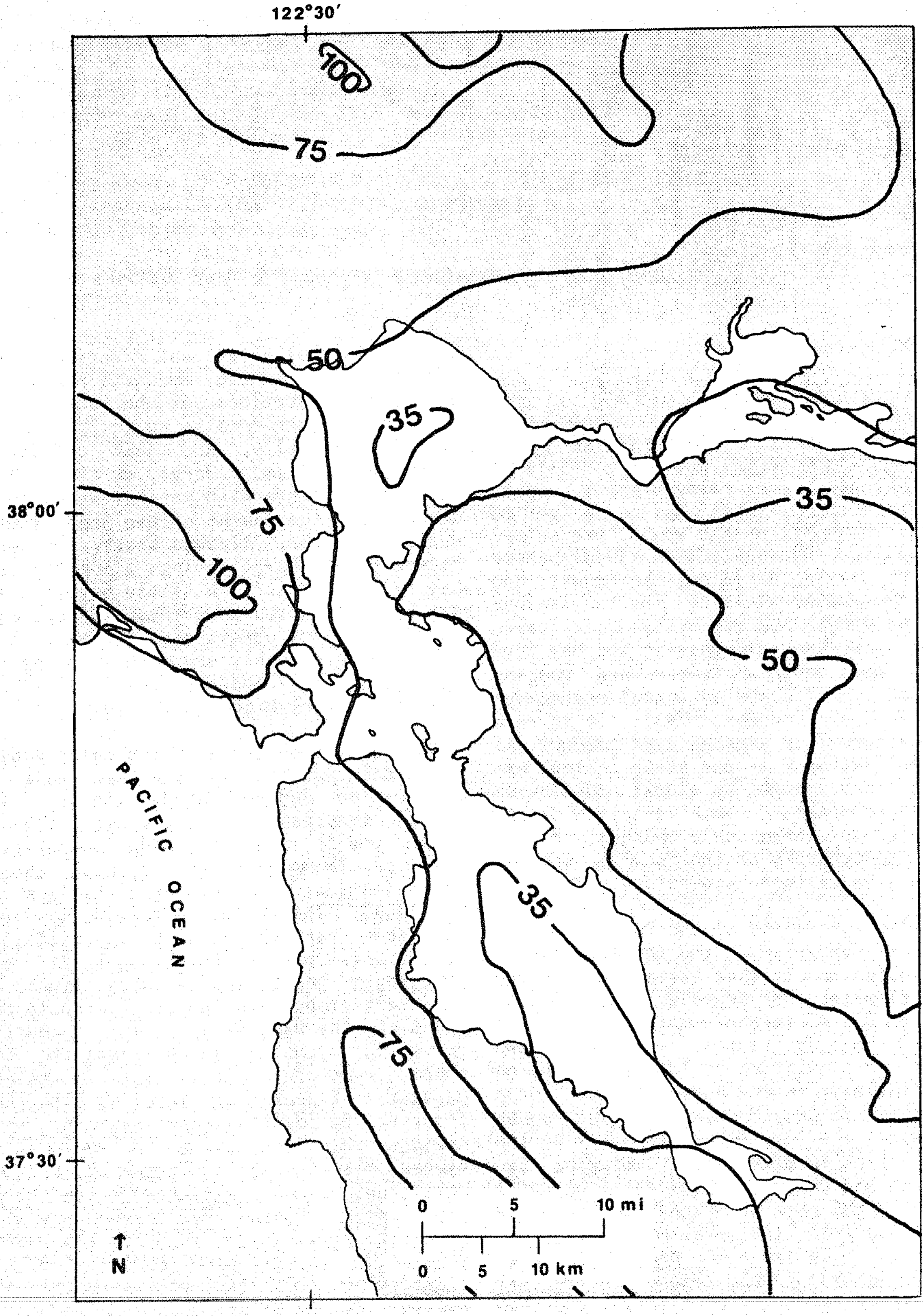

Figure 9. Annual precipitation in San Francisco Bay region (from Rantz 1971). Totals given in centimeters.

in the central bay to 180 cm in Suisun Bay (Blaney and Muckel 1955). Estimates for salt marsh vegetation are less, amounting to 94 cm for saltgrass (Distichlis spicata). The balance between rainfall and evaporative losses is easily affected by yearly weather variations which can result in differences in sediment and water salinity in wetlands.

The atmospheric interactions between the continental land mass and the Pacific Ocean influence two other weather phenomena: local prevailing winds and low clouds or fog. Prevailing winds are strongest in the summer due to the semipermanent high pressure area over the eastern Pacific Ocean. At the same time, sunny skies over California, Nevada, and Arizona cause strong surface heating. The low pressure cell thus created results in strong horizontal pressure differences and is responsible for the prevailing westerly winds. The air flow extends to an altitude of 600 m and therefore is often restricted to relatively narrow passages: the Golden Gate, the San Bruno Gap, the Petaluma Valley, and the Carquinez Straits. For example, Figure 10 shows the increase in wind speed at the San Bruno Gap (measured at the San Francisco Airport) as compared to less restricted areas further inland. Temperatures are cooler in more wind-swept areas compared to wetlands protected by the coastal mountains. The fetch across the bay affects the height of wind-generated waves. The observed erosion along the eastern shore of the south bay (Atwater et al. 1979) may be partially attributed to waves produced over a 20-km fetch (Figure 11). The shifting of the East Pacific High southward in the winter exposes the bay area to the successive passage of cold fronts. Despite strong southeasterly winds which accompany these storms, average wind speeds are lowest during winter months.

Low cloudiness or fog is a common condition in the bay area. In summer, it is formed offshore when moisture-laden air passes over the cold ocean and condenses. The fog moves inland at night as the interior land mass cools and retreats to the

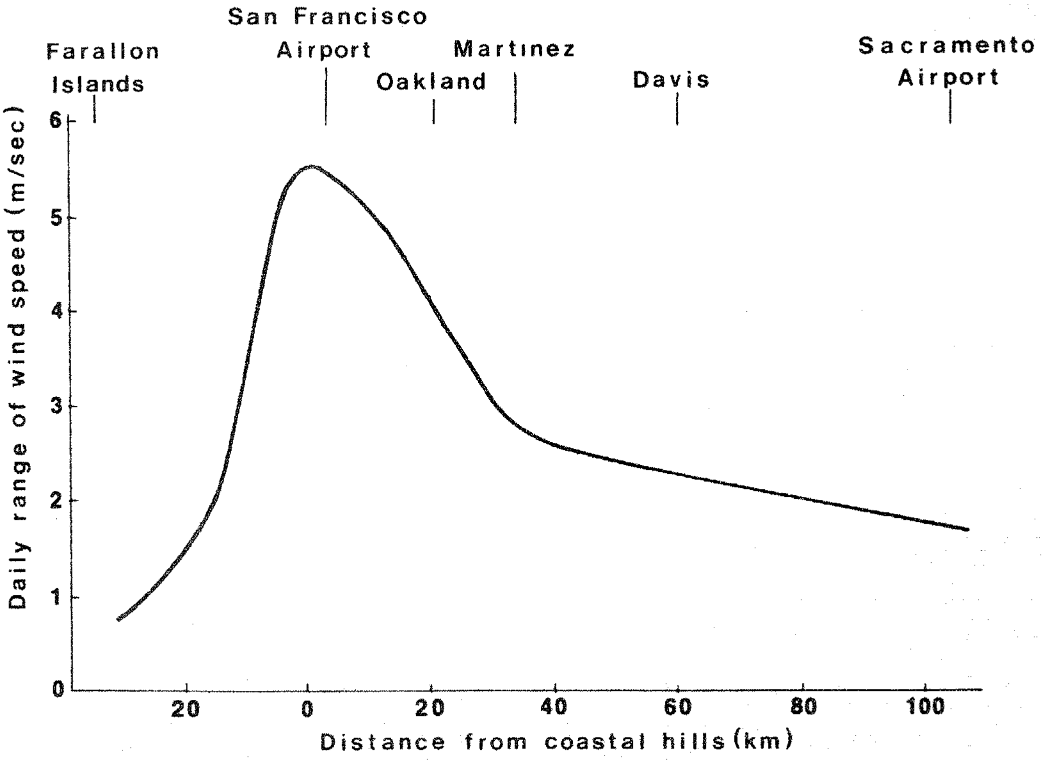

Figure 10. Daily range of wind speed as related to distance from coast and to local topography (from Root 1960).

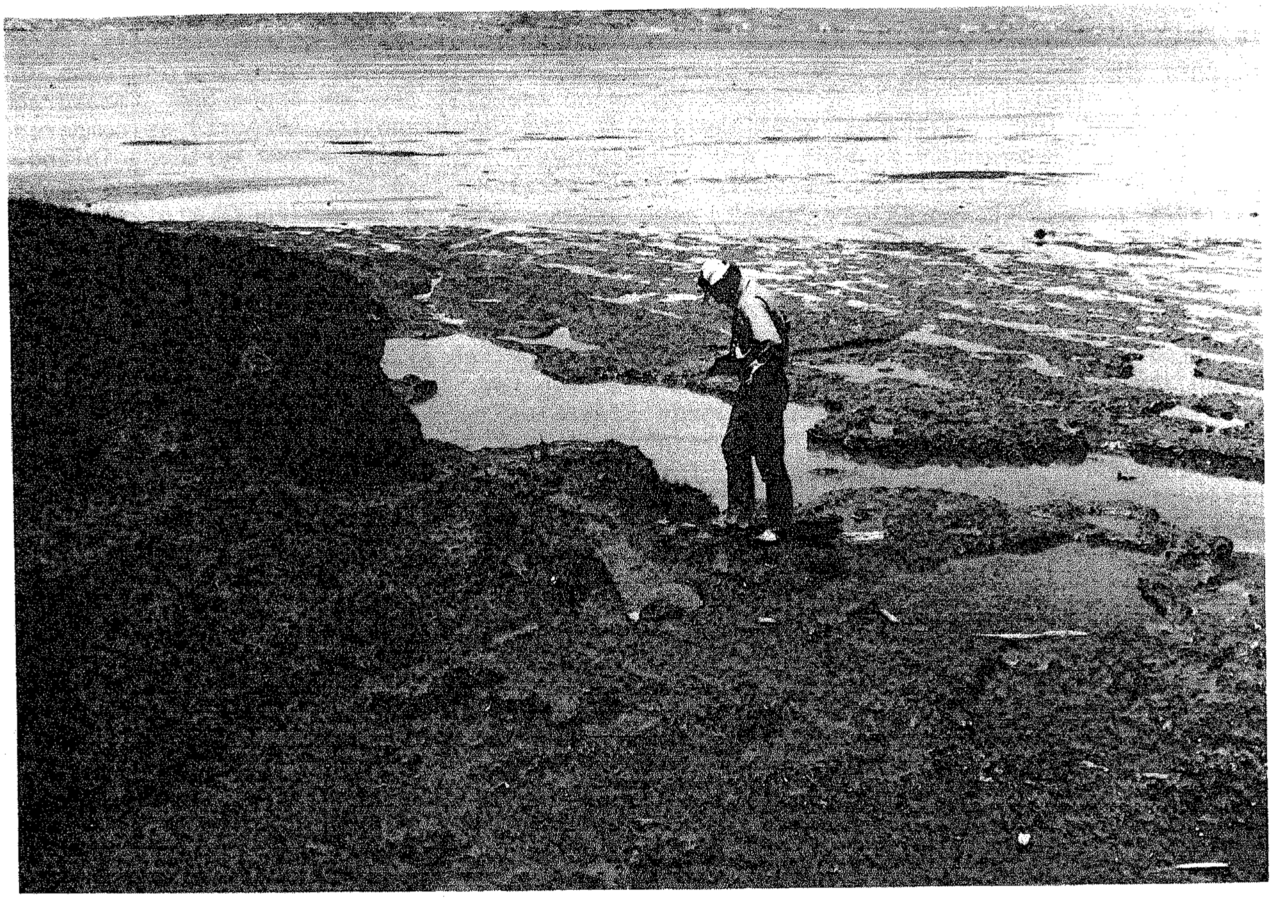

Figure 11. Erosion of tidal marsh shoreline in southern San Francisco Bay. Note sediment blocks scattered on mudflat. Clay bank also colonized by the burrowing isopod, Sphaeroma quoyana.

coast during the day. The amount and duration of the fog layer can vary daily affecting overall temperatures and amount of insolation. While summer fog is a coastal phenomenon and usually lifts by midday, winter fog or tule fog occurs over inland areas and is usually more persistent (Miller 1967). This type of fog is caused by radiation to the colder ground and condensation of the water vapor. Because of the weaker winds in winter, this type of fog may persist for days and can become extremely dense. It occurs most frequently over Suisun Marsh and the delta area.

In summary, the climate of San Francisco Bay varies locally within the overall Mediterranean pattern. The south bay has less rainfall and higher evaporative rates than the north bay. Therefore, one would expect sediment salinities to be higher in south bay wetlands. Prevailing winds impact eastern and northern shorelines with wind-generated waves and increase shoreline erosion rates. The incidence of fog may affect productivity by reducing solar radiation, however, no field measurements are available to estimate photosynthetic response under cloudy and full sun conditions.

4.2 MICROCLIMATES

Just as the overall climatic pattern is affected by regional and local conditions, the wetland environment can affect the microclimate of the plants and animals growing there. In an analysis of the energy budget of a south San Francisco Bay salt marsh, Felton (1978) studied the radiation, temperature and humidity profiles, and energy exchange beneath Pacific cordgrass (Spartina foliosa) and pickleweed (Salicornia virginica) canopies. The most significant factor affecting the microclimate was the periodic replenishment of surface and subsurface water by tidal inundations. Sediments with high moisture content have a higher heat storage capacity and therefore tend to moderate temperature extremes. In addition, the differences in canopy structure affected radiant energy transfer between the marsh surface and the surrounding air mass. The fluxes of energy within cordgrass and pickleweed in south San Francisco Bay are given in Figure 12. The more open nature of the Pacific cordgrass canopy resulted in a greater net radiation flux (the difference between incoming solar radiation (Q_T) and outgoing radiation = Q_N). Due to the higher moisture content of sediments at lower elevations, a greater percentage of the net radiation was absorbed by the sediment beneath Pacific cordgrass than beneath pickleweed (Q_G). The air temperatures (Q_H) were therefore lower in the Pacific cordgrass marsh. Latent heat exchange due to evaporation (Q_E) was less in the Pacific cordgrass than the pickleweed as a result of reduced air temperature and lower transpiration rates in cordgrass. All differences were more pronounced in summer when vegetation canopies were more developed. Tidal inundation dampened diurnal air temperature ranges and gradients. It also contributed to the net export by day of heat from the marsh to the bay waters and import by night.

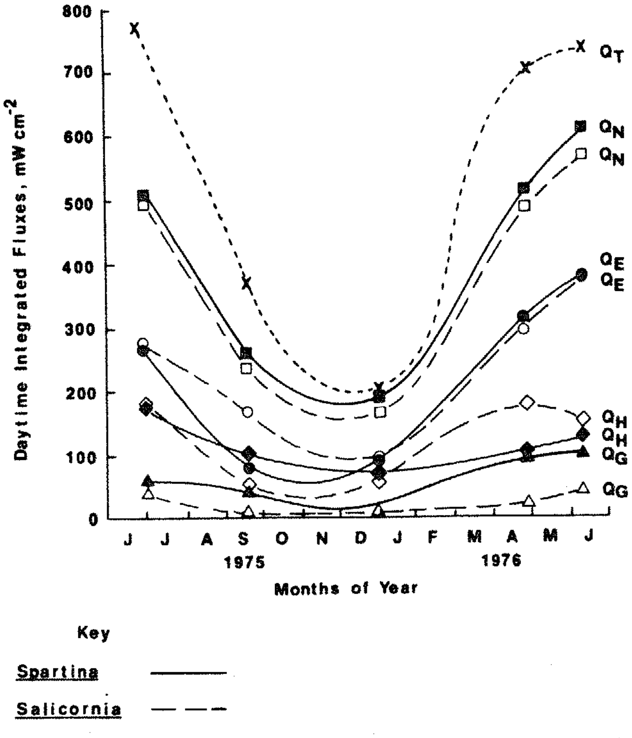

Figure 12. Energy fluxes in two salt marsh canopies in southern San Francisco Bay: one dominated by Pacific cordgrass (Spartina foliosa) and the other by pickleweed (Salicornia virginica). Symbols are described in text (from Felton 1978).

Such differences in radiation flux are significant when considering physiological and ecological processes related to primary production in marshes. Zedler (1980) has shown that algal mat production in Tijuana Estuary salt marsh is somewhat less than Pacific cordgrass and equivalent to jaumea (Jaumea carnosa). Productivity was nearly always lower under dense compared to open canopies. Based on the net radiation measurements of Felton (1978), algal mat production beneath pickleweed should be less than beneath cordgrass.

Felton (1978) also estimated the effects of the tidal marshes on local climate. The small tidal marsh she studied in south San Francisco Bay had only limited influence on humidification of air masses, slight frictional retardation of the wind, and a dampening of temperature extremes in the marsh itself and a few kilometers downwind. On a regional scale, one would expect that the loss of tidal marshes to urbanization has contributed to reduced humidity and greater temperature extremes.

4.3 SURFACE WATER FLOW INTO THE BAY AND ITS TIDAL MARSHES

Freshwater flows into San Francisco Bay have a critical influence on tidal wetland distribution in San Francisco, San Pablo, and Suisun Bays. Ever since Mall (1969) showed the relationship between soil salinity and marsh plant distribution, extensive studies have been undertaken to provide better management of freshwater flow to preserve the Suisun Marsh (California State Water Resources Control Board [CSWRCB] 1978). Surface freshwater flows into the bay include the

Sacramento-San Joaquin river system, the local drainage system, and water users. Groundwater sources are minor due to the impermeable bay mud underlying most tidal marshes.

The drainage basin of the San Francisco Bay system covers over 40% of the land area of California, or 163,000 km². Ninety percent of total surface flow enters the bay via the Sacramento and San Joaquin Rivers. Outflow from these rivers into the bay is termed delta outflow because of the confluence and mixing of the two rivers within a low lying delta area immediately east of Suisun Bay. Historically, delta outflow has varied considerably due to yearly variations in rainfall and snow pack thickness. During one particularly wet year (1862), fresh water flowed outward through the Golden Gate for 10 consecutive days and during the drought of 1931, salt water extended almost to Sacramento. Presently, delta outflow is controlled by numerous dams and pumping stations operated by state and federal agencies and can be estimated with some precision (Conomos 1979).

Between 1906-1977, total annual outflow has ranged between 7.7 x 10^9 m^3 to 5.8 x 10^{10} m^3 with a median of 2.8 x 10^{10} m^3 (CSWRCB 1978). If flow were continuous, this would amount to a discharge of approximately 880 m^3/sec. The pronounced seasonal period of rainfall (snowfall at higher elevations) followed by dry weather creates a cyclic pattern of delta outflow (Figure 13). Discharge is highest from January to April when direct runoff and snowmelt contribute to outflow and is lowest during the dry summer months. The seasonal variation in precipitation can result in a 10-fold difference in outflow when flood flows through the Yolo Bypass are considered (Conomos 1979).

The primary influence of delta outflow is on water salinities. Water salinities in Suisun and San Pablo Bays are directly affected by changes in delta outflow whereas the south bay is only influenced during extremely high flows. South bay salinities usually remain above 25 ppt even during normal winter outflows. The strong estuarine gradient in the north bay region influences the distribution of

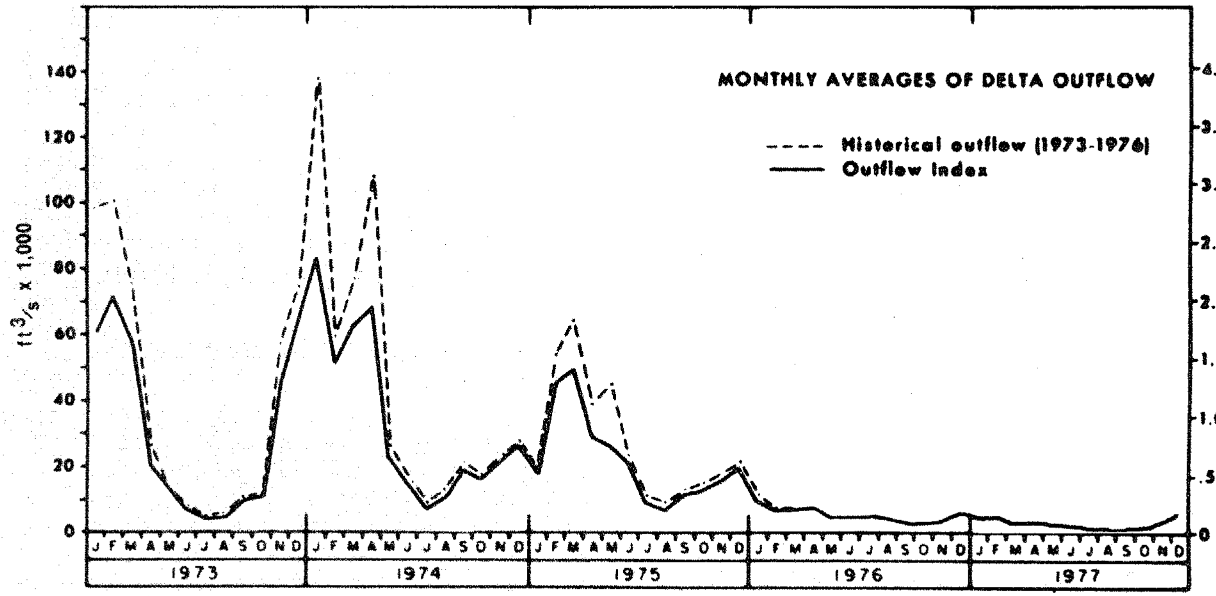

Figure 13. Monthly averages of delta outflow for the years 1973-1977. Historical outflow includes flood flows through Yolo Bypass, outflow index is standard calculation of delta outflow based on estimated flows in Sacramento and San Joaquin Rivers only. Years 1973-74 considered "normal" water years; 1976-77 considered drought years.

wetland vegetation, fresh and brackish water plants dominating Suisun Bay and salt marsh plants throughout San Pablo and central San Francisco Bay.

The local drainage basin has a total area of 8974 km², about 6% of the Sacramento-San Joaquin drainage basin (Selleck et al. 1966). Seven of the largest basins are described in Table 4. Flows in local rivers and creeks are highly seasonal and regulated, particularly in the south bay. Compared to delta outflow, local stream discharge is minor and affects only wetlands along the streams themselves. Except for the extensive wetland system along the Petaluma River, most of the local riparian wetlands have been eliminated by development and flood control projects.

Table 4. Gaged stream flow from seven largest drainage basins surrounding San Francisco Bay (from Selleck et al. 1966).

Stream	Region	Basin size (km^2)	Mean flow (m^3/sec)
Alameda Creek	South	1,800	0.61
Napa River	San Pablo	1,080	3.22
Coyote Creek	South	914	1.91
Sonoma Creek	San Pablo	396	1.85
Guadalupe River	South	383	-
Petaluma River	San Pablo	370	0.48
Pacheco Creek	Suisun	357	0.74

Discharge from water users such as industrial, residential, and agricultural sources accounted for approximately 3% of total inflow in 1978 (Russell et al. 1982). This may increase to 7% by the year 2000. Much of the discharge is from industrial or domestic water users. The water supply is provided from storage capacity in the Sierra and local reservoirs. This disrupts the natural distribution of freshwater by diverting upstream sources and discharging it in either large central bay diffusers or continuous flows through local streams. Under summer conditions in the south bay, freshwater sewage outflow exceeds natural runoff (Conomos 1979) and has resulted in the conversion of salt marsh to brackish marsh adjacent to streams used for discharge.

4.4 TIDAL CYCLES

The tidal cycle in the Pacific Ocean is mixed semidiurnal resulting in two cycles each tidal day (24.84 hr). Tidal heights of the two highs and lows each day differ (Figure 14). The differences are related to the position of the moon; nearly equal tides occur when there is no lunar declination with the earth's equator

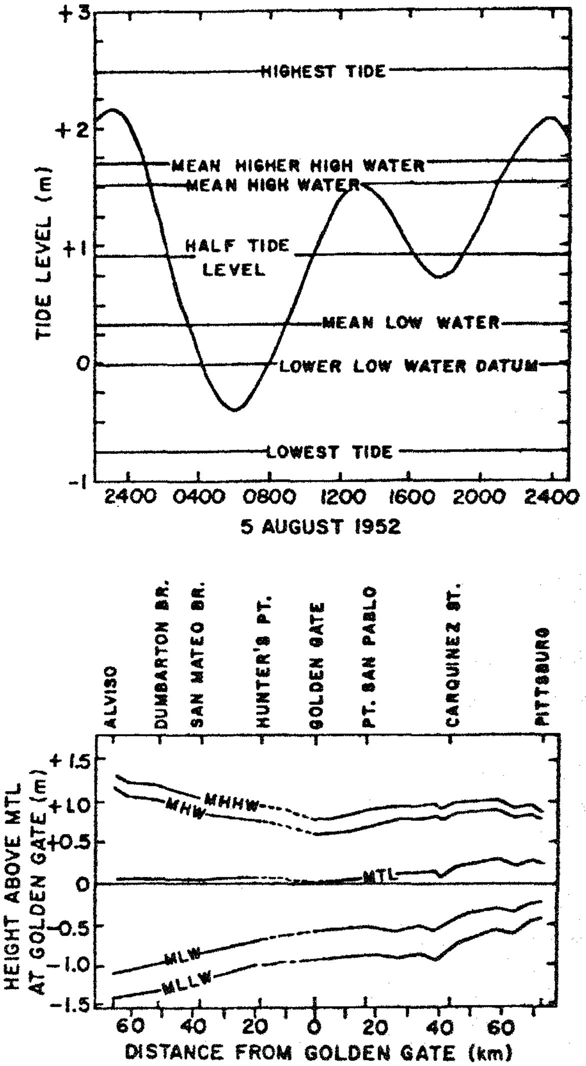

Figure 14. Top: Typical tidal cycle in San Francisco Bay with tidal datums indicated. Bottom: Change in elevations of tidal datums with distance south (left) and north (right) from the Golden Gate. Both from Conomos 1979 as modified from the US Army Corps of Engineers.

and greatest differences occur when the lunar declination is at a maximum (Conomos 1979). Tidal range also varies on a fortnightly cycle. The greatest tidal range (spring tide) occurs during times of the full and new moons and the smallest range (neap tide) occurs during quarter phases. The tidal datums resulting from this cycle are given in Table 5.

Tidal cycles in San Francisco Bay have a number of important effects on tidal marshes: the vertical extent of marsh vegetation, time of submergence and exposure, and tidal flushing. Tidal elevation and range varies with distance north and south of the Golden Gate (Figure 14). The tidal range increases substantially in the south bay (0.9 m greater than at the Golden Gate) affecting both the extent of intertidal mudflats and landward submergence at high tide. Decreasing tidal range and higher tidal datums in relation to National Geodetic Vertical Datum (NGVD) in the San Pablo and Suisun Bays contribute to a narrower and higher wetland configuration.

The time of submergence and exposure in relation to daylight varies seasonally and between basins. Most frequent and longest duration of daylight exposure occurs in the spring in the central bay and in the summer within San Pablo and Suisun Bays. Shellem and Josselyn (1982) found the period of most frequent daytime exposure coincided with the greatest macroalgal production on mudflats adjacent to tidal marshes. It probably also has an influence on microalgal production and rates of evaporation from wetland sediments.

Maximum tidal ranges occur in December-January and again in June. While both periods result in substantial flushing within tidal marshes, the winter tidal range may be heightened by high precipita-

Table 5. Abbreviations and definitions for various tidal datums (from Atwater et al. 1979).

Datum	Abbreviation	Definition
Mean higher high water	MHHW	Average height of the higher of the daily high tides
Mean high water	MHW	Average height of all high tides
Mean tide level	MTL	Plane halfway between mean high water and mean low water, also called half-tide level
Mean low water	MLW	Average height of all low tides
Mean lower low water	MLLW	Average height of the lower of the daily low tides. Adopted as plane of reference for hydrographic surveys and nautical charts of the west coast of the United States
Mean sea level	MSL	Average height of the water surface for all stages of the tide, determined from hourly readings
National Geodetic Vertical Datum of 1929	NGVD	The standard datum for heights across the nation. Formerly called the "U.S. Coast and Geodetic Survey sea-level datum of 1929," and originally determined from mean sea levels at 25 tide stations in the United States and Canada. Generally differs from local sea level so it is best regarded as an arbitrary datum that happens to be close to mean sea level

tion or runoff. A large portion of the detrital material accumulated from the previous growing seasons may be exported during this time. Although no experiments have tested this hypothesis, a large amount of saltmarsh vegetation can be observed floating in the bay during winter months.

4.5 SEDIMENT SALINITY IN TIDAL MARSHES

The concentration of salts in the marsh sediments is determined by numerous hydrologic and biologic factors (Table 6). The primary determinant is the mixing between ocean waters and freshwater flow from the Sacramento and San Joaquin Rivers. Lighter freshwater tends to flow over the denser salt water, but tidal currents and bay bathymetry cause mixing and create a weakly stratified salinity profile (Conomos 1979). A stronger horizontal salinity gradient is present in the north bay whereas the south bay is more uniform. Tidal inundation by various dilutions of ocean water, local climatic processes, and the marsh vegetation itself are responsible for the sediment salinities observed at any one locale.

Rainfall and delta outflow decrease wetland sediment salinities throughout the bay during winter and early spring months. Sediment salinity rises in the summer due to lack of rainfall, reduced delta outflow, increased evaporation, and higher evapotranspiration by the marsh vegetation. Sediment salinity also increases with increasing elevation due to longer periods of exposure and evaporation. Measurements of sediment salinities in marshes can vary depending on elevation and tidal flow in the marsh. Differences in methodology also contribute to difficulties in making comparisons. Table 7 compiles data on sediment salinities. In general, tidal wetlands in the north bay exhibit lower salinities than similar habitats in the south bay (Hayward Landing, Alameda Creek, and Palo Alto). In most cases, salinities in late summer are higher in pickleweed stands than in cordgrass. However, between the north and south bays, cordgrass occupies habitats with a wide range of sediment salinities. Based on these limited data, it appears that sediment salinities in tidal wetlands do not become hypersaline as Zedler (1982) has observed in southern California wetlands.

Table 6. Factors affecting sediment salinities in tidal marshes.

Factor	Increase (+) or decrease (-) salinity in sediments	Seasonal significance	
		Maximum	Minimum
Rainfall	-	Winter	Summer
Evaporation	+	Summer	Winter
Delta outflow	-	Spring	Fall
Local drainage	-	Winter	Summer-Fall
Sewage outflow	-	-	-
Tidal cycles	+	-	-
Evapotranspiration	+	Summer	Winter

Diked wetlands, however, do exhibit periods of hypersaline conditions, even in the brackish Suisun Marsh (Mall 1969). The situation is similar to lagoon systems in southern California where fresh and hypersaline conditions alternate (Zedler 1982). Winter rains reduce salinities in the upper levels of the sediment through percolation and dilution. Summer evaporation brings the trapped salts to the surface and inhibits vegetative growth. The result is a mosaic of vegetation: slightly elevated spots with annual vegetation surrounded by patches of pickleweed (_Salicornia virginica_) pockmarked with expanses of alkali flat with no vegetation.

4.6 SEDIMENTATION AND FORMATION OF DRAINAGE PATTERNS WITHIN TIDAL MARSHES

The formation of tidal marshes along the edges of San Francisco Bay has been dependent on sedimentation. As the rate of sea level rise slowed over the past 6,000 years, the rate of sedimentation has been sufficient to allow the expansion of tidal wetlands over previous tidal mudflats (Atwater _et al_. 1979). The primary source of sediment is the drainage basin of the Sacramento and San Joaquin Rivers which currently supplies 80% to 90% of total annual input. Most alluvial deposits of local streams and rivers have been obliterated by deposits of clay derived from the Sierra and Central Valley drain-

Table 7. Seasonal sediment salinities (ppt) within marshes in the San Francisco Bay region. Numbers taken from graphs or tables given by references. Averages taken for salinity measurements over sediment depth. When several measurements along a transect are given, salinity is from vegetative habitat with 100% cover of species cited. Apparent soil salinity method described by Mahal and Park (1976b). Soil paste is salinity at 100% saturation. Readings given in m-osm/g converted to ppt by multiplying by 29.25. (Cain and Harvey, 1983).

Location	Year	Method	Original units	Species	Jan	Apr	Jul	Oct	Reference
Suisun Marsh (diked wetland)	1963-5	5:1 soil extract	ppt	*Salicornia*	25	28	52	45	Mall(1969)
				Scirpus robustus	15	14	25	32	
Mare Island	1972-3	Apparent soil sal.	m-osm/g	*Salicornia*	-	15	23	31	Mahall and Park(1976b)
				Spartina	-	15	20	28	
Sonoma Creek	1979-80	Apparent soil sal.	ppt	*Scirpus robustus*	7	5	25	25	Pearcy *et al*(1981)
Muzzi Marsh	1982	soil paste	ppt	*Salicornia* (low)	5	10	12	13	Josselyn (unpubl)
				Salicornia (high)	10	5	26	17	
Marin Day School	1982	soil paste	ppt	*Spartina*	6	6	15	16	Josselyn (unpubl)
Hayward Landing	1980	soil paste	ppt	*Salicornia*	12	-	22	12	Perez (1981)
				Spartina	18	-	22	23	
Alameda Creek	1977	Apparent soil sal.	m-osm/g	*Spartina*	-	29	-	32	Cain and Harvey (1983)
Palo Alto	1977	Apparent soil sal.	m-osm/g	*Spartina*	-	34	-	31	Cain and Harvey (1983)

age. Present-day sediment loading is closely correlated with total delta outflow (Krone 1979). The estimated annual average is 3.69 x 10^6 mt/yr from delta outflow compared to 1.13 x 10^6 mt/yr from local streams (Krone 1966). If estimates of water diversion in future years are accurate, sediment loads from the Sacramento-San Joaquin drainage may decrease 60% by the year 2020.

Much of the sediment is deposited in San Pablo Bay during periods of high runoff. During periods of lower flow, greater settling occurs in Suisun Bay. The landward flowing saline bottom currents in the north bay and the increased flocculation of suspended particles in the region of initial fresh and saltwater mixing contribute to an entrapment zone for sediments. The entrapment zone or turbidity maximum is located where surface water is between 1 and 6 ppt, which includes eastern San Pablo Bay, the Carquinez Straits, and western Suisun Bay (Arthur and Ball 1979). Because strong tidal currents maintain channel depths, much of the sediment is deposited along the margins of the bay and in tidal marshes. During the period of hydraulic mining, much of Southampton Marsh was formed adjacent to Carquinez Straits (Gilbert 1917). Resuspension by currents and waves also contributes to eventual deposition in tidal marshes.

The size class distribution of particles in sediments within tidal marsh sediments is similar to that deposited on the bay bottom. It consists largely of fine clays and silts; approximately 60% by weight is in the clay size range and the remaining material is silt (Krone 1962). The depositional environment is important in determining size class distribution in wetlands; i.e. areas of frequent wave action have a lower content of fine particles compared to low energy areas. Nevertheless, clay represents the dominant substrate type in most tidal salt marshes.

The mineral composition of the clay fraction reflects the source regions (Krone 1962, Pestrong 1965). Montmorillonite composes the largest percentage and is derived from the Sacramento-San Joaquin drainage. Illite, or mica, is about half as abundant and is derived from the Coastal Ranges. The percentage of kaolinite is similar to illite. Visually, montmorillonite and illite appear as thin platelets. Kaolinite group minerals include tubular halloysite and platy kaolinite particles. The tight binding of the plate-like minerals when water is removed from the sediments (as when diking wetlands) causes shrinkage and leads to an overall subsidence in elevations (Krone 1982). Once dehydrated, the clays never totally rehydrate and such permanent elevation changes must be considered in wetland restoration planning.

Non-clay components include quartz, shell, organic matter, and iron flocs. The quartz sand component is usually less than 7% except in areas of tidal flushing or strong wave action. Shells are abundant in some wetland deposits, but are restricted to berms adjacent to the tidal marsh. The most abundant shell deposits are located in the south bay and form the basis for a cement industry. Organic matter is low in the few marsh sediments tested. Pestrong (1965) found that sediments underlying pickleweed had the highest organic content (avg 18%), followed by Pacific cordgrass sediments (avg 12%), and the tidal flat (avg 10%). Iron occurs as ferric hydroxide flocs in aerobic surface sediments and ferrous sulphide coating in minerals in anaerobic sediments (Krone 1962).

Rates of sedimentation in tidal marshes vary with sediment supply and elevation. The amount of suspended sediment in the water column is greatest in the north bay. Suisun and San Pablo Bays have suspended particulate concentrations averaging between 25 and 50 mg/l in the winter compared to 10 to 25 mg/l in the south bay (Conomos 1979). Much higher levels of suspended particles can be expected in shallow regions due to resuspension. Krone (1982) states than concentrations typically range from 50 mg/l during calm periods to more than 1000 mg/l during windy periods.

Low-lying areas (shallow ponds) can rapidly fill due to the constant influx of sediment. Converting wetlands to other uses does not decrease sediment supply as many marina and lagoon operators have discovered. In Palo Alto, deposition in the yacht harbor exceeds 60 cm/yr (Krone 1982). Increasing elevation, however, does limit the duration of submergence and hence leads to decreasing sedimentation. The sedimentation rate above mean high water (MHW) elevation is negligible. Unless additional alluvial material is deposited from the upland, tidal marsh sedimentation will reach equilibrium at approximately MHW. As rising sea level floods additional land surface, sedimentation occurs, and the tidal marsh develops landward. Only in regions where sedimentation exceeds the amount needed to keep pace with sea level changes do we see a progression of marshes over tidal flats. Precise descriptions of early wetlands are lacking. The presumption is that the prehistoric marsh topography consisted of broad plains at MHW edged by steeper slopes grading into mudflats and the entire system transected by meandering sloughs of various dimensions (Josselyn and Atwater 1982).

Pestrong (1965) wrote an extensive treatise on drainage patterns in bay tidal marshes. The basic dendritic pattern and meandering nature of the sloughs are very similar to that exhibited by terrestrial streams (Figure 15). The primary difference is the influence of bidirectional tidal flow as compared to unidirectional stream flow. The flood and ebb flows are strong in the main tidal channels with the

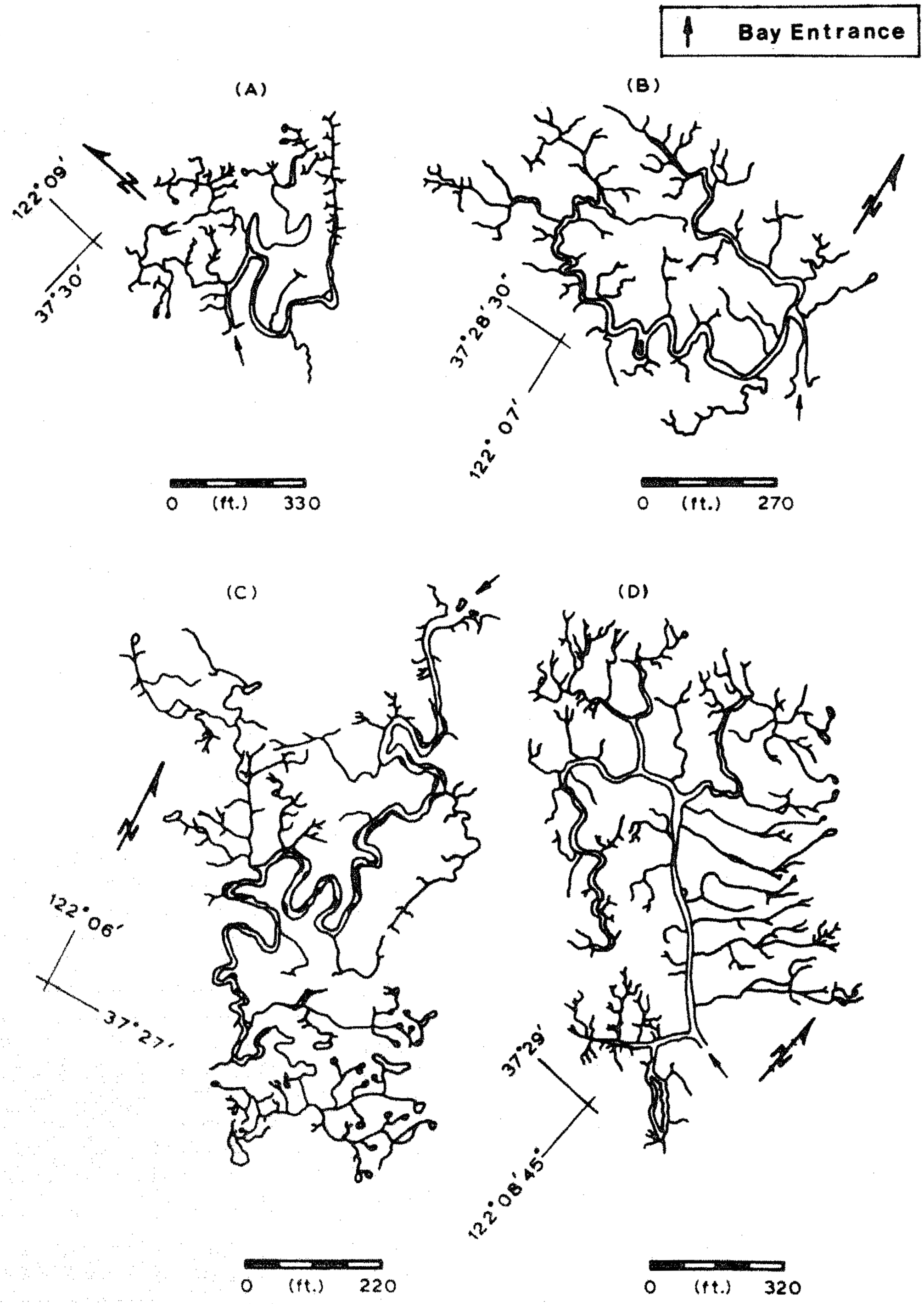

Figure 15. Typical drainage patterns for tidal marsh slough systems in south San Francisco Bay. Arrow denotes bay entrance. Mapped by Pestrong (1965).

ebb usually having the greatest velocity and duration. The smaller channels have significant flows only during the ebb cycle. The flood waters creep slowly up against the channel walls much like water filling a reservoir, as opposed to the accelerating flows of the ebb tides. Greatest sedimentation occurs in the back channels and on the marsh surface itself where vegetation further slows water velocity. As the marsh surface increases in elevation through time, the main tidal channels become more deeply incised in the marsh. Deposition of heavier particles along the top edge of the channel forms a low natural levee (Pestrong 1972). Pickleweed dominates the marsh plain and is easily undercut by tidal flow in the channel. The slumping of this material contributes to the migration of the channel and provides sloping elevations suitable for Pacific cordgrass colonization (Figure 16). Krone (1982) suggests that restoration designs incorporate this natural process by dredging channels with steep sides and larger dimensions than required. Natural sedimentation processes will fill in the sides of these channels providing excellent substrate for cordgrass invasion.

Tidal marshes are generally areas of sediment deposition over time; however, strong wave action can contribute to net loss of sediment. Chan and Hulberd (1978) have documented this process in the Corte Madera Ecological Preserve where wave action created by passenger ferries has undercut pickleweed. The average shoreline retreat along the marsh front was 0.95 m/yr. The introduced burrowing isopod (Sphaeroma quoyana) has also been implicated in contributing to marsh erosion by weakening banks beneath pickleweed (Carlton 1979). Pacific cordgrass has not been proven as effective in stabilizing eroding banks as smooth cordgrass (Spartina alterniflora) (Newcombe et al. 1979).

4.7 RESTRICTED TIDAL FLOWS

Restriction of tidal flows into wetlands by dikes and tide gates generally decreases the supply of sediment to the wetland. However, tidal flow velocities are also decreased and lead to greater deposition in channels. With less sediment reaching the marsh plain and greater deposition occurring in channels, the wetland topography becomes more uniform. Deposition in channels reduces water flow and contributes to isolated ponds which add to vector control problems. Overall, close attention must be focused on proper construction and maintenance of tidal control structures to provide adequate circulation in the wetland.

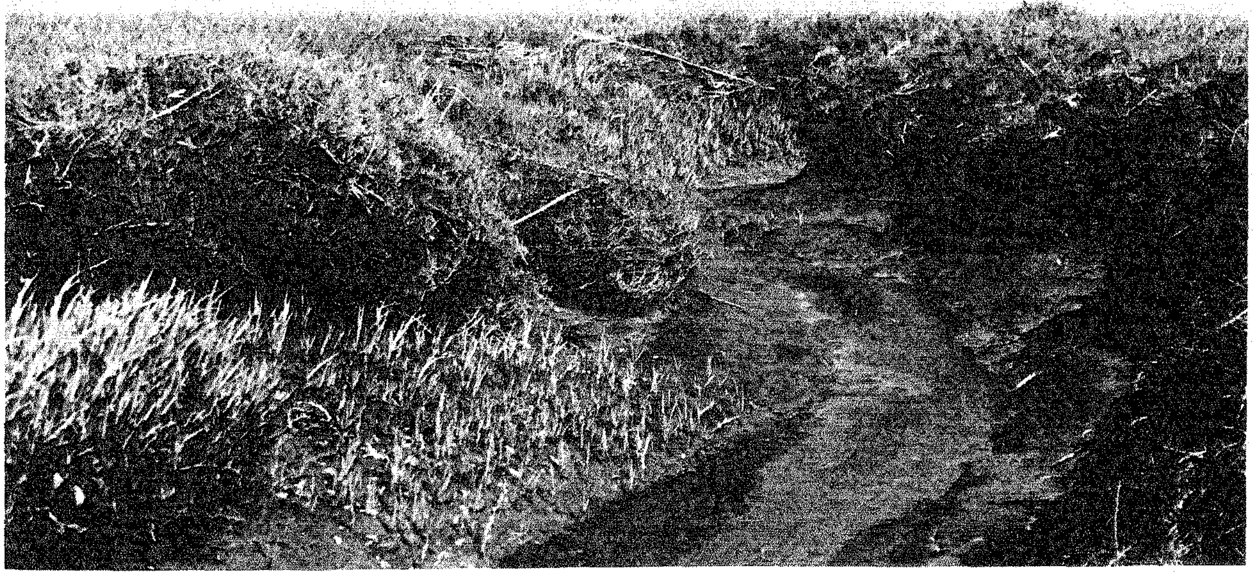

Figure 16. Slumping of channel banks in south San Francisco Bay. Note colonization of bank by Pacific cordgrass on bottom left (Photo by D. Spicher).

CHAPTER 5

PLANT COMPOSITION AND ZONATION IN TIDAL MARSHES

Tidal marshes are dominated by vascular plants. As the most obvious members of the tidal marsh community, they are often used to delimit boundaries. At first, the broad sweep of the wetland appears dominated by a few species with relatively sharp boundaries between adjacent communities especially at sites with steep slopes or sharp elevational changes. Upon closer examination of both the flora and fauna, gradation rather than disjunction is the rule as one moves from subtidal to intertidal and eventually to upland. The species which comprise the tidal marsh community appear to respond more to individual physiological tolerances than to well defined community boundaries. Thus, it is not unusual to observe tidal marsh plants in diked wetlands or at higher tidal elevations than normal due to freshwater discharge. In addition, zonation patterns between species within the tidal marsh community are observed. Physiological responses, interspecific competition, and physical factors (sedimentation, freshwater discharge) result in a dynamic balance between individual species obscuring boundaries. Because of the significance of various plant species to particular animals, it is important that an understanding of the factors responsible for zonation patterns be incorporated into the community description.

5.1 MAJOR PLANT SPECIES

The tidal marshes considered in this community profile can be divided into salt marsh and brackish marsh. Salt marsh is found throughout the south, central, and San Pablo bays. Brackish marshes dominate Suisun Bay and in areas of local freshwater discharge such as the Petaluma and Napa Rivers, and several south bay rivers which receive treated sewage effluent.

Salt Marsh

Pacific cordgrass (Spartina foliosa) and perennial pickleweed (Salicornia virginica) are the dominant species of the salt marsh community. Pacific cordgrass is usually found at lower intertidal elevations (mean tidal level [MTL] to mean high water [MHW]) and pickleweed at higher elevations (above MHW). Both species are perennial. Both produce viable seed, but once established appear to spread primarily by vegetative growth of rhizomes. Because of differences in anatomy, stature, physiology, and associated plant species, the two halophytes will be discussed separately below.

Pacific cordgrass (Spartina foliosa) is a member of the grass family (Gramineae). In older literature, it is referred to as S. leiantha. Its distribution is restricted to the Pacific coast of North America and extends from Humboldt Bay to Bahia de la Magdalena in Baja California (Macdonald and Barbour 1974). It is absent from many bays along the outer coast, but is common throughout San Francisco and San Pablo Bays. Pacific cordgrass is similar to many grasses, consisting of sheathed leaves surrounding a rigid culm which arises from an underground rhizome (Figure 17). It produces a single inflorescence containing many small flowers with male and female parts within the same flower (monoecious). It generally reaches a height of 0.5 to 1.5 m, however, a dwarf form has been described (Harvey 1976).

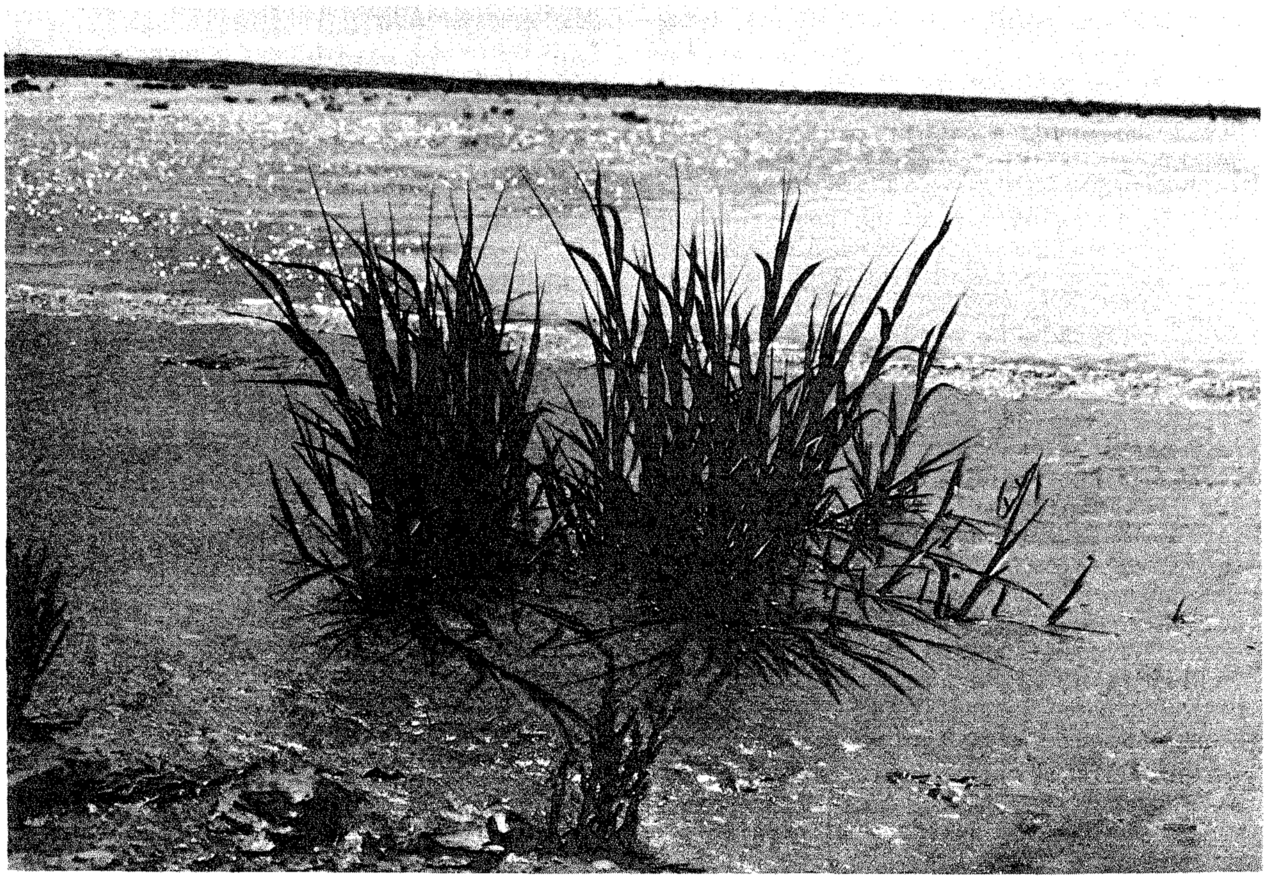

Figure 17. Pacific cordgrass (Spartina foliosa) colonizing a mudflat. Note shoots extending out from base along underground rhizomes. Plant not in flower.

The leaf anatomy of Pacific cordgrass is similar to other Spartina species, including the kranz anatomy typical of C-4 plants (Kasapligil 1976). In addition, structures called hydathodes are present which are responsible for active secretion of sodium chloride from the plant. The salt crystallizes on the surface of the leaves and is washed away by rain or tidal submergence. Water loss from the leaves is reduced by their curling inward so that the lower epidermis with its thick impervious cuticle is exposed while the upper surface with a thinner cuticle and more abundant stomata is protected from the drying action of the wind. The upright stem or culm and the underground stem or rhizome contain an extensive air passage or lacunal system. The lacunae are abundant in the peripheral cortex of the stems and are important in the diffusion of air to the lower regions of the plant which are often growing in anaerobic conditions. Two types of roots arise from the rhizome: anchorage roots and thinner, profusely branched absorption roots. The anchorage roots penetrate into deeper layers of the substrate whereas the absorption roots form an intricate mat in the upper layers of the mud. Both contain lacunae continuous with the stem. Diffusion of air from rhizomes and roots to the surrounding sediments can be important in supporting aerobes in an otherwise anaerobic environment.

The presence of two growth forms of Pacific cordgrass in south bay marshes has led investigators to question whether the difference is genetically or environmentally induced. A "robust" form grows at lower elevations and reaches 1.2 m in height and a "dwarf" form is found at higher elevations and grows to only 0.3 m tall (Harvey 1976). Parnell (1976) determined that both growth forms have a diploid chromosome number of 60. Using controlled culture methods, Cain and Harvey (1983) observed a significant decline in height for Pacific cordgrass with increasing sediment salinity. Robust forms grew less in sediment salinities above 11.7 ppt (0.4 osmole/kg H_2O) and dwarf forms were even shorter in salinities above 23.4 ppt (0.8 osmole/kg H_2O). Locations where dwarf plants were observed in the field had sediment salinities above 31 ppt (1.05 osmole/kg H_2O). The response observed for Pacific cordgrass plants in the bay differs markedly from that observed by Zedler (1977) in the Tijuana Estuary. In southern California, it is not unusual to observe normal (robust) height forms in sediment salinities above 34 ppt. Cain and Harvey (1983) suggest that other factors are probably involved as even the "dwarf" plants in laboratory culture grew taller than in nature. Similarly, Linthurst and Seneca (1980) observed that changes in sediment surface elevation had a marked effect on numerous sediment characteristics which affected growth in smooth cordgrass (Spartina alterniflora).

The physiology and photosynthetic response of Pacific cordgrass to increasing sediment salinities has been studied by Phleger (1971), Mahall and Park (1976b), and Pearcy et al. (1981). Similar conclusions were reached by all investigators: Pacific cordgrass grows best at lower salinities (less than 15 ppt), but will continue to grow at reduced rates at salinities as high as 35 ppt. Seed germination is also enhanced in lower salinity (Crispin 1976) and pretreatment in freshwater is suggested as a means to enhance germination when using seeds in restoration projects (Mason 1976). While it is apparent that Pacific cordgrass can grow at lower salinities than those measured at field locations, competitive interactions with other species (notably alkali bulrush [Scirpus robustus]) limits its spread (Pearcy et al. 1981).

Dispersal mechanisms for Pacific cordgrass are assumed to involve either seeds or vegetative fragments. Although conditions affecting seed germination for Pacific cordgrass have been well documented (Crispin 1976, Maguire and Heuterman 1978), little information is available to estimate dispersal and germination in the field. Despite flower production, seed production in Pacific cordgrass is limited (Mason 1976). In plants producing seed, viability reportedly exceeds 80% (Crispin 1976); however, germination percentages are less (Mason 1976). Heavy infestation by ergot (Claviceps) can reduce seed viability in certain marshes (Figure 18). Under field conditions, Crispin (1976) found less

Figure 18. Seeds of Pacific cordgrass infected by ergot. Ergot appears as dark, curved horns embedded in floral stem.

than 4% germination, and that as little as 0.5 cm of mud reduced emergence of seedlings. Newcombe and Pride (1976) reported nearly 100% germination when seeds were collected and stored in the laboratory prior to transplanting. Neither Josselyn and Perez (1981) nor Hopkins and Parker (in press) noted any seed of Pacific cordgrass germinating in their studies of seed banks in bay tidal marshes. Nevertheless, natural establishment of Pacific cordgrass has occurred in several marsh restorations (Faber 1980, Cuneo 1982), though whether by seed or vegetative means was not documented. Most authors recommend transplanting stems or plugs of Pacific cordgrass to establish it in marsh restoration sites (Harvey et al. 1982, Zedler et al. 1982).

Few vascular plant species are found associated with Pacific cordgrass. Pacific cordgrass is generally monospecific between MTL and MHW (Hinde 1954, Atwater and Hedel 1976). Pickleweed, however, will frequently spread into the upper range of cordgrass. Germinating seeds of other marsh plants are infrequently observed among Pacific cordgrass but survival is negligible (Hopkins and Parker in press). Micro- and macroalgae are present although no species listing has been developed as for southern California wetlands (Zedler 1977). Of the macroalgae, Enteromorpha and Ulva are frequently seen tangled on Pacific cordgrass culms especially in spring months (Shellem and Josselyn 1982).

Macdonald and Barbour (1974) noted the presence of a different growth form of Pacific cordgrass in Humboldt Bay. It grows in compact, closely spaced tussocks occupying the zone normally inhabited by pickleweed. It occupies a similar habitat in a marsh restoration site along Corte Madera Creek and grows adjacent to the normal rhizomatous growth form. Preliminary research indicates the transplanted form shows no growth dormancy, flowers earlier than the native form, and does not produce rhizomes (Spicher pers. comm.). It appears very similar to gulf coast cordgrass (Spartina spartinae) (H.T. Harvey, pers. comm.). Further research is imperative in order to determine whether this form will spread into local marshes as other introduced species have. Until such research is completed, individuals proposing marsh restoration should not use plants from outside the bay area for transplanting (Zedler et al. 1982).

The second major plant species found in salt marshes is perennial pickleweed (Salicornia virginica)(Figure 19). Its scientific name is occasionally listed as Salicornia pacifica based on Mason's (1957) acceptance of Standley's (1916) interpretation. Most modern literature, however, synomymizes S. pacifica under S. virginica (Munz 1959). Given its present interpretation, Salicornia virginica has a widespread distribution on both the Atlantic and Pacific coasts. It, by far, covers greater area of salt marsh habitat in the bay than any other species. It is normally found at elevations above MHW. It also grows in areas without tidal influence such as diked wetlands because it can tolerate high sediment salinities during the dry season.

Pickleweed is a perennial and forms extensive, intertwining above-ground branches about 0.5 m tall. The plant is a succulent and consists of a woody stem surrounded by succulent leaves. The flowers are inconspicuous and embedded in the upper portions of the stem of the inflorescence. Male and female flowers are on separate plants (dioecious). The seeds produced are deeply embedded in the stem and are released in the fall and winter when the stem withers and decays away.

Pickleweed is adapted to saturated soils and high salinities. Within the stem and root, aerenchymous tissue is present containing air spaces to allow diffusion of oxygen to the roots (Anderson 1974). The root system does not penetrate as deeply as that of Pacific cordgrass and the air passage system is not as well developed. Pickleweed is a succulent and can store excess salts within vacuoles. It does not possess salt glands for active secretion; instead, as plant parts accumulate salts, they are sloughed off. This process frequently occurs in the fall and winter and is accompanied by the loss of chlorophyll (green) pigment and development of anthocyanin (red) pigment.

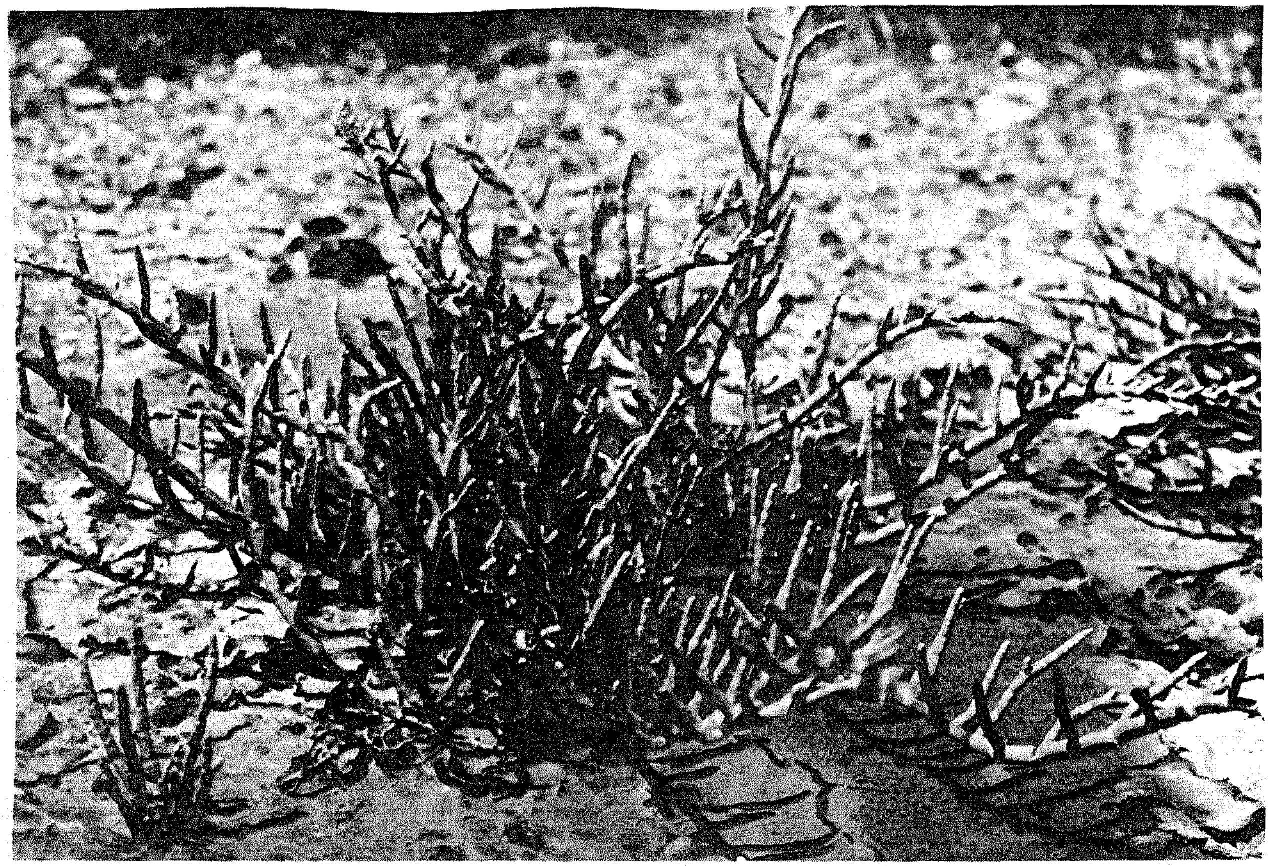

Figure 19. Perennial pickleweed (Salicornia virginica).

Pickleweed is a C-3 plant and fixes carbon dioxide via the Calvin cycle. Pearcy *et al.* (1981) found that carbon dioxide uptake in short-term experiments is unaffected by salinities ranging between 0 and 30 ppt; however, long-term growth rates (accumulation of tissue weight) are reduced at salinities above 20 ppt. Maximum growth is reached at 10 ppt suggesting that moderate salinities are necessary to provide NaCl as a solute to maintain osmotic balance in the cells. Temperature optimum for pickleweed is between 25° and 27°C. Maximum rates of photosynthesis occur at 2000 μein/m^2/sec. Pickleweed does not reach light saturation, perhaps due to the poor light absorbing ability of its photosynthetic stems. This is reflected in its extremely low photosynthetic rate at light intensities below 500 μein/m^2/sec. Clearly, pickleweed is adapted to saline substrates, warm temperatures, and high light intensities; all of which are ingredients of its environment.

Pickleweed spreads rapidly by vegetative means. Its sprawling, low lying stems produce many new upright stems each spring. Buried stems also produce uprights. Josselyn and Perez (1981) observed that broken stems buried at a marsh restoration site were the first to produce new growth, even prior to the restoration of tidal action. Seed production is also extensive (Figure 20). Hopkins and Parker (in press) counted germinating seeds, over 90% of which were pickleweed seeds, at densities of 2100-3175/m^2 in sediments of a San Pablo Bay marsh. Germination peaked in early April; however, by mid-June, 96% of the seedlings had died. Apparently competition with existing plants occurred since seedling survival in marsh restoration sites was much higher (Newcombe and Pride 1976). Martindale (unpubl) observed an ascomycete fungus (Camarosporum) infecting pickleweed seeds in a south bay marsh. Its significance in reducing seed viability is unknown. In general, seed dispersal mechanisms appear to be adequate

Figure 20. Seedlings of perennial pickleweed. Mature plants pulled aside to show density of seedlings.

Figure 21. Annual pickleweed (Salicornia europaea).

for pickleweed as most authors recommend letting it "volunteer" in marsh restorations (Harvey *et al*. 1982).

A number of halophytes are found associated with pickleweed. Generally, these species are found as patches within the pickleweed marsh or form upland boundaries around the marsh. *Jaumea carnosa* and sea arrowgrass (*Trichochin maritima*) are examples of the former whereas marsh rosemary (*Limonium californicum*) is an example of the latter. An annual species of pickleweed (*Salicornia europaea*) is often observed in marsh restorations at elevations slightly below the perennial species (Figure 21). As the perennial form becomes established, it extends down further and displaces annual pickleweed (Josselyn, pers. obs.).

Small depressions or slight elevations can break the extensive distribution of perennial pickleweed and create conditions favorable to other species. Gumplant (*Grindelia stricta*) and salt grass (*Distichlis spicata*) are often found on natural rises within pickleweed or along the upland edge of the marsh (Figures 22 and 23). Depressions are caused by the death of pickleweed after it is covered by wrack material during high tides. Oliver and Reilly (1981) observed rapid colonization by *Jaumea carnosa*, alkali heath (*Frankenia grandifolia*), and salt bush (*Atriplex* spp) of disturbed areas creating a mosaic of vegetation. Over several years, pickleweed may re-establish itself, but its competitive ability is dependent upon tidal elevation. It is more likely to recolonize patches at lower than higher elevations. One species which is always found in association with pickleweed is dodder (*Cuscuta salina*). It is a parasitic plant which appears as bright orange threads intertwining among the pickleweed

Figure 22. Flowers of gumplant (Grindelia stricta).

Figure 23. Salt grass (Distichlis spicata).

(Figure 24). Its leaves are reduced to minute scales and it produces small, white flowers from May to September. Although, at times, dodder can appear to completely cover its host plant, it usually does not kill it.

Lists of species associated with pickleweed in various bay marshes are given in Atwater et al. (1979). Brief descriptions with common names are given in Table 8. Faber (1982) also provides a guide with illustrations to common wetland plants in California.

Regulatory agencies have sought to use marsh plants as indicator species for determination of jurisdictional limits (Briscoe 1979). Harvey et al. (1978) investigated the occurrence of marsh, upland, and non-indicator species for several sites in San Francisco Bay. Most of the species given in Table 8 were considered marsh species, closely associated with pickleweed. Only fat-hen (Atriplex

Figure 24. Saltmarsh dodder (Cuscuta salina) on perennial pickleweed.

Table 8. Vascular plant species associated with pickleweed (Salicornia virginica).

Species	Common name	Description	Location
Distichlis spicata	Saltgrass	Narrow spike leaves	Upper zone
Atriplex patula	Halberd-leaved saltbush	Tall; triangular leaves	Upper zone
Frankenia grandifolia	Alkali heath	Low; bush; small pink flowers	Upper zone
Grindelia humilis	Marsh gum-plant	Tall; composite flowers	Upper zone
Limonium californicum	Marsh rosemary	Basal leaves; tall inflorescence	Upper margin
Jaumea carnosa	Jaumea	Spreading; fleshy leaves	Intermixed
Cuscuta salina	Salt marsh dodder	Orange stems; white flowers	On pickleweed
Cordylanthus mollis ssp mollis	Soft bird's beak	Purple; fleshy leaves	In pickleweed
Salicornia europaea	Annual pickleweed	Bushy annual	Lower zone
Spergularia marina	Salt marsh sand spurry	Low; spreading plant	Disturbed ground
Cotula coronopifolia	Brass-buttons	Low; yellow flowers	Disturbed ground

patula ssp hastata) and saltgrass were found to range extensively in both upland and marsh habitats and to be of limited value in delimiting marsh habitat.

Brackish Marsh

Brackish marshes were once quite extensive throughout Suisun Bay and at scattered locations where local runoff reduced salinities. The balance between saline and freshwater conditions is delicate and fluctuates seasonally. As a result species typical of salt and freshwater wetlands intermix, and the community is reflective of local environmental conditions. This section will provide a generalized description of the species composition.

The dominant genera of the brackish tidal marsh are Scirpus and Typha. Like the salt marsh, dominant species vary with elevation. Atwater and Hedel (1976) identify three major zones: low marsh (MTL or lower), middle marsh (MTL to mean higher high water [MHHW]), and high marsh (at or above MHHW). Harvey et al. (1977) identify five major zones: low-low, high-low, low-high, high-high, and peripheral. They do not provide any indication of tidal levels associated with each zone except to note a continuum from lower to higher tidal elevations. Nevertheless, the descriptions they provide of vegetation found at various elevations support a three zone pattern: a low marsh dominated by California bulrush (Scirpus californicus); a middle marsh with a mixture of cattails (Typha spp) and bulrushes (Scirpus olneyi and S. robustus); and a high marsh with a varied group of halophytes including saltgrass and the Baltic rush (Juncus balticus). It is important to remember that the plant composition of brackish tidal marshes is very different from the more extensive diked wetlands of Suisun Marsh. These wetlands are managed for waterfowl food plants such as alkali bulrush (Scirpus robustus) and brass buttons (Cotula coronopifolia).

California bulrush (Figure 25) is found at lower elevations, eventually replacing Pacific cordgrass around Carquinez Straits. It extends to just below MTL at Benicia and to below MLLW in the delta. Apparently, it is able to tolerate greater submergence with fresher conditions. California bulrush grows from an underground rhizome and produces an upright culm or stem up to 4 m tall. Leaves are reduced to basal sheaths. The culm is the primary photosynthetic tissue. The culm is characterized by being only slightly triangular as opposed to more prominent ribs of alkali bulrush. Inflorescences are produced near the tip of the culm. California bulrush is easily confused with the common bulrush (S. acutus) which differs by being rounded in cross-section throughout its length and having floral bristles which are barbed (Mason 1957). The California bulrush is felt to represent the dominant species of the lower marsh (Atwater and Hedel 1976). A subspecies of the tufted hairgrass (Deschampsia caespitosa ssp holciformis) is occasionally found at lower elevations as well (Josselyn, pers. obs.).

Figure 25. California bulrush (Scirpus californicus) in flower.

At elevations between MTL and MHHW, two other species of bulrush (Scirpus olneyi and S. robustus) and two species of cattail (Typha latifolia and T. angustifolia) dominate tidal brackish marshes. Alkali bulrush is more prevalent in San Pablo Bay and the Carquinez Straits where salinities are low enough to allow it to grow but high enough to preclude growth of other bulrushes and cattails (Atwater and Hedel 1976). In the portions of Suisun Marsh managed for waterfowl, alkali bulrush (an important waterfowl food plant) is one of the most abundant species (Mall 1969). In the tidal marshes of Suisun, Olney's bulrush (S. olneyi) and the cattails (Typha spp.) are more prevalent.

Alkali bulrush is a leafy sedge 0.5 to 1.5 m tall. It can reproduce vegetatively from tuberous underground rhizomes. Seeds are produced in pendulous heads at the top of the plant and are thought to be a prime food source for waterfowl. Mall (1969) found that seed production was greatest when submergence was six months or longer and spring sediment salinities were maintained below 26 ppt. Pearcy et al. (1981) observed declines in both photosynthetic rate and growth at all salinities tested, indicating that freshwater conditions are more favorable compared to the field conditions in which it is normally found. They suggested that alkali bulrush reaches its greatest abundance in tidal marshes subject to seasonal salinity changes (0 to 25 ppt). It grows rapidly in spring when sediment salinities are close to zero. The taller canopy of alkali bulrush eventually shades out the lower growing pickleweed. As sediment salinities rise in late summer, alkali bulrush becomes dormant. It is more tolerant of higher salinities during this period than its potential freshwater competitors such as California bulrush (*Scirpus californicus*) and cattails (*Typha* spp). In marshes with low sediment salinities throughout the year, these latter species become more prevalent and can shade out the shorter alkali bulrush. For the wetland studied, Pearcy *et al*. (1981) concluded that pickleweed dominates when saline conditions exist year-round; California bulrush flourishes when no or little salt is present in sediments; and alkali bulrush grows in situations with freshwater conditions in spring and saline conditions in summer.

Olney's bulrush (*Scirpus olneyi*) is most abundant in Suisun Bay and the delta. It is easily distinguished by its height (up to 2.5 m tall) and sharply triangular stem. It is more tolerant of submergence than the narrow leaved cattail (*Typha angustifolia*) but less tolerant of high sediment salinities (Mall 1969). On the other hand, Atwater and Hedel (1976) observed Olney's bulrush growing in San Pablo Bay where water salinities were typically near 20 ppt.

Cattails (*Typha* spp) are difficult to identify due to frequent hybridization particularly between the common cattail (*T. latifolia*) and the narrow leaved cattail (*T. angustifolia*) (Mason 1957). The former has light green leaves and the pistillate and staminate flowers are continuous on the spike whereas the latter has dark green leaves and there is a break between the upper staminate and lower pistillate flowers. Of eight species sampled in Suisun Marsh by Mall (1969), the narrow leaved cattail was second to pickleweed for sediment salinity tolerance. It is apparently more tolerant of higher sediment moisture than pickleweed and therefore is found in pockets which retain water between tidal cycles.

In the high marsh or peripheral halophyte zone (MHHW and above), a number of species typical of both freshwater and saline marshes are found. Where salinities are high, pickleweed (*Salicornia virginica*), saltgrass (*Distichlis spicata*), fat-hen (*Atriplex patula* ssp *hastata*), and gumplant (*Grindelia humilus*) are found. In areas of lowered salinity, brass buttons (*Cotula coronopifolia*) and the baltic rush (*Juncus balticus*) are more prevalent. Many other species extend into this zone including an endangered species (state listed): *Lilaeopsis masonii*. The exact distribution of species is dependent on period of submergence, sediment salinity, and interspecific competition. Atwater *et al*. (1979) provide a complete list of species found in the Suisun tidal marshes. Because of the extensive diking in Suisun Marsh, little of the high marsh remains except at Joice Island, Roe Island, and some areas along the south shore of Suisun Bay.

5.2 ZONATION PATTERNS OF WETLAND VEGETATION

Vertical distribution

The elevational distribution of marsh plants in tidal marshes is a distinctive feature. From a distance, sharp boundaries appear between plant species, whereas close examination reveals a gradual shift in species composition. Although elevation with respect to tides appears to be the primary determinant of species distribution, many species can be found in discrete patches at elevations in which they are not expected. Attempts to develop definitive relationships between species distribution and tidal elevations have not been successful in other regions (Eleuterius and Eleuterius 1979). Tidal sloughs, minor changes in marsh topography, differences in sediment characteristics, local hydrologic factors, and competition can all affect the pattern of species distribution.

Early work by Hinde (1954) attempted to relate the vertical distribution of salt marsh plants to tidal elevations and the length of submergence in each zone. He described three major zones of a salt marsh in the south bay (Palo Alto): the *Spartinetum* (+1.6 to 2.5 m above mean lower low water [MLLW]), the *Salicornietum* (+1.9 to 3.1 m above MLLW), and the *Distichlidetum* (+2.1 to 3.1 m above MLLW). He hypothesized that the lower extent of each of these zones was determined by the physiological limitations of the dominant species to prolonged submergence. Submergence times greater than 21 continuous hours limited Pacific cordgrass whereas pickleweed was even less tolerant of prolonged submergence (Table 9). Pickleweed grew best when emergence was greater than or equal to the period of submergence and Pacific cordgrass dominated when the period of submergence was greater than emergence. It did not survive when the length of submergence was four times greater than emergence. Hinde also observed that the frequency of long periods of emergence during the daytime was greatest in April through July at lower elevations. The extended periods of daytime emergence at low elevations corresponded to the initiation of growth in Pacific cordgrass. When longer periods of submergence returned, the taller plants were able to extend their photosynthetic leaves above tidal influence. On the other hand, pickleweed does not grow very tall but is exposed to longer periods of emergence at the MHW level. Based on recent photosynthetic measurements, such conditions are ideal for pickleweed which is a relatively poor light absorber (and therefore does best in high light intensities) and is little affected by elevated sediment salinities (Pearcy *et al*. 1981).

Mahall and Park (1976c) examined the factors of soil aeration and tidal immersion directly. They measured soil oxygen diffusion rates in the field and conducted greenhouse experiments with Pacific cordgrass and pickleweed under various periods of submergence. No significant differences in oxygen diffusion rates were obtained between plots occupied by either plant indicating that conduction of oxygen to the roots of pickleweed does not limit its seaward distribution as hypothesized by Hinde (1954). On the other hand, Mahall and Park (1976c) did observe a significant decline in growth for pickleweed exposed to longer and deeper tidal submergence. They did note that pickleweed growing in Pacific cordgrass was more robust and taller than within its normal elevational range suggesting that reduction in available light during submergence may limit pickleweed growth. They also hypothesized that greater leaching of nutrients and organic compounds during submergence may occur from pickleweed than from cordgrass.

Table 9. Tidal data for the Palo Alto Salt Marsh (from Hinde 1954).

Level above MLLW (m)	Total emergence in daylight per year (hr)	Total submergence in day and night per yr. (hr)	Ratio of total emergence/submergence
+3.1 highest *Salicornia*	4,001	1,753	4.05
+2.9	-	2,855	2.07
+2.5 highest *Spartina*	2,807	3,901	1.25
+2.3	2,147	4,922	0.78
+2.0 lowest *Salicornia*	1,477	6,026	0.45
+1.6 lowest *Spartina*	988	7,039	0.24
+1.5	829	7,385	0.19

Mahall and Park (1976b) were able to show a relationship between sediment salinity and zonation. Pickleweed was able to withstand greater absolute salinity and sudden changes in salinity to a greater extent than could Pacific cordgrass. They observed no significant decline in shoot growth in pickleweed in salinities ranging from 12 to 37 ppt whereas Pacific cordgrass shoot growth declined rapidly above 16 ppt. Field measurements indicated that the transition zone between these two species occurred at about 24 ppt as measured in the summer. In establishing a water budget for both species, they observed that Pacific cordgrass is much less effective at excluding ions from entering its roots than pickleweed. Ustin *et al*. (1982) confirmed these results and noted that pickleweed grew in sediments which had a lower water potential (hence greater salinity) than Pacific cordgrass. This difference was most pronounced in the late summer.

The sediment salinity pattern in bay tidal marshes is determined by tidal inundation, freshwater discharge, and evaporation. Sediment salinities are generally lowest in winter due to the seasonal rainfall and runoff. With the reduction of rainfall and increased evaporation in summer, sediment salinities rise, especially at higher elevations. The more frequent submergence at lower elevations maintains salinities closer to that of the bay water. The most rapid transition in sediment salinities occurs at approximately MHW, the same elevation where pickleweed replaces Pacific cordgrass. Salinity is, therefore, the major factor influencing vegetative zonation in salt marshes. Length of submergence is important in its affect on available light and perhaps in oxygen availability to plant roots. The taller Pacific cordgrass can extend further into the bay and the shorter pickleweed is limited to upper, more exposed elevations. Pacific cordgrass also has larger aerenchyma tissue (lacunae) compared to pickleweed. Although both can tolerate anaerobic conditions, Pacific cordgrass is probably able to survive longer periods of submergence.

The factors affecting zonation patterns in brackish marshes are less well understood. Mall (1969) was able to delineate the differences in sediment moisture, organic content, and salinity which affected the distribution of a number of plant species within diked wetlands of Suisun Marsh (Table 10). Presumably, these factors would also play a role in tidal marshes. Due to the greater number of species in brackish marshes and the large year-to-year variation in delta outflow, species zonation patterns are more complex and may be a result of past conditions as well as current factors. Zedler (1982) has observed how single flood events can have a marked effect on species composition which is continued in non-flood years.

Estuarine gradient (Horizontal distribution)

Both the vertical and horizontal zonation patterns in bay tidal marshes change with increasing distance inland (Table 11). The primary influence is the reduction of salinity in the water flooding the marshes and therefore lower sediment salinities. Atwater and Hedel (1976) noted elevational changes with respect to tidal levels for several species from the delta to the Golden Gate. For example, the California bulrush is found from MLLW to MHW in the delta, but only extends slightly below MTL in Carquinez Straits. Pickleweed is found at greater elevations as one moves inland. Alkali bulrush grows extensively at mid-tide elevations in Suisun Bay but is found only in isolated high marsh patches in San Pablo Bay.

Ustin *et al.* (1982) examined the distribution of three marsh plants

Table 10. Ranges of sediment salinities, organic matter content, and percent soil moisture in which specific marsh plants dominate in diked wetlands of Suisun Marsh. Measurements made on soil extracts diluted with 5 parts distilled water to 1 part sediment. All measurements in root zone (0 to 30).

Species	Percent moisture	Mean annual salt in root zone (mmho/cm)	Percent organic matter content
Scirpus olneyi	100-150	2-4	10-15
Juncus balthicus	25-125	2-4	9-12
Distichlis spicata	100-200	10-20	12-20
Atriplex hastata ssp *patula*	75-150	10-20	17-30
Cotula coronopifolia	100-125	5-7	10-20
Salicornia virginica	100-150	12-25	20-25
Scirpus robustus	125-175	10-20	25-60
Typha angustifolia	150-250	5-10	25-35

Table 11. Tidal ranges for marsh plants at several locations in San Francisco Bay (from Atwater and Hedel, 1976).

Species	Richardson Bay	San Pablo Bay	Carquinez Straits	Delta
Spartina foliosa	MTL-MHW	<MTL-MHW	-	-
Scirpus californicus	-	-	<MTL-MHW	<MLLW-MHW
Salicornia virginica	<MHW- > MHHW	<MHW- >MHHW	>MHHW	-
Scirpus olneyi	-	-	MHHW	>MTL

(Pacific cordgrass, pickleweed, and alkali bulrush) near their distributional limits in San Pablo Bay. They found areas where alkali bulrush grew in a narrow zone between Pacific cordgrass and pickleweed. Sediment salinities in this zone were inhibitory to the growth of alkali bulrush during the summer months. Its survival in this zone was dependent on the reduction of sediment salinities in the spring by heavy delta outflow. Its period of most rapid growth was from May to June and by July when sediment salinities were rising, growth ceased. Flower and seed production occurred infrequently, underground rhizomes initiated almost all new seasonal growth. By July, alkali bulrush exceeded both Pacific cordgrass and pickleweed in height and its dense canopy inhibited the spread of either species into its zone. Year-to-year survival was dependent on seasonal freshwater inflow, although the underground rhizomes of alkali bulrush can remain dormant during drought years and resprout when sediment salinities are reduced.

Long term changes in species composition have been noted by Atwater (1980) on Browns Island at the eastern end of Suisun Bay. Based on fossil evidence, saltgrass has replaced more freshwater species such as the common reed (Phragmites communis) and the alkali bulrush. He estimates this change has occurred over the past 1000 years. Short term changes have also been observed as during a severe drought (1976-77) when Pacific cordgrass became established in areas formerly supporting California bulrush in Southampton Marsh on the Carquinez Straits (Atwater et al. 1979).

The importance of seasonal reductions in salinity as a determinant of species composition along the estuarine gradient is further supported by evidence from Rollins (1973) for managed wetlands in Suisun Marsh. He observed a highly significant correlation between the salinity of tidal water (applied through tidal gates) and the resulting sediment salinity in the 0 to 30 cm depth. This was further related to the plant community. Leaching of salts by applying low salinity water in the spring greatly increased the survival of brackish water plants such as alkali bulrush.

In summary, both vertical and horizontal distribution patterns of tidal marsh species appear closely tied to sediment salinities. While tidal inundation is important as a source of moisture and salts, other hydrologic and climatic factors interact to create conditions favorable to a few species. Seasonal variation further complicates the patterns observed because the prevalence of vegetative reproduction in marsh plant species allows each to respond rapidly to favorable conditions. Plant competition appears most significant in areas of overlap between saline and brackish marshes.

5.3 TRANSITION ZONE (PERIPHERAL HALOPHYTES)

The transition zone represents the change in plant species composition from typical wetland species (hydrophytes) to upland species. It is frequently referred to as representing an upper boundary for wetlands and therefore has gained some legal significance (Briscoe 1979). MHW serves as the jurisdictional limit for the Army Corps of Engineers under the Rivers and Harbor Act of 1899. Few community analyses, however, have been able to verify consistent relationships between tidal datums (the statutory boundaries) and plant species indicators. Instead, transitional communities vary from site to site in their elevational distribution (Frenkel et al. 1981). Josselyn and Atwater (1982) concluded that geologic phenomena (subsidence, sedimentation), human interference (diking, filling), and problems in precise leveling in broad marsh plains compound the difficulties in relating tidal elevations to past and current distributions of plant species. Use of marsh vegetation alone to locate jurisdictional boundaries has been rejected in some courts (Briscoe 1979).

The transition zone is significant ecologically. Of the six animals listed as rare or endangered in bay tidal marshes, four utilize the region between MHW and the upland for breeding and/or feeding (Table 12). Both plant species listed as rare or endangered occupy the transition zone. Many other animals use the transition zone to escape extreme high tides or winter floods. Diking of wetlands has impacted this habitat to the greatest extent by creating a sharp boundary between tidal marshes and the upland (dike slope).

Harvey et al. (1978) have reported on the transition zone limits for several wetlands in California, one of which was in San Francisco Bay. They found that no plant species were typical or limited only to the transition zone. Instead, they used a method that required an a priori decision be reached on whether a species was typically wetland or upland. Using these species as indicators, they determined transition zone limits using percent cover data. Upper limits were measured at the point where marsh plants comprised less than 5% cover and lower limits where upland plants were represented by less than 5% cover. The upper and lower transition limits for a marsh near Palo Alto were +1.25m ± 0.26 and 0.83m ± 0.12 above MHW, respectively. The average width of the transition zone was 3.11m ± 3.43. A similar approach was taken by Frenkel et al. (1981) for Oregon marshes. The mean upper and lower limits in their study were 0.58 and 0.36 m above MHW or approximately 0.7 m lower than those found by Harvey et al. (1978). Although it is a useful tool in delimiting wetlands, the relation of the transition zone with respect to tidal datums varies and cannot be used as a consistent jurisdictional marker.

Table 12. Rare and endangered animal and plants species in bay tidal marshes (from Jones and Stokes and Assoc. 1979; Atwater et al. 1979). S = California state or California Native Plant Society listing; F = Federal listing. Not included in table are species which are not limited to tidal marshes although they may sometimes be observed there, ie. California brown pelican, American peregrine falcon, etc.

Species	Habitat	Rare	Endangered
Salt marsh harvest mouse (*Reithrodontomys raviventris*)	salt, brackish		F,S
California black rail (*Laterallus jamaicensis coturniculus*)	salt, brackish	S	
California clapper rail (*Rallus longirostris obsoletus*)	salt		F,S
Soft bird's beak (*Cordylanthus mollis* ssp. *mollis*)	salt, brackish	S	
Jepson's pea (*Lathyrus jepsonii*)	brackish	S	

CHAPTER 6

ANIMAL INHABITANTS OF TIDAL MARSHES

6.1 HABITATS

The apparent monotony of pickleweed (Salicornia virginica) and the bulrushes (Scirpus spp.) in San Francisco Bay tidal marshes is broken by a variety of habitats which support a diverse group of animals. Ranging in diversity and size from protozoans to harbor seals, the animals utilize the wetlands for resting, feeding, breeding, and protection from predators. This chapter will introduce the kinds and abundances of animals and the habitats they utilize. The animals discussed fall into four major categories: invertebrates, fish, birds, and mammals. The invertebrates are the most diverse, ranging from infaunal organisms within the sediments of bay marshes to the numerous species of crustaceans, insects, and spiders which occupy the mud surface and plant canopy. The vertebrates are less numerous, but usually more apparent in the habitats they occupy: fish can be abundant in tidal channels and marsh pools, birds feed on adjacent mudflats and a few nest in the marsh vegetation, and mammals are generally restricted to higher ground within the marsh and adjacent upland.

The term habitat can be applied to a broad spectrum of regions from the set of physical and chemical conditions surrounding a single species to those around a large community (Clements and Shelford 1939, Odum 1971). In reference to tidal marshes, the habitats considered are: transition or peripheral halophyte zone, salt pannes and pools, the vegetated marsh, channels (including mosquito ditches) and sloughs, and the adjacent mudflat (Figure 26). Salt pannes are generally flat, unvegetated areas in the high marsh whereas pools are depressions which usually contain water. The term pothole is used to refer to pools which are formed from plugged tidal channels. Channels are generally deeper than wide and sloughs are wider than deep. Channels are incised in the high marsh and sloughs

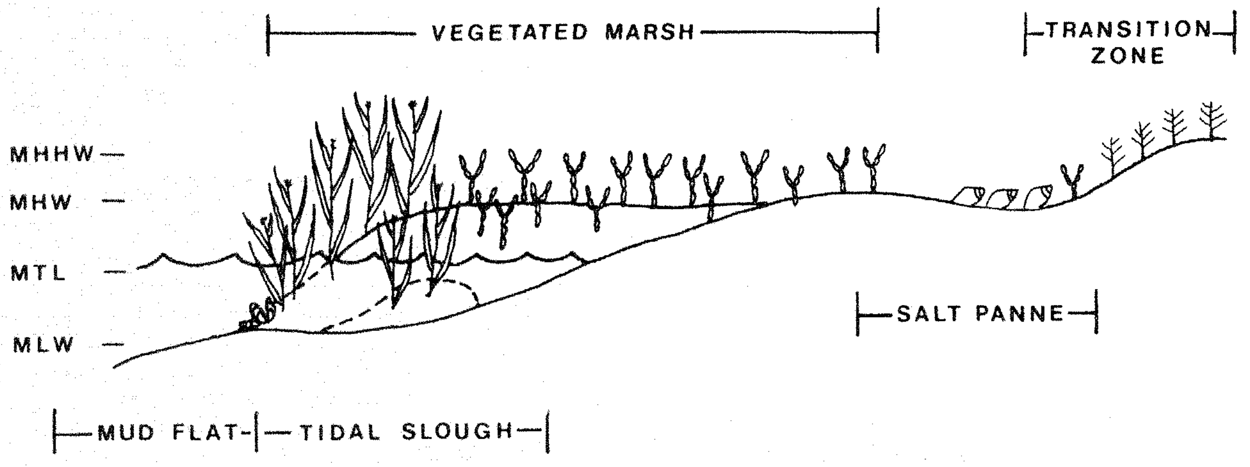

Figure 26. Habitats discussed within profile in relation to tidal datums. Tidal sloughs extend into low marsh, and tidal channels (not shown) extend through high marsh.

meander through the low marsh. The terms used here are compared to the classification scheme developed by Cowardin et al. (1979) in Table 13.

6.2 INVERTEBRATE FAUNA

The invertebrate fauna in tidal marshes can be divided into three major groups: benthic infauna, epifauna, and terrestrial arthropods. The infauna and epifauna are largely derived from marine and estuarine groups whereas the insects and spiders are terrestrial and aquatic forms which invade the marsh community. Review articles on these groups in San Francisco Bay are included in Macdonald (1977), Carlton (1979), and Cameron (1972). Taxonomic treatments are given in Smith and Carlton (1975) and Carlton (1978).

Infauna

The distribution of the benthic infauna within tidal marshes has not been well studied and must be inferred from studies of tidal creeks and mudflats immediately adjacent to tidal marshes. For the purpose of this community profile, a tidal elevation of + 0.5 m (above MLLW) was selected as the boundary between mudflat and tidal marsh organisms. This elevation approximates the maximum depth of channels draining tidal marshes (Pestrong 1965).

Extensive studies have been completed over the past 70 years on the distribution and abundance of subtidal and intertidal mudflat communities (see Nichols 1973 for review). The results indicate that sediment texture and salinity are the most significant physical factors affecting benthic species. Studies in other estuaries confirm these findings (Maurer et al. 1977, Boesch 1977). In San Francisco Bay, the distribution of strictly marine organisms is limited to the central bay. At the extreme ends of the bay exist populations of fresh and brackish water faunas. Between these two extremes is found a complex, extremely variable mosaic of communities highly dependent on local physical, chemical, and biological factors (Nichols 1973). Nichols (1979) attributes the high degree of patchiness to the effects of intermittant disturbance of the substrate either by wave and current action or by biotic disturbance such as predator activity, accumulations of decaying drift algae, and burrowing activity.

Anthropogenic influences such as sewage pollution, freshwater diversion, and introduction of exotic species further complicate the clarification of the factors affecting benthic community struc-

Table 13. Comparison between habitats discussed in this profile and those listed by Cowardin et al. (1979) .

	Vegetated marsh	Channels and sloughs	Salt pannes	Transition zone
System	Estuarine	Estuarine	Estuarine	Estuarine
Subsystem	Intertidal	Intertidal	Intertidal	Intertidal
Class	Emergent wetland	Unconsolidated shore	Unconsolidated shore	Emergent wetland
Subclass	Persistent	Mud	Mud	Persistent
Dominance	Cordgrass Pickleweed Bulrush	*Macoma*	*Cerithedia*	-
Modifier	Saline Brackish	Regularly flooded	Irregularly flooded	Temporarily flooded

ture. Carlton (1979) lists over 90 species of invertebrates which have been introduced to the bay through intentional transplanting (oysters, clams) or accidental establishment (by association with oyster culture, shipping, fishing activity). Many of the introduced organisms dominate the benthic and intertidal mudflat community. As successful colonizers, the introduced species are highly adapted to the disturbed environments present in the shallow waters of the bay (Nichols 1979). Thus, tidal marshes and their surrounding mudflats offer haven to a diverse group of native and introduced invertebrates.

Among the typical mudflat infaunal organisms penetrating tidal marsh environments, the Baltic clam (Macoma balthica L.[=Macoma inconspicua Broderip and Sowerby, 1829]) has been investigated in the south bay by Vassallo (1969). The greatest abundance of the Baltic clam was at +0.8 m above MLLW (maximum elevation of the study transect) with an average density at that elevation of 1062 ind/m^2. She attributed the greater abundance of Baltic clams at higher elevations to their adaptation to disturbed environments, eg. wave action. In addition, predation pressure on the adults by the channeled whelk (Busycotypus canaliculatus) and on the spat by an amphipod (Ampelisca milleri) is reduced at higher elevations.

The Baltic clam is a deposit feeder, and Black (1980) found that feeding by both large and small animals was greater at low tide (mudflat exposed) than at high tide. In addition, estimates of feeding rates suggested that food resources on the mudflat may be limiting and that input by tidal action is necessary to sustain population growth. In San Francisco Bay, the abundance of the Baltic clam in regions of greater physical disturbance and higher tide levels may be a response to food input and stranding by waves and a longer period of exposure for feeding.

An introduced species, the ribbed mussel (Ischadium [=Modiolus] demissum) inhabits a slightly higher intertidal habitat and is most abundant within the Pacific cordgrass (Spartina foliosa) zone. The ribbed mussel was probably introduced between 1860 and 1910 via the importation of eastern oysters (Crassostrea virginica) from the Atlantic coast (Carlton 1979). On the Atlantic coast, the ribbed mussel is a common estuarine species occurring within the smooth cordgrass (Spartina alterniflora) zone (Lent 1967). Its upper limit is apparently controlled by desiccation and thermal stress and its lower limit by lack of suitable attachment sites and predation (Lent 1969, Wells 1958). In San Francisco Bay, the ribbed mussel is commonly found in clumps, at least half-buried in the mud, with its byssal threads attached to the rhizomes of Pacific cordgrass or other mussels.

Langlois (1980) studied a population of ribbed mussels in the south bay. Greatest densities were observed along the outer edge of the Pacific cordgrass zone and declined with increasing elevation (Table 14). He did not observe any difference in average size of individuals on either a seasonal or elevational basis. Growth rates, however, were significantly faster within the Pacific cordgrass zone than in the pickleweed. Based on field studies of growth increments, he developed growth curves which provide an estimate of the age of various-sized mussels (Figure 27). During the two years of his study (1977-79), he observed little to no new establishment of young. A severe drought occurred during this study period, and the resulting high salinities in the south bay may have affected reproduction and recruitment. Predation and mortality of adults is high; however, it is not known what factors may limit spat fall or development. Population densities of adults may limit survival of spat and

Table 14. Population biology of the ribbed mussel (Ischadium demissum) (from Langlois 1980).

	Spartina edge	Upper Spartina	Salicornia
Density (#/m^2)	412	156	12
Avg. size (mm)	69	70	68
Growth rate (mm/30 days)			
Size class			
30-40mm	1.07	0.98	0.2
60-70mm	0.12	0.08	0.04
Season at max. growth	March-May	March-May	March-May
Mortality of adults	61%	22%	61%
Predation	12%	0	0

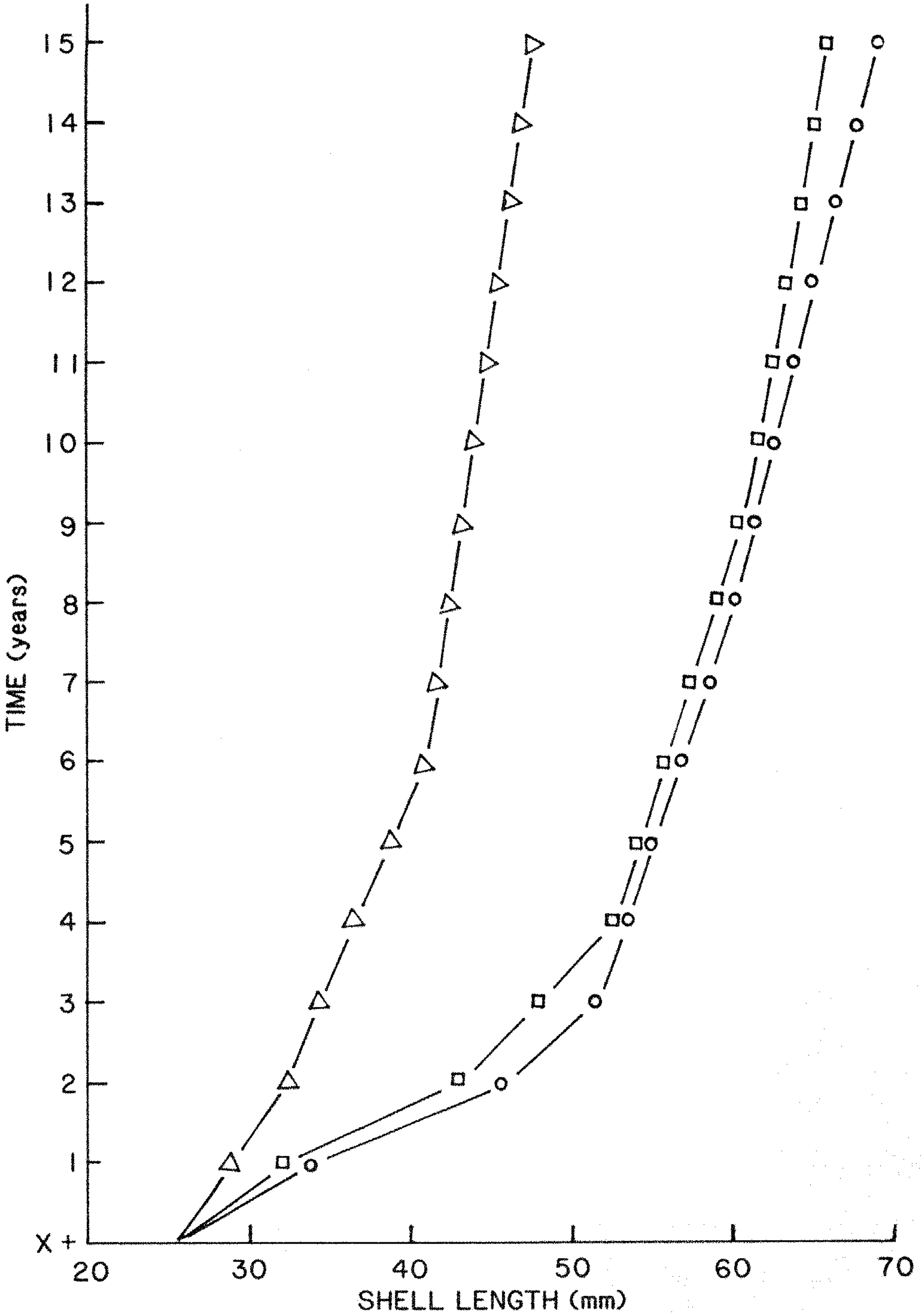

Figure 27. Estimated growth curve for the ribbed mussel (*Ischadium demissum*) in three habitat types. Circles represent growth at bayward edge of Pacific cordgrass, squares represent growth at landward edge of Pacific cordgrass, and triangles represent growth in pickleweed (from Langlois 1980).

small mussels. San Francisco Bay populations appear to be long lived (avg age = 14 yrs), to be stable in numbers, and to experience periods of low recruitment.

Another introduced infaunal species inhabits a slightly higher elevation. The burrowing and boring isopod (Sphaeroma quoyana) was probably introduced into the bay during the 1850-90's by shipping activity from Australia and Asia (Carlton 1979). It is found abundantly in San Pablo Bay and in the south bay where it burrows into mud banks from MSL to MHW (Figure 28). At the higher elevations, its burrows undercut the pickleweed zone and weaken the clay substrate, often facilitating the erosion of the shore by wave action (Figure 29). Ricketts et al. (1968) state that it burrows for protection and feeds on algae. Rotramel (1971) described it as a filter feeder, gathering detritus on the setae of its first three pairs of legs. Adults are active swimmers at night and the isopod can rapidly colonize available substrates (Schneider 1976).

Schneider (1976) studied a population of Sphaeroma quoyana on Tubbs Island in San Pablo Bay (Table 15). Although reproduction is continuous, S. quoyana release greater number of young in the spring, and the population reaches maximum size in the fall. The population at the lowest tidal level was limited by burrow collapse in the soft mud whereas firmer mud at higher levels provided more permanent burrows. Two size class cohorts were identified during the year and an individual isopod probably lives 1 to 1 1/2 years. Growth at all levels is fastest from March to May. Another isopod,

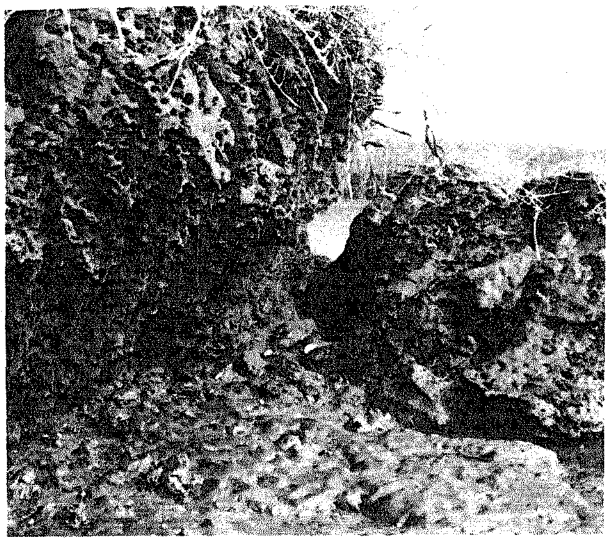

Figure 29. Marsh bank heavily colonized by Sphaeroma quoyana. Recent slumping of bank occurred on right.

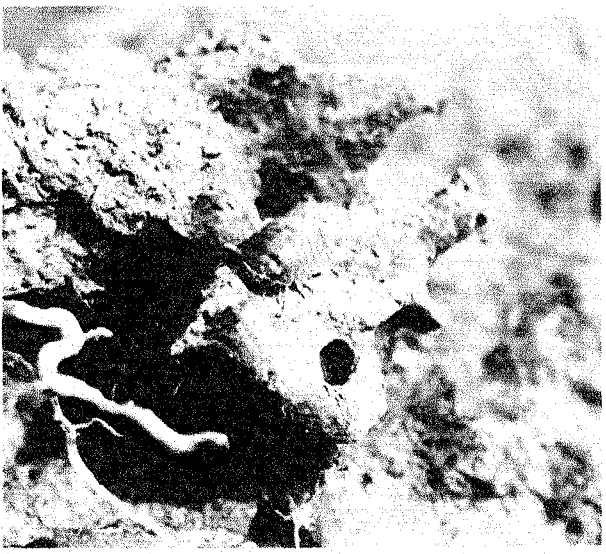

Figure 28. The burrowing isopod (Sphaeroma quoyana).

Table 15. Population biology of the burrowing isopod (Sphaeroma quoyana) (from Schneider 1976). Elevations given are referenced to MSL. Density calculated from quadrats taken on vertical face of mud bank.

	+1.35m	+1.56m	+1.76m
Density(#/m^2)			
March (min)	936	2,646	220
October (max)	3,307	23,637	14,619
Growth rate (mm/30 days) averaged over year		0.64	
season of max growth		Mar-May	

Iais californica was observed as a commensal on S. quoyana. I. californica apparently feeds from the setae of S. quoyana on particles of detritus. Approximately 1/3 of the adult S. quoyana carried I. californica, usually two per animal.

Much less is known for other infaunal organisms in bay tidal marshes. Several large polychaetes (Capitella capitata, Streblospio benedicti, Eteone californica), tube forming amphipods (Corophium spinicorne, Grandidierella japonica) and small bivalves (Gemma gemma, Tapes japonica) can be abundant in tidal wetlands. Quantitative studies conducted on a low mudflat in the Pacific cordgrass zone in south bay indicated that polychaetes are most abundant (91%), followed by oligochaetes (6.2%), bivalvia (1.9%), and amphipods (0.5%) (Fox 1981). Total numbers varied depending on substrate softness (moisture content) from a mean of 500 ind/m^2 to 2500 ind/m^2.

Epifauna

Scurrying crabs, parading mudsnails, and jumping amphipods are usually far more evident to the casual observer than are infauna. The epifaunal organisms are important as detrital processors, algal grazers, and predators. They utilize the structural diversity of the tidal marshes for protection as well as for food resources. Omnivory is probably the rule for most macroconsumers in the salt marsh (Montague et al. 1981). Zedler (1982) has emphasized the significance of algal mats to energy flow for epifaunal macroconsumers.

The Crustacea and Grastropoda are the most common epifaunal organisms. Several large organisms dominate: the yellow shore crab (Hemigrapsus oregonensis), mud snail (Ilyanassa =[Nassarius] obsoleta), and amphipod (Orchestia traskiana). The former two are generally found along the bottom and banks of tidal sloughs and the latter within the litter beneath pickleweed. Three gastropods (Assiminea californica, Ovatella myosotis, and Cerithidea californica) can be locally abundant especially in the higher marsh.

The yellow shore crab (Hemigrapsus oregonensis) burrows into the mudbanks of tidal sloughs. It commonly feeds within the tidal sloughs at night and remains in its burrow during the day. Occasionally, the native lined shore crab (Pachygrapsus crassipes) and the introduced xanthid crab (Rithropanopeus harrisii) are also found in tidal marsh sloughs. The latter is most abundant in the north bay and extends up the river to Stockton (Ricketts et al. 1968). Hermit crabs (Pagurus) have been observed living in burrows of the burrowing isopod (Sphaeroma quoyana) (Cal Acad. Sci. 1977).

The mudsnail (Ilyanassa obsoleta) is by far one of the most abundant epifaunal organisms within tidal sloughs and adjacent mudflats. It was first recorded for the bay in 1907 and was probably introduced from the Atlantic via oyster importation (Carlton 1979). It has largely displaced the native hornsnail (Cerithidea californica) from its once extensive distribution throughout the bay to a limited habitat within high marsh salt pannes in the south bay (Race 1982). The mudsnail feeds on algal-rich substrates, as its stomach contents consist of 75% algae and 25% decomposer microbes (Wetzel 1976). Mudsnails are most active when submerged and congregate around drainage tributaries during low tide to reduce moisture loss (Schaeffer et al. 1968). Thus, it is not unusual to observe extensive populations at low tide which outline the drainage pattern of the marsh.

Race (1981,1982) has studied the population ecology and documented the displacement of the native hornsnail (Cerithidea californica) (Table 16). In estuaries and lagoons outside of San Francisco Bay, the hornsnail typically inhabits pickleweed (Salicornia virginica) marshes, intertidal creeks, and mudflats. In San Francisco Bay, it is limited primarily to high marsh pannes surrounded by pickleweed. During winter months, it retreats to edge habitats beneath the pickleweed. In spring, dispersing hornsnails colonize submerged pannes. Others which begin to migrate to tidal channels exhibit behavioral avoidance when encountering the introduced mudsnail and

Table 16. Popluation biology of the hornsnail (Cerithidea californica) in a south bay marsh (from Race 1981,1982). Numbers in parenthesis indicate sample size.

	Tidal creeks	Salicornia edge	Submerged panne
Density ($\#/m^2$)			
January (min)	0	500	0
July (max)	250*	100	1000
Summer growth rate (mm/30 days)			
Initial size			
<15mm	1.0(3)	2.6(18)	4.0(1)
>25mm	0 (14)	0.2(258)	1.1(18)
Season of maximum growth	Summer		

*Limited to creeks colonized by snails moving from pannes.

are effectively displaced from mudflats. The mudsnail also feeds on egg cases and juveniles of the hornsnail, thereby thwarting further dispersal. The mudsnail is less thermally resistant than the hornsnail and cannot tolerate the warmer conditions in the salt pannes. As long as the panne receives some tidal inundation, the hornsnail grows rapidly during the summer months. It will usually not, however, attempt to colonize upper tidal channels when thermal conditions cause the mudsnail to retreat to lower tidal levels. Steeply eroded banks in areas of Sphaeroma quoyana infestation can limit the ability of the hornsnail to migrate out from the pickleweed marsh.

Two other snails located in the pickleweed marsh, Assiminea californica and Ovatella myosotis, are usually found together, although the latter is in greater numbers. Fowler (1977) investigated the occurence of the two species in a Palo Alto salt marsh. Both occupy the same habitat type (dense pickleweed); however, O. myosotis is more gregarious. Their stomach contents and fecal material appeared identical except for slightly greater mud content in O. myosotis. The ability of the two snails to coexist may be based on food resource partitioning. The radula and radular mass of A. californica are in a highly maneuverable snout which is narrower than that of O. myosotis. Thus, A. californica can obtain food from small crevices that have not been cleared by the broad scraping activity of O. myosotis.

Little work has been done on the amphipods within bay tidal marshes. Several species are quite abundant, including the native species: Anisogammarus confervicolus, Orchestia traskiana, and Hyale plumulosa; and an introduced species: Grandidierella japonica. The amphipods live in the detrital accumulations beneath the pickleweed and feed on live and dead material by shredding large particles. Lopez et al. (1977) noted increased microbial activity on detrital material grazed by the amphipod Orchesita grillus. By shredding particles into smaller sizes, the amphipods expose greater surface area for microbial attachment and activity. Amphipods, therefore, provide an important link between vascular plant production and the microbial processes in the marsh.

Terrestrial arthropods

Insects and spiders are among the most abundant animals within tidal salt marshes. For one species of springtail (Collembola) which feeds on dead plant material, Cameron (1972) estimated an average yearly density of $27,713/m^2$ in a salt marsh along San Pablo Bay. This density is for a single species out of 103 collected. Similar results have been observed in Georgia salt marshes where the planthopper (Prokelisia) reaches abundances of 5000 to $50,000/m^2$ when feeding on smooth cordgrass (Spartina alterniflora)(Pfeiffer and Wiegert 1981). Of course, the species which has received the most attention is the salt marsh mosquito (Aedes). Abatement districts have been formed to respond to the disease and nuisance problems associated with mosquitos. Since the early part of the 19th century, ditching to increase tidal flow has been extensively used in tidal and diked wetlands. More recently (following WWII), pesticide application has received widespread use (Provost 1977). All studies of insects in bay tidal marshes have been undertaken during this period and it is usually assumed that they have adapted to the pesticide application and are, in some cases, resistant (Lane 1969).

Several studies have sampled insect populations in tidal marshes: Lane(1969) in south bay; Cameron (1972) in San Pablo Bay; and Balling and Resh (1982) along Petaluma River and in Suisun Bay. Because different sampling methods and analytical methods were used in each study, comparisons are difficult. For example, based on species lists, less than 10% overlap in species composition was present between Lane's (1969) and Cameron's (1972) studies. On an ordinal level, greater overlap is seen; i.e. flies, gnats, midges, and mosquitos (Diptera) dominated both tidal marshes (Table 17). Species in the Coleoptera, Homoptera, and Hymenoptera were also common. Differences in sampling techniques (i.e. sweeping vs harvesting plant material) accounts for much of the variation observed (Lane 1969). However, the two sites differ in salinity and tidal regimes, factors which are particularly important in structuring insect populations in salt marshes (Foster and Treherne 1976).

Comparisons based on population numbers also differ between marshes (Table 18). In the brackish Petaluma Marsh, Acarina (mites and ticks) dominated (Balling and Resh 1982) whereas Homoptera (leaf hoppers and aphids) and Diptera (true flies) occurred in greater numbers in the salt marsh studied by Lane (1969). Homoptera were most abundant in Pacific cordgrass and pickleweed and were replaced by Diptera within saltgrass (*Distichlis spicata*). The presence of a delphacid planthopper (*Prokelisia* sp.) accounted for the high numbers of Homoptera in the Pacific cordgrass zone and a chironomid midge (*Pseudomittia* sp.) was the most abundant dipteran within saltgrass. The brine fly (*Ephydra cinerea*) was particularly abundant in high marsh salt pannes. Amongst the mats of macroalgae (*Enteromorpha* sp.), the waterboatman (*Trichocorix reticulata*) was common, and fed on the algae as well as midge and mosquito larvae.

Table 17. Taxonomic composition of insects in tidal marshes (from Cameron 1972; Lane 1969).

Location	Habitat	Order	Percentage of total number of species	Number of species
Tolay Creek, San Pablo Bay	*Spartina*	Diptera	40	34
		Coleoptera	21	18
		Hymenoptera	15	13
		Homoptera	8	7
		Thysanoptera	7	6
	Salicornia	Diptera	40	29
		Coleoptera	22	16
		Hymenoptera	13	9
		Homoptera	8	6
		Thysanoptera	8	6
Fremont, South Bay	*Spartina/ Salicornia*	Diptera	46	43
		Homoptera	13	12
		Lepidoptera	12	11
		Hemiptera	9	8

Table 18. Relative abundances (percentage of total number collected) of terrestrial arthropods in bay tidal marshes.

Location	Habitat	Order	% of total
Fremont, South Bay (Lane 1969)	*Spartina*	Homoptera	58
		Diptera	35
		Coleoptera	4
	Salicornia	Homoptera	76
		Diptera	11
		Hemiptera	9
	Distichlis	Diptera	63
		Homoptera	17
		Hemiptera	15
Petaluma Marsh (Balling and Resh 1982)	*Salicornia*	Acarina	51
		Diptera	15
		Hemiptera	10
		Araneae	8

Balling and Resh (in press) recently reported on the life history of waterboatmen (*Trichocorixa reticulata*) in ponds in the Petaluma Marsh. They found that the number of generations produced annually was dependent on the pond longevity. Ponds which dried during late summer contained overwintering, non-reproducing adults while water filled ponds produced another generation. Other factors which modified generation time were: prolonged period of oviposition (usually over a 2-week period), variable egg development time (0-11 days), variable instar development rates, and inter-pond differences in recruitment of adults. Through these various life history adaptations, waterboatmen are able to either accelerate or delay development and subsequent generations as conditions permit.

Mosquito larvae (*Aedes* spp.) are also abundant in high ponds and have received much attention due to the human and animal diseases the adult mosquito can transmit. *Ae. dorsalis* and *Ae. squamiger* are the major species produced within salt marshes. Larvae from the former are found in tidal salt marshes from March to October with peak abundance in August, while the latter produces larvae in both tidal and diked marshlands from November to April with peak abundance in January (Telford 1958, Bohart and Washino 1978). The larvae of both species can tolerate salinities from 2 to 61 ppt. Balling and Resh (1983b) studied the abundance of larvae in high ponds and potholes in marshes throughout the bay. In addition, they took various morphometric measurements of the ponds, measured physical factors, and determined abundance for other insects. Through multiple regression analysis, they found that 62% of the variation in mosquito occurrence could be accounted for by the elevation of the pond. Ponds higher than 1.6 m above MLLW (referenced to the Golden Gate tidal range) most frequently contained mosquito larvae. Abundance of larvae was positively correlated to pond elevation, presence of emergent vegetation, and pond area. They concluded that tidal flushing was probably the most significant factor in reducing larval survival, and that ponds above MHW represent the vast majority of mosquito producing areas. Of these, ponds less than 100 m^2, or if greater than 100 m^2, containing 30 % emergent vegetation, reducing larval survival, were the most likely candidates for ditching. The presence of waterboatmen was negatively correlated with mosquito larval occurrence. This was not due to any predator-prey relationship, but to the drought resistant eggs of the mosquito allowing it to ovidepositin higher elevation ponds.

In addition to catagorization and studies of individual species, classification based on feeding guilds is another way to examine insect populations. Cameron (1972) classified the population in a San Pablo Bay marsh as 50% herbivore, 35% saprovore (detritivore), and 15% predator. In both Pacific cordgrass and pickleweed, he observed an increase in herbivore diversity with increasing aboveground biomass. Predator diversity, consisting mostly of spiders, increased with increasing herbivores. High predator diversity caused a decline in herbivores during mid-summer. Saprovores reached maximum diversity during winter when litter was more available (Figure 30). Lane (1969) did not classify all species into feeding guilds, but did notice increasing numbers and diversity with increasing above-ground biomass of Pacific cordgrass. He noted greater numbers of herbivores on

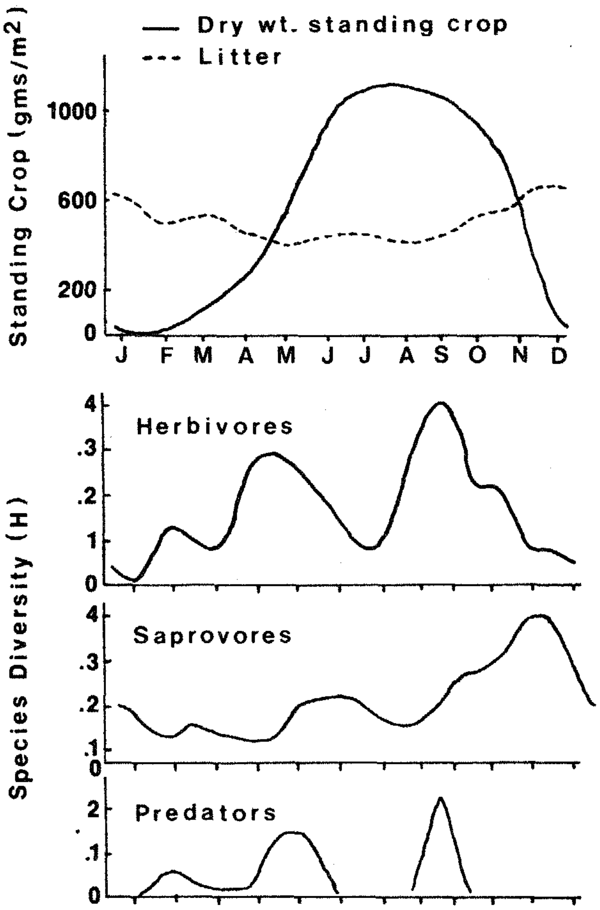

Figure 30. Top: Standing crop of live pickleweed (*Salicornia virginica*) and dead material (litter). Bottom: Changes in species diversity in insects classified as herbivores, saprovores, and predators. Species diversity calculated as Brillouin (H). (from Cameron 1972).

Pacific cordgrass compared to pickleweed. A chloropid fly (*Corticaria*) was especially abundant on the inflorescences of Pacific cordgrass. Spiders were the chief predators and fed heavily on the brine fly (*Ephydra cinerea*).

Balling and Resh (1982) found that age and morphology of mosquito ditches affect insect community structure. Community diversity was lowered near newly excavated mosquito ditches compared to open marsh. Eight-year-old ditches and natural channels, however, had greater diversity than nearby open marsh. This difference was especially pronounced during the summer dry season. They suggested that the higher biomass of pickleweed near channels provided greater food and shelter. Reduced sediment salinities also decreased physiological stress for the insects. In the winter high tides and increased runoff washed out insects near channels. No significant difference was observed between ditches and open marsh in Suisun Marsh where plant diversity was greater and annual salinity fluctuation reduced.

Overall distribution of invertebrates

The distribution and abundance of invertebrates in tidal marshes have been altered greatly through intended or inadvertant introductions and vector control activities. Changes in the hydrology of the San Francisco Bay system due to upstream water management have also influenced invertebrate communities (Hedgpeth 1979). The result is a mix of species unlike any other along the west coast of North America, even in comparison to nearby embayments like Bodega and Tomales Bays.

Zonation patterns of invertebrates in tidal marshes, unlike rocky shores, are difficult to observe due to the presence of sediments and dense vegetation. Individual species, however, are distributed within tidal ranges which depend on their morphological and physiological adaptations (Table 19). Recent work on rocky shores suggest that physical factors (temperature, desiccation, long period of emergence) are the primary determinants of the upper limit to individual species whereas biological factors (competition, predation) affect the lower limits reached by organisms (Carefoot 1977). The information on tidal marsh infauna and epifauna support these general conclusions. The Baltic clam (*Macoma bathica*), the ribbed mussel (*Ischadium demissum*), and the hornsnail (*Cerithidea californica*) are largely limited by increased predation and competitive exclusion at lower intertidal elevations and by harsh physical conditions at high levels. The hornsnail is more tolerant of desiccation than the introduced mudsnail (*Ilyanassa obsoleta*) and, therefore, has found a refuge in the high intertidal zone.

Table 19. Benthic invertebrates collected in three San Francisco Bay salt marshes located in Corte Madera: Muzzi Marsh, Creekside Park, and Triangle Marsh. Diamond indicates introduced species according to Carlton (1979). Habitats defined as: I - Channels, banks, sediments within 0.5 m NGVD; II - Pacific cordgrass zone; III - Rocks and rip-rap; IV - High marsh pools; V - Pickleweed zone. Samples collected in Habitats I, II, and V using coring devices and sieving through 0.5 mm mesh. Hand and net methods used in Habitats III and IV. Data provided by J. Buchholz and E. Lazo-Wasem.

	-Habitat-				
	I	II	III	IV	V
Cnidaria (Coelenterata)					
Anthozoa					
Nematostella vectensis	○	○			
Nematoda					
UID nematodes	○	○		○	○
Annelida					
Polychaeta					
Capitellidae					
◆ Capitella capitata	○	○			
Heteromastus sp.	○				
Nereidae					
Nereis procera	○				
Phyllodocidae					
Eteone californica	○	○			
Serpulidae					
◆ Mercierella enigmata			○		
Spionidae					
◆ Polydora ligni	○	○			
◆ Streblospio benedicti	○	○			
Arthropoda					
Mandibulata					
Crustacea					
Ostracoda					
Cylindroleberis sp.	○	○		○	
Copepoda					
UID Harpactacoid	○				
Cirripedia					
Balanus glandula			○		
Malacostraca					
Mysidacea					
Neomysis mercedis	○				
Tanaidacea					
◆ Tanais sp.	○	○			
Isopoda					
Gnorimosphaeroma oregonensis	○				
◆ Iais californica	○				
Ligia occidentalis			○		
◆ Sphaeroma pentodon	○				
Amphipoda					
Anisogammarus confervicolis	○				
Corophium spinicorne	○	○			
◆ Grandidierella japonica	○				
Hyale plumosa	○	○			
Melita sp.	○	○	○		
Orchestia traskiana			○		○
O. georgiana			○		
Decopoda					
Hemigrapsus oregonensis	○		○		
◆ Palaemon macrodactylus	○				
Labiata					
Insecta					
Hemiptera					
Trichocorixa reticulata				○	
Diptera					
Paraclunio alaskensis	○	○			
Coleoptera					
UID larvae		○			
Chelicerata					
Araneae					
UID spiders			○		○
Acarina					○
Mollusca					
Grastropoda					
Prosobranchia					
Assimineidae					
Assiminea californica					○
Nassariidae					
◆ Nassarius obsoletus (=Ilyanassa obsoleta)	○				
Bivalvia					
Myidae					
◆ Mya arenaria	○	○			
Mytilidae					
◆ Ischadium demissum					
Mytilus edulis			○		
Tellinidae					
Macoma balthica	○	○			

Substrate also affects distribution of intertidal invertebrates. Firm burrowing substrate is needed for the isopod (*Sphaeroma quoyana*), rocky substrate for the lined shore crab (*Pachygrapsus crassipes*), and abundant plant litter for amphipods. Thus, the availability of such microhabitats leads to a mosaic of populations overlying the basic zonation patterns.

Insects have approached marshes from a terrestrial habitat. Their distribution is largely dependent on availability of plant material and, in some cases, they have adapted to individual plant species and the physical factors surrounding those plants. The development of a waterproof integument, efficient osmoregulatory systems, and physiological adaptations to submergence have enabled insects to invade tidal marshes (Foster and Treherne 1976).

6.3 FISH COMMUNITIES IN TIDAL WETLANDS

Scientists have long hypothesized that estuaries and their surrounding tidal marshes are important nursery areas for fishes (Gunter 1967). Estuaries and shallow tidal channels provide protection, food, and reduced osmoregulatory stress for juvenile fish. Much has been written on the significance of salt marsh detrital material in fish diets (Darnell 1967, Odum *et al*. 1972). Both commercially important and non-game species have been studied in relation to their dependence on tidal marshes. Skinner (1962) has reviewed former and present distributions of commercial fisheries in relation to bay tidal marshes. Smith and Kato (1979) partially attribute the decline of commercial fisheries in San Francisco Bay to wetland habitat loss. Yet, few studies have examined fish utilization of tidal marshes in the bay. Of the 121 species recorded for the bay, Jones and Stokes Assoc. (1979) listed only 16 species expected to occur in tidal marshes but indicated that no definitive data exist to enumerate uses or abundances.

A recent study by Woods (1981) documented seasonal use of a tidal slough system at the Hayward salt marsh restoration in the south bay. She used three collection techniques (otter trawl, minnow trap, and gill net) and found marked differences among the fish species collected (Table 20). Of the 22 species collected, the two most abundant species throughout the year were the topsmelt (Atherinops affinis) and the arrow goby (Clevelandia ios). They comprised 75% of the total catch. The yellowfin goby (Acanthogobius flavimanus) and the staghorn sculpin (Leptocottus armatus) were also common. Spring and summer months yielded the greatest abundance of the top four species; few to none were collected in winter months. The majority of the fishes caught were juveniles suggesting that the tidal sloughs provide a nursery habitat for these species. Other studies in the south bay confirm the significance of topsmelt and gobies within shallow slough systems (Jones and Stokes Assoc. 1979). Additional species frequently sampled are: shiner surfperch (Cymatogaster aggregata) and three-spined stickleback (Gasterosteus aculeatus). The latter species is more common in the upper reaches of tidal channels and mosquito ditches, along with the mosquitofish (Gambusia affinis)(Balling et al. 1980).

The topsmelt (Atherinops affinis) is well adapted to estuarine conditions. Carpelan (1955, 1957) found it to be the most abundant fish in salt ponds, tolerating salinities up to 80 ppt. It apparently also tolerates diurnal temperature ranges of 12°C and an annual range of 25°C to a maximum of 33°C. Alcorn et al. (1980) observed no decline in the abundance of topsmelt in a salt marsh slough subject to an untreated sewage effluent spill. Topsmelt are bottom grazing fish, feeding on diatoms, detritus, insect larvae, and amphipods (Moyle 1976). Swift currents in tidal sloughs may resuspend these materials. Although topsmelt are abundant in shallow waters offshore from tidal marshes, they are never found as the dominant species (Green 1975). Eggs and larvae are only infrequently collected

Table 20. Total number of fish caught within tidal sloughs at the Hayward salt marsh restoration (June 1980 - May 1981) (from Woods 1981).

Species	Ottertrawl	Minnow trap	Gill net	Total #	Total %
Topsmelt (Atherinops affinis)	2829	1	61	2891	43
Arrow goby (Clevelandis ios)	2172	0	0	2172	32
Yellowfin goby (Acanthogobius flavimanus)	692	9	8	709	10
Staghorn sculpin (Leptocottus armatus)	566	5	7	578	8
3-spined stickleback (Gasterosteus aculeatus)	144	26	0	170	2
Starry flounder (Platichthys stellatus)	83	0	0	83	1
Longjaw mudsucker (Gillichthys mirabilis)	15	28	0	43	0.6
Northern anchovy (Engraulis mordax)	24	0	2	26	0.4
Leopard shark (Triakis semifasciata)	0	0	20	20	0.3
- (Other species 13 sp)	19	0	21	40	0.6

offshore and usually in low numbers (Eldridge 1977). In the Tijuana estuary in southern California, Norby (1982) found that the abundance of topsmelt eggs and larvae were positively correlated with algal mats, particularly *Enteromorpha*. The algal mats grew more abundantly in low velocity tidal channels in marshes. Thus, it appears that topsmelt are very dependent on tidal marshes for juvenile survival and are able to tolerate the fluctuating and sometimes harsh conditions as adults.

The gobies found in tidal marshes are also tolerant of widely fluctuating conditions. Both yellowfin goby (*Acanthogobius flavimanus*) and the longjaw mudsucker (*Gillichthys mirabilis*) can be found in freshwater (Moyle 1976). They are bottom feeders, utilizing small invertebrates, diatoms, and small fish. The longjaw mudsucker is of commercial importance as a baitfish and can be locally depleted by bait collectors (Moyle 1976).

The presence of leopard sharks in shallow tidal sloughs is also related to their benthic feeding habits. de Wit (1975) determined that polychaetes comprised 64% of the stomach contents of leopard sharks in the south bay. Other food items included: crabs (13%), shrimp (9%), clams (7%), and fish and fish eggs (10%). Of the fish, atherinid eggs and juveniles were most abundant. Russo (1975) was unable to confirm the significance of intertidal feeding for the leopard shark, but noted a greater abundance of intertidal organisms in the stomachs of brown smoothhounds (*Mustelus henlei*). Apparently, sharks of both species are important bottom feeders and can be significant predators in tidal sloughs.

In San Pablo Bay, greater numbers of juvenile anadromous fish and adult freshwater fish are observed. Madrone Associates (1977) observed large numbers of juvenile striped bass (*Morone saxatilis*) in their three-year study of Napa Marsh sloughs (Table 21). Similar abundances have been observed in Marin County wetlands by Josselyn (unpubl). During summer months, when salinities are higher, typical estuarine species such as the yellowfin goby and the staghorn sculpin (*Leptocottus armatus*) are prevalent. The reduction in salinities during periods of high delta outflow allow delta smelt (*Hypomesus transpacificus*) and tule perch (*Hysterocarpus traski*) to extend further seaward in the north bay. All of the fish feed on similar food: small benthic invertebrates and insects.

Moyle *et al*. (1982) sampled the fish community in the tidal sloughs of Suisun Marsh. Of the 39 species collected, 2 were endemic to the Delta; 13 were native marine, estuarine, or anadromous species; 5 were freshwater; and 18 were introduced

Table 21. Fish collected in the Napa Marsh Slough: 1973-1976 (from Madrone Assoc. 1977).

Species	Season of max numbers	Total # caught	Percent of total caught
Striped bass (*Morone saxatilis*)	summer	1,672	50
Delta smelt (*Hypomesus transpacificus*)	winter-spring	488	14
Yellowfin goby (*Acanthogobius flavimanus*)	summer-fall	246	7
Tule perch (*Hysterocarpus traski*)	winter	201	6
Pacific staghorn sculpin (*Leptocottus armatus*)	summer	181	5
Splittail (*Pogonichthys macrolepidotus*)	summer	129	4

species. The most common species were present as year-round residents with more freshwater forms present in the winter-spring period (Table 22). Striped bass (*Morone saxatilis*), particularly juvenile forms, were the most abundant fish. The juveniles fed primarily on the opossum shrimp (*Neomysis mercedis*), and adults fed on other fish. *N. mercedis* is a significant component in the diets of most other fish as well. They noted that dietary overlap was greatest among introduced species and seasonal species whereas native residents had the least overlap in food resources. Most of the species were channel feeders with only a few feeding within the vegetation of the tidal marshes.

An introduced species which has assumed great importance in salt and brackish marshes around San Francisco Bay is the mosquitofish (*Gambusia affinis*). Mosquitofish are tolerant of a wide range of temperatures (4° to 37°C) and salinities (Moyle 1976). They tolerate low oxygen levels by utilizing the upper few millimeters of the water column. They are omnivorous and opportunitistic feeders. They will consume abundant quantities of mosquito larvae as well as any other appropriately sized organisms such as algae, zooplankton, and benthic invertebrates. They generally prefer relatively open water areas and do not penetrate areas of dense vegetation. Krumholz (1948) has reviewed their reproduction and population ecology and found that most fish live less than 15 months. Growth is dependent on food supply and temperature. Four broods may be released each year.

Mosquitofish are generally released for mosquito larval control into salt and

Table 22. The ten most common fish species collected in Suisun Marsh (1979-81) (from Moyle *et al*. 1982). Asterisk indicates introduced species.

Species	Percent of Catch	Seasonality	Feeding type	Primary food
Striped bass (*Morone saxatilis*)*	28	resident	carnivore	*Neomysis*, fish
Splittail (*Pogonichthys macrolepidotus*)	18	resident	omnivore	*Neomysis*, debris
Three-spined stickleback (*Gasterosteus aculeatus*)	16	resident	benthic carnivore	polychaetes, copepods
Tule perch (*Hysterocarpus traski*)	9	resident	benthic carnivore	amphipods
Longfin smelt (*Spirinchus thaleichthys*)	8	winter-spring	planktivore	*Neomysis*
Prickly smelt (*Cottus asper*)	6	resident	benthic carnivore	amphipods
Yellowfin goby (*Acanthogobius flavimanus*)*	3	resident	benthic carnivore	*Neomysis*
Sacramento sucker (*Catostomus occidentalis*)	3	spring	detritivore	benthic copepods, debris
Common carp (*Cyprius carpio*)*	2	resident	-	-
Staghorn sculpin (*Leptocottus armatus*)	2	spring	benthic carnivore	*Neomysis*

brackish ponds. Artifical ditches in the high marsh or pickleweed zone can provide refuge for mosquitofish during low tides and aid in their dispersal to other areas in the marsh. Balling et al. (1980) found that mosquitofish density was three times greater in ditched areas (11 fish/m^2) than unditched areas (4 fish/m^2). A greater proportion of juveniles were found in ditched areas. An experimental ditching program indicated that the juvenile fish migrated to new areas via channels rather than through submerged vegetation at high tide. In addition to larger populations of mosquitofish, ditched wetlands contained twice as many other species of fish as unditched areas. Their study focused on ditches which enhanced circulation. Ditches designed simply to drain the high marsh would be less effective in supporting diverse fish communities because they lack standing water at low tide.

Much remains to be learned about fish communities in bay tidal marshes. Synoptic studies of open bay and marsh habitats are required to understand the dependence of various species on the tidal slough system. The few species most frequently caught in marsh sloughs are physiologically adapted to changing and extreme conditions. These attributes allow them to exploit the abundant food resources of the marsh in the absence of other potential competitors. We are only beginning to understand how slough morphology affects the productivity and distribution of tidal marsh fish. Norby (1982) found that relatively deep channels with low tidal velocities provided the best spawning habitat for topsmelt, longjaw mudsucker, northern anchovy and staghorn sculpin. The design of circulation channels in marsh restorations should benefit from such increased knowledge.

6.4 BIRDS USING TIDAL MARSHES

San Francisco Bay marshes play an extremely important role in the migration of birds through the Pacific flyway. Most of the available data relate to waterfowl, especially gamebirds. In 1968, California Department of Fish and Game [DFG] estimated that sixty percent of the canvasbacks (Aythya valisineria) and over 20% of the greater and lesser scaups (Aythya sp.) and surf scoters (Melanitta perspicillata) in the Pacific flyway utilized the bay wetlands (California Dept. Fish and Game [DFG] 1968). The percentage use varies considerably each year and has declined more recently (R. Lowe, pers. comm.). Northern pintails (Anas acuta) are more abundant, but only 9% of the total population are estimated to use bay wetlands. Most of the waterfowl utilize the open water and adjacent salt ponds, scattered freshwater marshes, or the managed diked wetlands of Suisun Marsh (Gill 1977, Bollman et al. 1970).

The majority of birds utilizing San Francisco Bay tidal marshes are migratory and do not breed in this area. Bollman et al. (1970) observed the greatest number of birds during the spring and fall (Figure 31). During the 1964 and 1965 censusing seasons, over 3.5 million birds were counted each year. Fifty-five percent were shorebirds and 34% waterfowl. Of the habitats surveyed, mudflats and saltponds had the highest bird densities and vegetated marsh areas the lowest. Herons, coots, and terns had the highest percentage observations in tidal marshes relative to other species; however, their total numbers were low (Table 23). Shorebirds were the most abundant birds in tidal marshes. Bird censusing in the Bollman et al. (1970) study was conducted on ebbing tides. Cogswell (1981) observed marked differences in bird populations in tidal marshes during various tide phases. Mudflat feeders, such as shorebirds, utilized open areas in the marsh when outer mudflats were covered and retreated to islands and levee banks at the highest tides. During low tide, they followed the retreating water edge, feeding on the newly exposed mudflat. Fish-eating birds such as herons and egrets usually remained in the marsh and fed along sloughs or in shallow ponds. Other fish-eating birds, such as terns and cormorants, were attracted to concentrated fish populations in tidal sloughs during ebbing tides. Ducks were most abundant at high tide periods when 95% to 100% of the marsh surface was covered. Thus, the Bollman et al. (1970) study probably underestimated bird utilization in tidal marshes.

Numerically the most abundant species found in tidal marshes are the shorebirds (Figure 32). The more common species

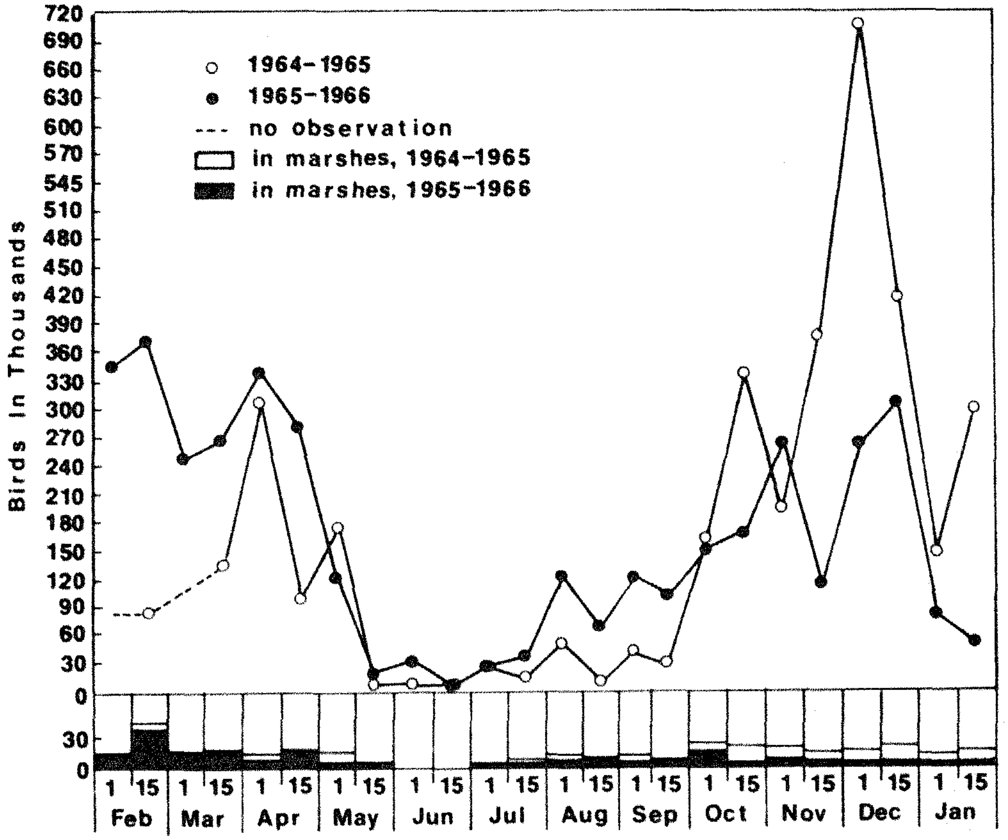

Figure 31. Top: Total number of birds observed at 13 sites in San Francisco Bay during 1964-66. Habitats surveyed at each site included: tidal marsh, mudflats, salt ponds, open water, and other. Bottom: Number of birds in thousands observed at 13 bay sites within tidal marshes for 1964-65 and 1965-66 (from Bollman *et al*. 1970).

include: American avocet (*Recurvirostra americana*), long-billed dowitcher (*Limnodromus scolopaceus*), dunlin (*Calidris alpina*), marbled godwit (*Limosa fedoa*), semipalmated plover (*Charadrius semipalmatus*), willet (*Catoptrophorus semipalmatus*), black-necked stilt (*Himantopus mexicanus*), and various sandpiper species (*Calidris* spp). Most are migratory and usually feed on adjacent mudflats or salt ponds. Of the shorebirds, only the American avocet, black-necked stilt, and snowy plover (*Charadrius alexandrinus*) establish nests and breed in this region (Gill 1977). Shorebirds are extremely active feeders and may have a significant impact on their prey organisms (Quamman 1981). Recher (1966) hypothesized that population density of shorebirds on bay tidal flats was controlled by available feeding space and that food was generally abundant relative to the metabolic requirements of the birds. He did notice differences in prey selectivity among shorebirds (Table 24). The American avocet and willet were least selective whereas the semipalmated plover was the most selective. Feeding methods and major prey items also differed among species allowing for some resource partitioning on the mudflat. Within tidal marshes, most feeding activity is restricted to tidal sloughs and high marsh pools. At extreme high tides, shorebirds may congregate in dense masses awaiting the exposure of their feeding habitat. Kelly (1976) observed that willets and marbled godwits habitually used certain high tide roosts in the salt marsh, moving approximately 1 km between the roost and the mudflat. Slight variations in the topography of the marsh and the protection afforded by the

Table 23. Birds counted monthly in 13 tidal marshes around San Francisco Bay during 1964-65 (from Bollman et al. 1970). Other habitats counted were: open water, tidal flats, salt ponds, and other (in flight).

Bird type	Number of birds in tidal marsh		% of total counted within tidal marshes	
	1964	1965	1964	1965
Pelicans	170	95	1.5	0.7
Shore birds	67,950	125,700	3.3	6.2
Loons	0	2	0.0	2.9
Cormorants	640	395	9.0	3.2
Herons	1,280	2,852	23.0	31.0
Ducks	17,750	19,200	1.4	1.5
Geese	0	20	0.0	5.0
Grebes	210	140	1.7	0.4
Coots	2,560	14,170	7.2	29.4
Gulls	500	14,450	0.3	3.6
Terns	700	800	6.6	3.8
Total	91,760	177,824	2.5	4.6

vegetation may reduce metabolic losses due to wind chill and extreme high tides.

Fish-eating birds such as herons and egrets frequent tidal marsh areas at all tide levels. Though they are never very abundant, their size and graceful appearance make them more apparent to the casual observer. They are easily disturbed by human activity and are flushed more readily. They feed along tidal sloughs, posing quietly at the water's edge and making rapid stabs at prey items (Figure 33). They prefer to nest in tall trees or bulrushes, but will use small shrubs adjacent to tidal marshes (Gill 1977).

Resident bird species which rely on tidal marshes for breeding and nesting are most impacted by habitat loss (Table 25). Foster (1977) estimated that populations of salt marsh yellowthroat (Geothlypis trichas sinuosa) have been reduced by 80% to 95% in the last 100 years, and California clapper rails (Rallus longirostris obsoletus) were once so abundant that sportsmen would kill thousands in a single week (Shellhammer and Harvey 1982). Because of their current or potential endangered status, studies have been com-

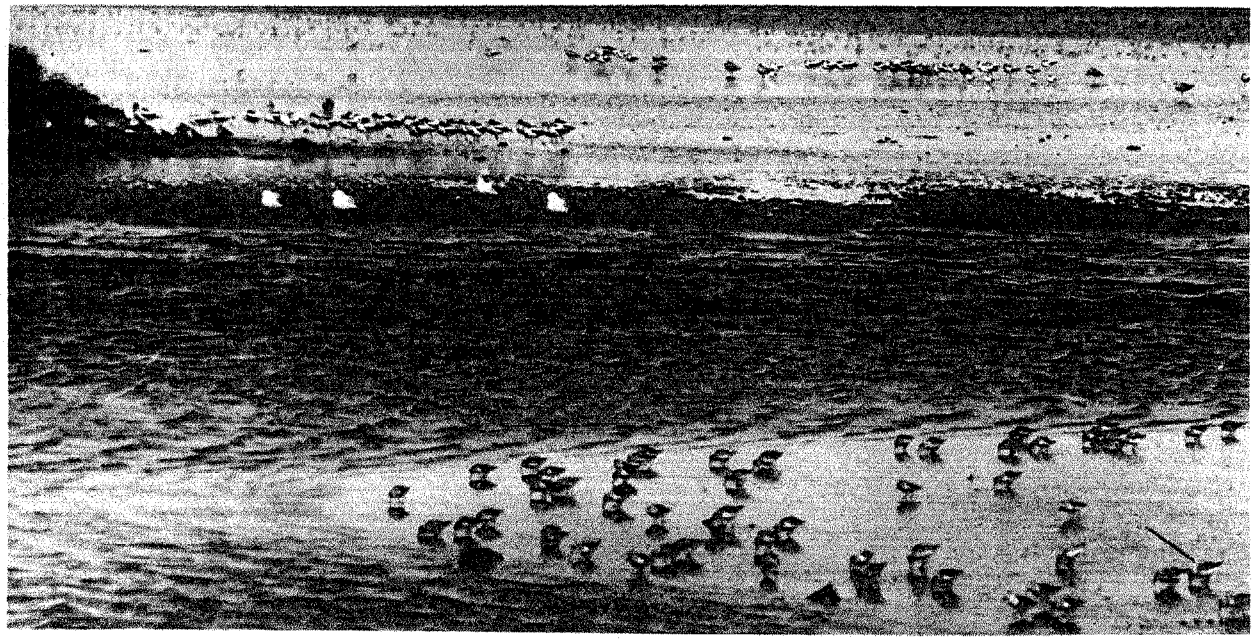

Figure 32. Mudflat offshore of tidal marsh in south San Francisco Bay populated by shorebirds including sandpipers (foreground), American avocets (middle left and top right), and dowitchers (middle right) (Photo by D. Spicher).

Table 24. Prey diversity and feeding techniques for various shorebirds in bay tidal marshes (from Recher 1966).

Species	Prey diversity (H)	Feeding Method	Depth in mud of effective feeding (cm)	Major prey item	Median size of prey (mm)
American Avocet	1.23	sweeping	surface	small bivalves	<6
Dowitcher	1.02	deep probe	8	polychaetes	6-12
Marbled godwit	0.86	deep probe	15	polychaetes	6-12
Semi-palmated plover	0.19	rapid peck	surface	polychaetes	6-12
Willet	1.33	probe	5	small bivalves	<6
Western sandpiper	1.17	rapid peck	2	ostracod	<6

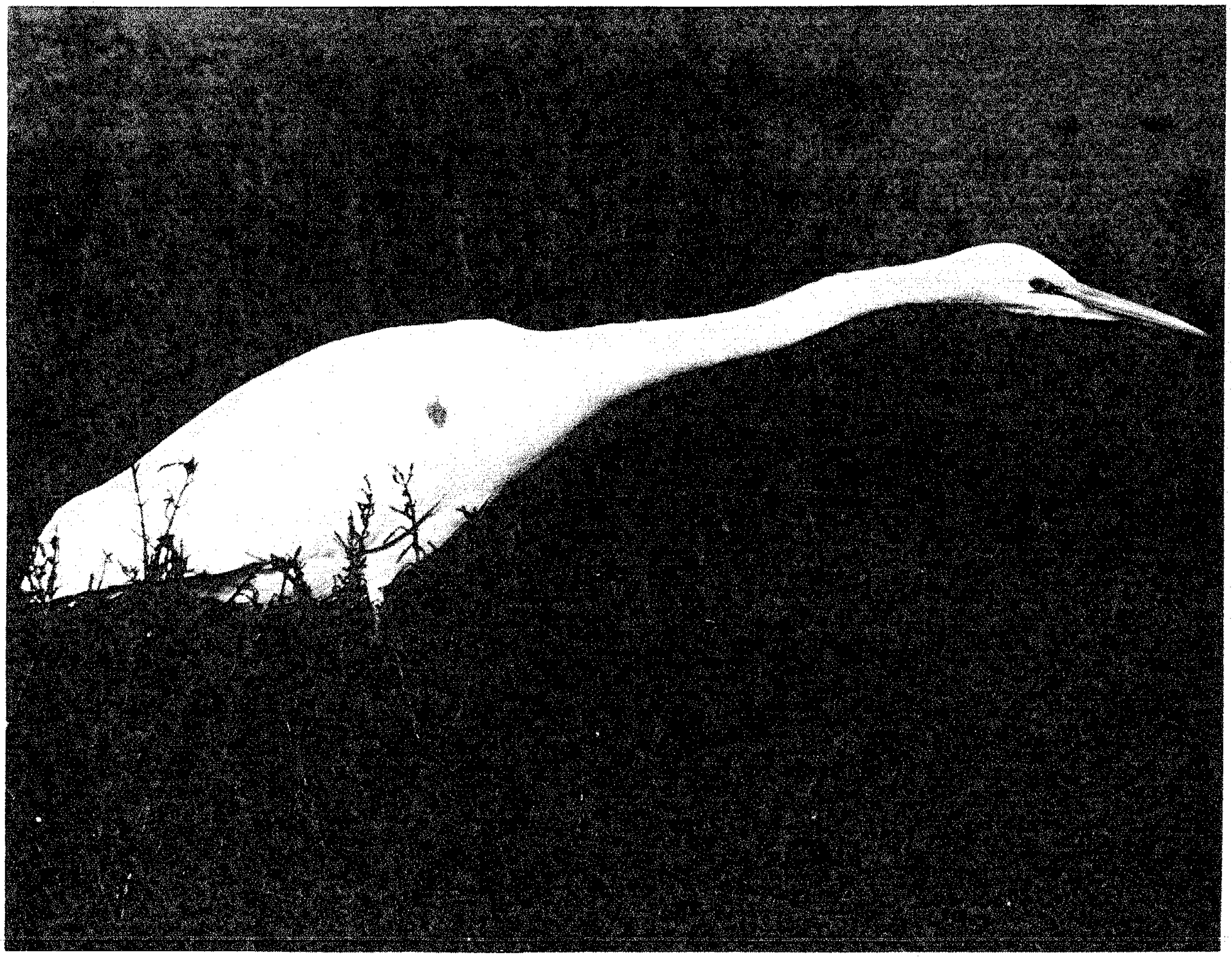

Figure 33. Great egret within pickleweed (Photo by L.V.J. Compagno).

Table 25. Breeding bird populations within tidal marshes of south San Francisco Bay during 1971 (from Gill, 1977).

Species	Nesting habitat	Peak nesting	Mean clutch size
Great blue heron	Tops of coyote bush, bulrush	May	3.63
Black-crowned heron	Gumplant/ pickleweed	May	2.89
Snowy egret	Gumplant/ pickleweed	June	3.20
White-tailed kite	Tops of coyote bush	May	3.50
Marsh harrier	Pickleweed/ cordgrass	May	5.00
California clapper rail	Cordgrass/ pickleweed	May	6.83
Long-billed marsh wren	Cordgrass/ cattails	May	-
Red-winged blackbird	Salt marsh	May	-
Savannah sparrow	Pickleweed/ levee	May	3.60
Salt marsh song sparrow	Pickleweed/ cordgrass	April	2.90

pleted which assess the population biology of these resident species.

The salt marsh song sparrow (Melospiza melodia) is a resident species which establishes small territories within pickleweed along tidal sloughs and channels (Figure 34). Three races, each numbering between 2000-5000 mated pairs, occur in the bay area: Alameda (M. m. pusillula), Samuel's (M. m. samuelis), and Suisun (M. m. maxillaris)(Walton 1978). Within suitable habitats, population densities range between 5 to 30 pairs/hectare. Isolation of these races is due to limited dispersal of young and the distances between adjacent populations. Johnston (1956a) estimated the mean dispersal distance of young from hatch site to nesting site as 185 m, and Walton (1978) observed that channels greater than 50 m wide were effective barriers to dispersal. Distances between adjacent populations range between 1 km in Suisun Marsh to 10 km in south bay (Walton 1978). Any further habitat loss will lead to greater isolation.

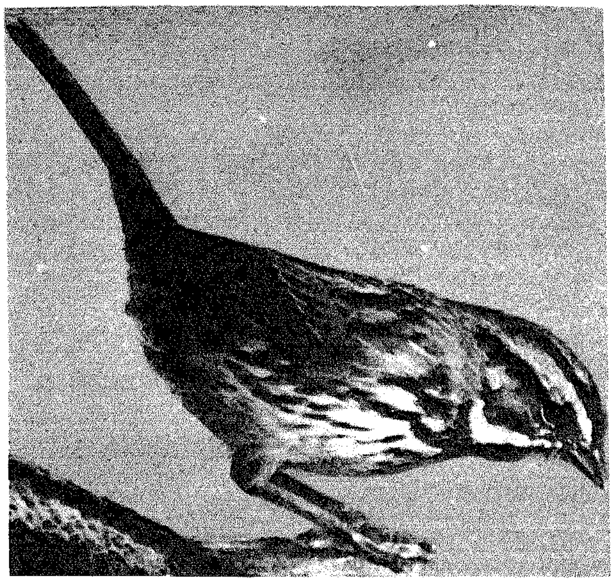

Figure 34. Salt marsh song sparrow (Photo by L.V.J. Compagno).

Territoriality in the salt marsh song sparrow is observed throughout the year, but is strongest in March in association with nesting. Territories range in size from 350 to 650 m^2 and are located almost exclusively within pickleweed at a distance not greater than 10 m from a waterway (Johnston 1956b, Walton 1978, Collins and Resh in press). Territory size is at a minimum during the nesting season due to both an increase in the availability of food (seeds and insects) and the greater concentration of activity near the nest. The most successful nests are built in the canopy at a height above highest high tides of spring, yet low enough in the canopy to conceal the young from raptors. For the Petaluma marshes, Collins and Resh (in press) determined that nests must be at least 25 cm above the ground and the vegetative cover over 50 cm tall to afford relatively safe nest sites. Territory size is also dependent on the type of waterway adjacent to the nesting site. Collins and Resh (in press) found that smaller territories occurred adjacent to natural channels and sloughs (avg = 387 and 498 m^2, respectively) rather than to mosquito control ditches (avg = 644 m^2). The authors attributed the reduced territory size to greater food availability (concentration) along natural waterways due to higher plant biomass and diversity. Vegetation is equally important during the post-nesting season. The numbers of salt marsh song sparrows were positively correlated with the vegetation height and percent cover of coyote bush (*Baccharis pilularis*). Coyote bush, apparently, provides both an importrusesant roosting structure and a summer food resource. The authors conclude that although mosquito control ditches are not a preferred habitat for the salt marsh song sparrow, the increased system of waterways has resulted in a higher carrying capacity for this species in the marsh.

The salt marsh yellowthroat (*Geothlypis trichas sinuosa*) nests in freshwater marshes in the spring and summer, and during the winter spreads into adjacent salt marshes. Dispersal is along tidal sloughs and channels. Foster (1977) observed that disturbed areas between fresh and salt marsh habitats restrict movements. Site fidelity may also be important in restricting movement outside the natal locality. Population size is low; Gill (1977) estimated only 25 to 30 pairs in Coyote Hills, and Foster (1977) found a few sites with only one to two pairs. Planning for wetland enhancement and restoration must include consideration of means to encourage the dispersal of both the song sparrow and yellowthroat.

The California black rail (*Laterallus jamaicenisis coturniculus*) and the California clapper rail (*Rallus longirostris obsoletus*) were historically widely distributed throughout northern California. The destruction of tidal salt marsh habitat upon which they depend for food and breeding has decimated the populations resulting in designation of "rare" status for the former (California Dept Fish and Game 1978) and "endangered" status for the latter (California Dept Fish and Game 1978, USFWS 1979).

The California black rail, although rare throughout its range in California, is fairly common in San Francisco Bay. It is not frequently observed, however, due to its secretive nature. It is more abundant in brackish areas such as the Petaluma River, the Napa River, and Suisun Slough. Evens and LeValley (1981) estimated 150 birds in a marsh near Port Chicago (Suisun Bay) and 40 birds have been counted in the Petaluma Marsh (Evens and Page 1983). It appears to be more frequent in winter, though this may be an artifact of the difficulty in observing birds during the March to June breeding and nesting period. High tides during the winter tend to drive birds out of the marsh to higher ground and within sight of observers.

Evens and Page (1983) found that the density of California black rails in the Corte Madera Ecological Reserve salt marsh was correlated with areas containing 90%-97% cover by pickleweed and a high degree of understory penetrability. The latter attribute was defined as the relative ability of a 4.2 cm object (diameter of a black rail) to pass through the pickleweed understory. Canopy height in this type of habitat averaged 29 cm. No association with channels was found. Insects and crustaceans are listed as the primary food of the black rail (Jones and Stokes Assoc. 1979). Predation on the rail occurs primarily during extreme high tides when birds seek cover along the marsh periphery or at the top of emergent vegetation. Evens and Page (1983) reported attacks on rails by the northern harrier (*Circus cyaneus*), a great egret (*Casmerodius albus*), and a great blue heron (*Ardea herodias*). Tall vegetation located above tide level apparently provides a refuge for the rail and protection from predators.

Due to its endangered status, more studies have been conducted on California clapper rail (Figure 35). Once widely distributed in northern California, breeding populations are now restricted to San Francisco Bay and Elkhorn Slough. Nonbreeding individuals have been found in Humboldt, Morro, and Tomales Bays (Gill 1979). The rail is restricted to tidal salt marshes; however, individuals have recently been found on Joice and Grizzly Islands in Suisun Bay (Shellhammer and Harvey 1982). The rail typically utilizes small tidal sloughs as foraging habitat and rests in either Pacific cordgrass or pickleweed. Cordgrass supports the highest densities of rails due to isolation from feral predators and Norway rats, the cover provided from raptors, and the proximity of preferred feeding areas.

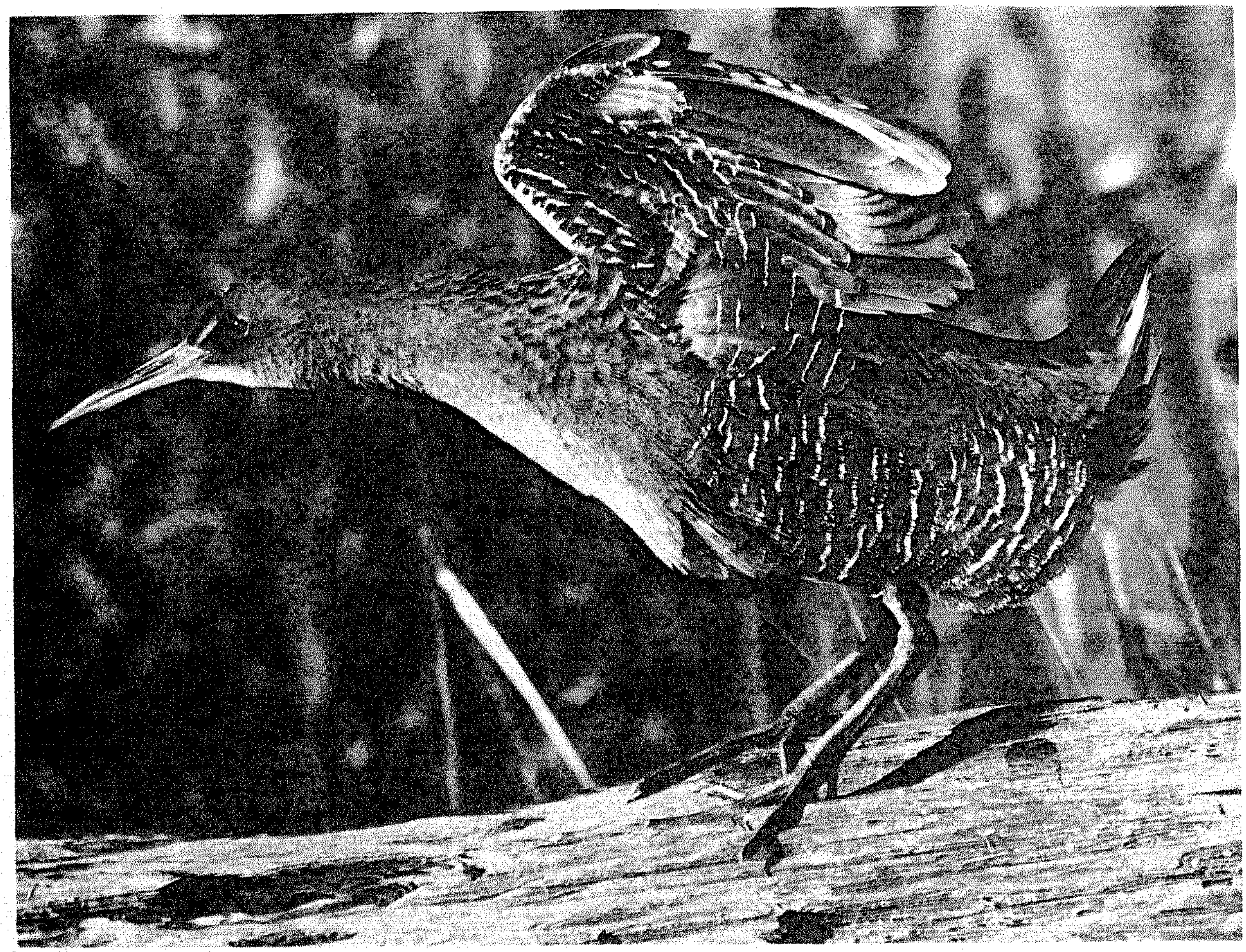

Figure 35. California clapper rail (Photo by L.V.J. Compagno).

The food of the California clapper rail consists of 85% animal matter and includes the ribbed mussel (Ischadium demissum), the Baltic clam (Macoma balthica), the yellow shore crab (Hemigrapsus oregonensis), and spiders. Rails will also feed on small mammals, including harvest mice (Figure 36). Its preference for ribbed mussels leads to the frequent observation of missing toes among adult rails (Figure 37). Apparently mussels clamp down on rail feet inserted in their mantle and remain attached until dislodged or the toe is lost. Mussel shells are often observed in or around the nest indicating that the birds can dislodge the shell from its substrate. This is contrary to DeGroot's (1927) hypothesis for the demise of the California clapper rail: young chicks drowning while being held between the valves of a mussel.

California clapper rails build their nests between mid-March and July. In a Corte Madera marsh, Evens and Page (1983) found that most clapper rail nests were located within 1.5 m of a channel, and only a few were observed further than 3 m. The rails generally preferred small channels, the average minimum size being 36 cm deep and 63 cm wide. The most common nest type is built within Pacific cordgrass utilizing cordgrass stems for the nest (Figure 38). Other plants may provide habitat for nesting including pickleweed and gumplant (Grindelia humilis). The nest usually is built off the ground and can move upwards during the highest tides. Average clutch size is between 6-8 eggs. Harvey (1980) observed a 38% hatching success and 56% nesting (nest producing young) success. Fledging success has not been determined. For

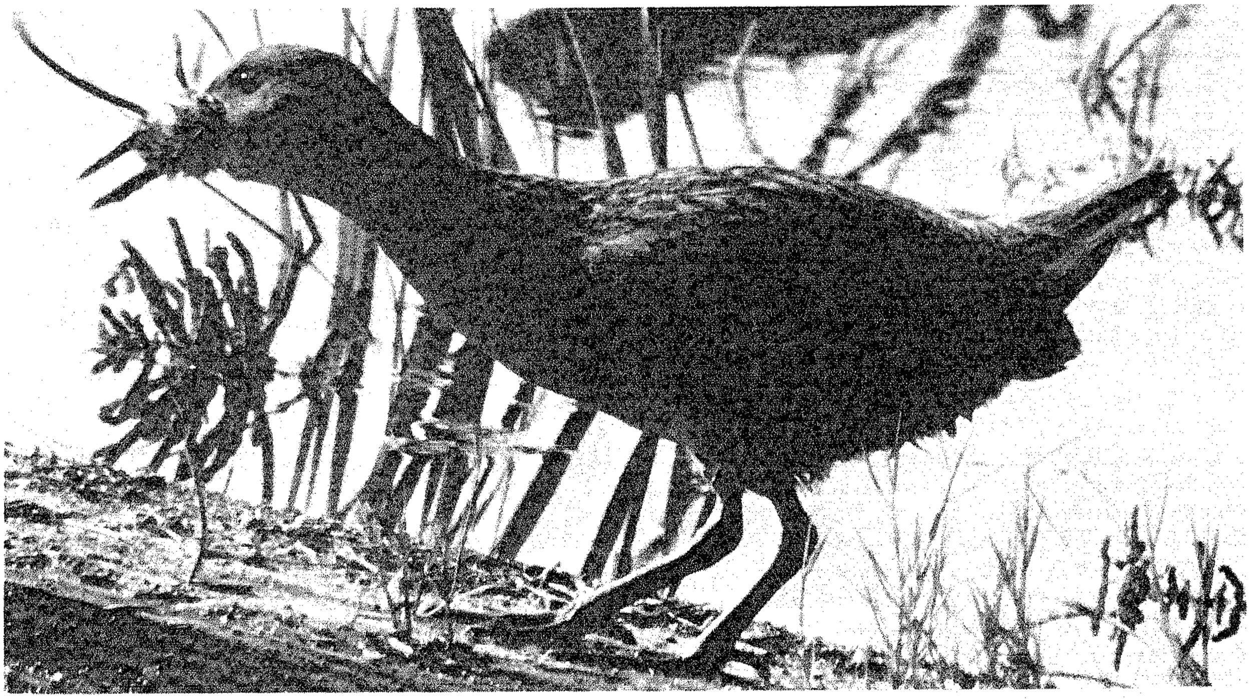

Figure 36. California clapper rail feeding on harvest mouse. Mouse identified from previous photos. Prey was captured while retreating from marsh at high tide (Photo by L.V.J. Compagno).

Figure 37. Adult California clapper rail with attached ribbed mussel. Note missing toe at far left (Photo from Applegarth 1938).

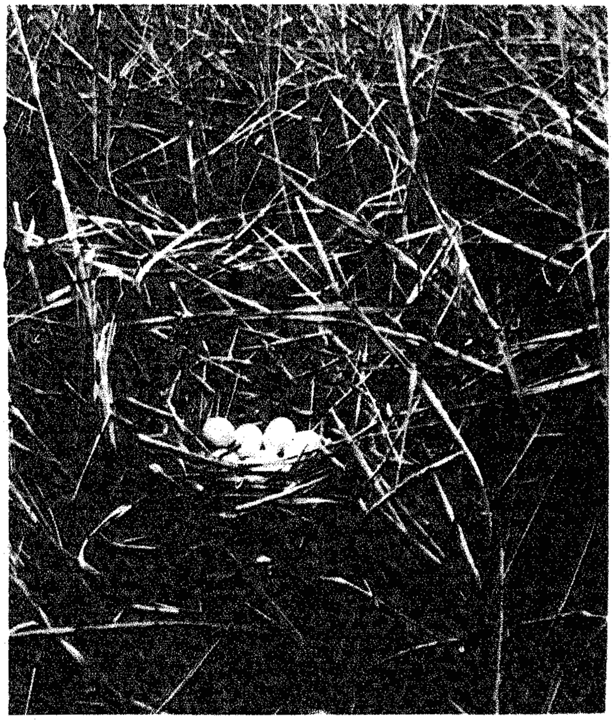

Figure 38. Clapper rail nest built within Pacific cordgrass (Photo from Applegarth 1938).

downy young, the Norway rat is probably the most significant predator whereas adults are preyed upon by the red-tailed hawk, peregrine falcon, barn owl, and northern harrier. In a year-long study, Evens and Page (1983) found 11 carcasses of young and adult birds out of an estimated population of 44 birds. Most dead birds were found along an abandoned boardwalk in the marsh, suggesting that the raptors utilize this artifical perch for stalking and feeding on their prey.

Adult California clapper rails have a limited dispersal. They generally remain hidden amongst the tidal slough vegetation and fly only short distances along the slough (Shellhammer and Harvey 1982). Gill (1979) estimated the rail population for the period of 1971-5 as between 4,200 to 6,000 individuals, with 55% located in the south bay and 45% in San Pablo Bay. Shellhammer and Harvey (1982) cite more recent surveys which estimate the south bay population at half of the 1971-5 population. Breeding population densities average 1.5 rails/ha (Gill 1979, Harvey 1980, Evens and Page 1983). Shellhammer and Harvey (1982) recommend an acquisition, management, and research/education plan to protect the California clapper rail. It is likely that the other resident bird species discussed above will benefit from these efforts.

6.5 MAMMALS FOUND IN BAY TIDAL MARSHES

Prehistoric and historic evidence support the conclusion that bay tidal marshes were once rich in the abundance and diversity of mammalian inhabitants. Roosevelt elk (Cervus canadensis roosevelti) and tule elk (C. c. nannodes) were abundant as well as black-tailed deer (Odocoileus hemionus columbianus). Predators such as the grizzly bear (Ursus californicus) and mountain lion (Felis concolor californica) were frequent. Hunting and the livestock industry combined to reduce the numbers of these large mammals by the early 20th century. Other valuable furbearing mammals, such as mink (Mustela vison) and river otter (Lutra canadensis brevipilosus), were hunted and drastically reduced. Marine mammals, such as the harbor seal (Phoca vitulina) which utilized tidal wetlands as haul-out areas, were equally sought after. Legislative protection (either through licenses or total protection) have brought better management to mammalian resources, but populations have suffered irreversible declines due to habitat loss and urbanization.

Many small mammals can be found in bay tidal marshes (Table 26). Many simply use the marsh as a foraging area or for dispersal and are usually found around the upper fringes of the marsh. Only two species are totally dependent on the tidal wetland: the Suisun shrew (Sorey sinuosus) and the salt marsh harvest mouse (Reithrodontomys raviventris). The latter is designated as an endangered species (US FWS 1979). A protected species, the harbor seal (Phoca vitulina), has consistently utilized a salt marsh in south bay as a rookery (Fancher and Alcorn 1982).

The salt marsh harvest mouse (Reithrodontomys raviventris) consists of two populations: a northern (San Pablo and Suisun Bays) subspecies (R. r. halicoetes) and a southern (Corte Madera, Richmond, south bay) subspecies (R. r. raviventris). It frequents both salt and brackish water habitats, and both diked and non-diked areas. Its preferred habitat is pickleweed, where it feeds on green vegetation and seeds. Both Haines (1964) and Fisler (1963) studied the water intake by harvest mice and found that the northern subspecies regulates its intake of salt to about the same level at all concentrations offered it, but the southern subspecies prefers to consume considerable salt water, decreasing only after 0.4 molar is reached. It has generally been assumed that the mice spend their entire life within the salt marsh, however, Zetterquist (1977) observed small numbers in marginal (non-tidal marsh) habitats in the south bay. It is probable that diked land with suitable vegetation will harbor significant populations. Ideal habitat conditions are listed by Shellhammer and Harvey (1982) as: 100% plant cover of which at least 60% is pickleweed and approximately 30-50 cm tall. The mice can swim or retreat to higher ground during high tides. Fisler (1965) noted that individuals will not leave thick cover or traverse bare areas. Thus, the highly disturbed nature of most remaining habitats greatly limits dispersal. The

Table 26. Mammalian uses of bay tidal marshes (from Madrone Assoc. 1977; Jones and Stokes Assoc. 1979). Non-specific use refers to uses such as dispersal, resting, roosting, and occasional movement. Key: 0 = obligatory use; X = common use, but not obligatory.

Species	Habitat	Breeding	Feeding	Non-specific
Insectivora:				
Vagrant shrew (*Sorex vagrans*)	salt, brackish	X	X	X
Suisun shrew (*Sorey sinuosus*)	brackish	0	0	0
Lagomorpha:				
Blacktail jackrabbit (*Lepus californicus*)	salt, brackish		X	X
Brush rabbit (*Sylvilagus bachmani*)	salt, brackish		X	X
Rodentia:				
California ground squirrel (*Citellus beecheyi*)	salt, brackish			X
California vole (*Microtus californicus*)	salt, brackish			X
House mouse (*Mus musculus*)	salt, brackish	X	X	X
Muskrat (*Ondatra zibethica*)	brackish	X	X	X
Norway rat (*Rattus norvegicus*)	salt		X	X
Salt marsh harvest mouse (*Reithrodontomys raviventris*)	salt, brackish	0	0	0
Carnivora:				
Mink (*Mustela vison*)	brackish		X	
River otter (*Lutra canadensis*)	brackish	X	X	X
Striped skunk (*Mephitis mephitis*)	brackish		X	
Harbor seal (*Phoca vitulina*)	salt	X		X

density of animals is difficult to determine and must be based on number of trap nights necessary to capture one mouse. Shellhammer and Harvey (1982) give 77 trap nights/mouse for San Pablo Bay, 213/mouse for south bay, and 272/mouse for Suisun Bay. The densest populations were found in Tolay Creek Marsh (Tubbs Island), Fagan Marsh (Napa River), Newark Slough (near FWS headquarters), and the Collinsville marshes in Suisun Bay. Recommendations for the recovery of the salt marsh harvest mouse call for preservation of habitat, particularly large areas of 200 hectares or more. Connections between suitable habitat are necessary and should be at least 20 m wide and have 100% cover by pickleweed (Shellhammer and Harvey 1982).

The largest mammal utilizing salt marshes is the harbor seal (*Phoca vitulina*). Since 1928, harbor seals have been observed hauled-out along Mowry Slough in the south bay. The seals are typically hauled out on pickleweed and saltgrass at high tide and on the mudflat at low tide. Numbers fluctuate seasonally with the greatest numbers (100-300) observed from April to May during the pupping season (Fancher and Alcorn 1982). As many as 100 pups have been observed here (Figure 39). Between 1972 and 1976, the percentage of pups born each year increased from 17% to 25% in the south bay (Fancher 1979). Other tidal marsh sites in the bay where harbor seals haul-out include: Green Island, Guadalupe River, Corkscrew Slough (Bair Island), and Tubbs Island (R. Lowe, pers. comm.)

6.6 SUMMARY

Tidal marshes contain a great diversity of animal life dependent on the protection and food provided by the vegetation. Each species has unique requirements which enable it to tolerate the difficult conditions of the marsh habitat

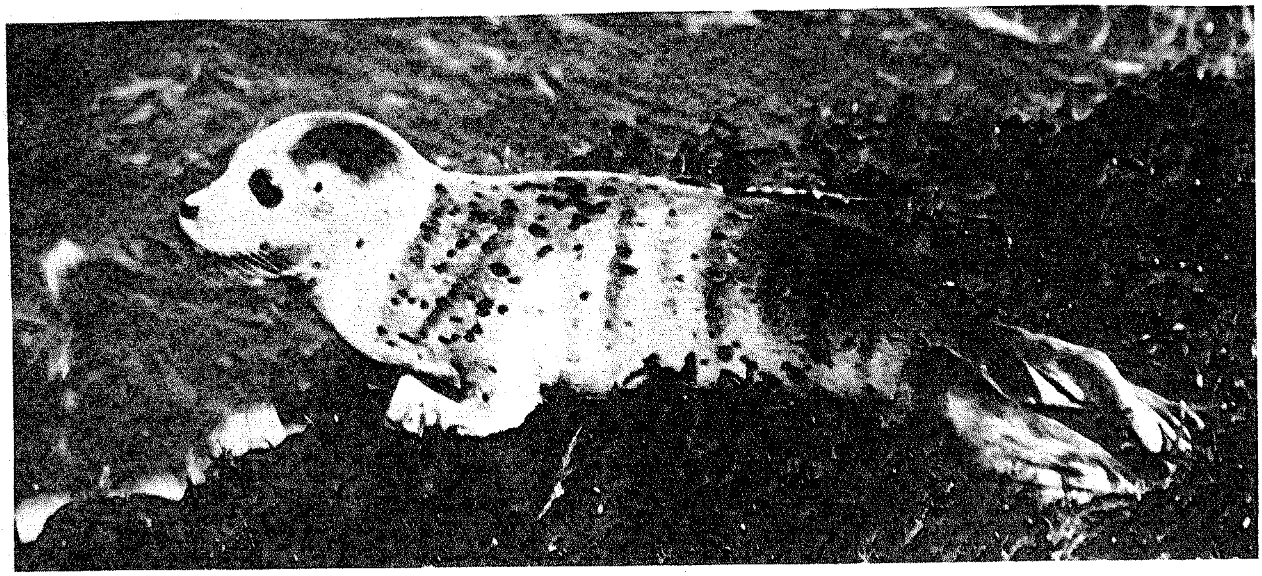

Figure 39. Harbor seal pup hauled-out on tidal marsh in south San Francisco Bay (Photo from Applegarth 1938).

(salinity, desiccation), while benefiting from high productivity of the marshes and protection from either land or water-oriented predators. The swift tidal currents bring suspended particulates to filter feeders and support an exchange of nutrients which stimulates benthic algal growth for the grazing epifauna. Fish invade the tidal marsh at high tide, grazing heavily on the benthic fauna. At the same time, fish-eating birds congregate at the slough edge and consume the fish concentrated there.

The marsh vegetation itself is little affected by the numerous animal denizens. Certain insects may cause minor damage to the above-ground biomass or birds may utilize stems for nests or feed on the seeds. The vegetation serves more as the architecture around which the animals structure their existence. It is an important element as disturbance can decrease animal movement or affect availability of nesting sites. It is, therefore, important to know as much as possible about the vegetational requirements of various animal species in order to properly manage for their continued survival within limited habitats.

CHAPTER 7

COMMUNITY METABOLISM OF BAY TIDAL MARSHES

No holistic studies have been completed on bay marshes from which detailed energy flow models can be developed to describe the interrelationships between plants and animals. Models developed from Atlantic coast marshes do provide a starting point (Pomeroy and Wiegert 1981). Great caution must be exercised in directly applying such models to Pacific coast wetlands because of substantial differences in climate, hydrology, and the organisms present (Zedler 1982). San Francisco Bay marshes present further complications due to the large number of introduced organisms which superimpose interspecific competition effects over factors normally controlling the native populations. In addition, gradual changes in species composition along the estuarine gradient may invalidate a single model approach.

San Francisco Bay tidal marshes are distinctive from Atlantic coast wetlands in several respects. First, the Mediterranean climate results in a marked seasonal difference in the hydrologic regime; evaporation over the year far exceeds annual rainfall. Second, pickleweed (Salicornia virginica) covers a larger area of tidal marsh compared to Pacific cordgrass (Spartina foliosa). Much of the literature for Atlantic coast marshes is based on the role of smooth cordgrass (Spartina alterniflora) in production, decomposition, and nutrient cycling. No comparable data exist for pickleweed dominated marshes. Third, diking and filling have destroyed 95% of the historic tidal wetland in the past 170 years. The remaining marshes are often altered or influenced by adjacent activities. It is unlikely that scientists will ever be able to reconstruct the significance of prehistoric tidal wetlands to estuarine functioning. Atlantic coast marshes are more extensive and, although impacted by human activity, can be more easily examined in their natural environment.

Several aspects of marsh function have not been examined at all for bay marshes. No information is available on microbial activity in the sediments. Rates of organic matter decomposition, sulfate reduction, denitrification, and other microbial processes have not been determined. Measures of nutrient levels in bay marshes are few and no information is available on the role of nutrients in marsh production. Microalgal production is unmeasured. Each of these measures plays a significant role in models developed for other marshes (Pomeroy and Wiegert 1981, Zedler 1982), and without them, a severe limit is placed on conceptual models for bay wetlands.

Quantitative models, therefore, must await further studies. This chapter reviews those areas where data have been collected, and where appropriate, linkages will be made. Weaknesses should be apparent and, it is hoped, will provide stimulus to further study.

7.1 PRIMARY PRODUCTION

Primary production is the most frequently measured parameter of community metabolism in bay tidal marshes. It is also one of the most difficult to interpret due to variability between and within marshes. Some of the variability can be attributed to differences in sampling techniques (quadrat size, sampling frequency, method of calculation). All of the studies for bay marshes have used the above-ground harvest method which underestimates biomass lost to herbivores, decomposers, and export from the marsh. Most studies have relied on either a single end-of-season harvest or on minimum and maximum collections. The use of the Smalley (1958) method relies on more frequent sampling and includes both live and dead components; however, loss of material by decomposition between sampling intervals is not considered. Turner (1976) determined that the end-of-season estimate yielded the lowest estimates and that Smalley's method, though yielding higher estimates, can be affected by uncorrectable errors when live biomass is declining. Onuf et al. (1978), in a study of succulents in a southern California wetland, found that the production estimated from the harvest method was 1/2 to 1/3 that determined from tagging individual plants. On the other hand, his highest estimate for pickleweed, using the tagging method, was 286 $g/m^2/yr$. This is the lowest value reported for the Pacific coast. Zedler (1982) concluded that despite unresolved difficulties in assessing salt marsh production, estimates based on periodic harvesting are the only comparable data available.

Production estimates for bay tidal marshes (Table 27) are well within the range of those reported for both Pacific and Atlantic coast marshes (Turner 1976, Eilers 1979, Zedler et al. 1980). Turner (1976) reported annual production on the Atlantic coast of 300 to 550 g dry wt/m^2 for smooth cordgrass at the same latitude as San Francisco Bay (38° N). The higher estimates for Pacific cordgrass might be accounted for by the longer growing season (10 mos) and milder winter climate. Estimates for pickleweed are as high or higher than Pacific cordgrass. There seems little justification to conclude that vascular plants in Pacific coast wetlands are less productive than Atlantic coast habitats (Onuf et al. 1978).

Less information is available on below-ground biomass for bay tidal marshes. Good et al. (1982) reviewed the significance of below-ground biomass and production. Below-ground biomass often exceeds above-ground standing crop, and the production contributes to the overall stabilization and build-up of the marsh substrate. The amount of below-ground biomass varies with species, depth in the sediment, and season. Mahall and Park (1976a) found that roots and rhizomes of Pacific cordgrass were more abundant at the 5-15 cm level compared to pickleweed in which over 50% of the below-ground biomass was in the upper 5 cm of sediment. The root to shoot ratio was about 3.65 for Pacific cordgrass and 0.55 for pickleweed. Spicher (1982) measured an average root-shoot ratio of 1.1 for pickleweed at various elevations in a marsh restoration near Corte Madera. For comparison, the root-shoot ratio of smooth cordgrass ranges between 1.2 to 5.3 for the short form and 0.4 to 8.2 for the tall form (Good et al. 1982). In general, root-shoot ratios for perennial marsh plants exceed 4.0 and annual species range between 0.14 to 0.46. Sampling has not been conducted frequently enough to estimate productivity of below-ground parts; however, based on root-shoot ratios, it can be assumed that bay marsh plants are equivalent to, or lower than, the Atlantic coast plants surveyed to date.

Zedler (1980) observed that the net primary productivity of benthic microalgae was 0.8 to 1.4 that of the vascular plant overstory in southern California marshes and emphasized the significance of the relatively open canopy of these marshes to high algal production. Zedler (1982) hypothesized that algal productivity can form the basis of a significant grazer food chain as opposed to a detrital food web based on decaying vascular plants. Despite its potential significance to bay wetlands, no measurements of microalgal production have been made.

Macroalgal biomass and production by various species of green algae (Enteromorpha and Ulva) is highest during spring and summer months when daytime low tides are most frequent, thereby providing high light intensities. Shellem and Josselyn (1982) estimated peak standing crops for Enteromorpha clathrata at 15 g dry wt/m^2 in May and net annual production of 270 g C/m^2. This estimate was for a mudflat adjacent to the salt marsh and production is probably lower beneath the marsh canopy. It is within the range given for microalgae (185-341 g $C/m^2/yr$) in the marsh studies by Zedler (1980).

Table 27. Summary of estimated annual vascular plant production for selected species in bay tidal marshes. All studies use end-of-season biomass to estimate production, except those reported by Josselyn (unpubl) which is estimated using the Smalley method. Single values are averages for one site. Ranges refer to averages at several locations in a single marsh.

Species	Location	Year	Estimated Annual Production (g dry wt/m^2)	Quadrat Size (m^2)	# quadrats/ station	Sampling frequency per year	Reference
Spartina foliosa	Tolay Creek San Pablo Bay	1968	1400	0.25	5	52	Cameron (1972)
	Mare Island San Pablo Bay	1972	274	0.125	8	1	Mahall and Park(1976a)
	Petaluma River	1972	689	0.125	8	1	Mahall and Park(1976a)
	Creekside Park Corte Madera Creek	1982	950[1]	0.20	5	7	Josselyn (unpubl)
	Corte Madera Bay	1982	710-1120[2]	0.20	5	7	Josselyn (unpubl)
Salicornia virginica	Tolay Creek San Pablo Bay	1968	1050	0.25	5	52	Cameron (1972)
	Mare Island San Pablo Bay	1972	820-958	0.125	8	2	Mahall and Park(1976a)
	Petaluma River	1972	590	0.125	8	2	Mahall and Park(1976a)
	Petaluma River	1979	604-1462[3]	0.25	10	2	Balling and Resh(1983b)
	Muzzi Marsh Corte Madera Bay	1982	950-1500[4]	0.10	10	2	Josselyn (unpubl)
	Creekside Park	1982	600-1000[4]	0.10	4	7	Josselyn (unpubl)
Salicornia europaea	Muzzi Marsh Corte Madera Bay	1982	720	0.10	4	7	Josselyn (unpubl)
Scirpus robustus	Sonoma Creek San Pablo Bay	1979-1980	3160	0.25	-	1	Pearcy *et al* (1981)
	Suisun Marsh	1979-1980	604-1840[5]	0.25	-	1	Pearcy *et al* (1981)
	Creekside Park Corte Madera Creek	1982	790[6]	0.20	5	7	Josselyn (unpubl)
Scirpus californicus	Delta	1977	2500	0.12	5	1	Atwater *et al*. (1979)

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[1] Stations taken in tidal channel in mid-marsh area

[2] Range is for stations located over entire intertidal distribution of Pacific cordgrass located directly on bay mudflat

[3] Range is for stations located adjacent to natural channels and mosquito ditches

[4] Range is for stations located over entire intertidal distribution of pickleweed located in restored marsh

[5] Range is for stations in diked wetland subject to variations in flooding regimes and sediment salinity

[6] Station located adjacent to freshwater drainage pipe

A rough estimate of the contribution of tidal marshes to overall bay production can be made from existing data. Cole (1982) and Cole et al. (unpubl) measured net production by phytoplankton using C-14 techniques. Their estimates were averaged for both deep and shallow sites. Annual production for south bay was estimated at 130 g C/m², for San Pablo Bay at 110 g C/m², and for Suisun Bay at 94 g C/m². Assuming a bay-wide average of 115 g C/m² (based on relative areas), multiplying by the total surface area of the bay (1.24×10^9 m²) gives an estimate of 1.4×10^{11} g C for the year. Average marsh production is 360 g C/m² (assuming an average production of 800 g dry wt/m² and a percent carbon of 45). Area of tidal marsh is 1.25×10^8 m². The estimated annual marsh production is 4.5×10^{10} g C. This is approximately 25% of the combined phytoplankton and marsh annual production. It does not include contributions from benthic micro- and macroalgae nor production in diked wetlands not subject to frequent tidal action. Because phytoplankton and vascular plant production are utilized in very different ways within the estuarine food web, judgements on their relative significance are difficult to make. Marsh production, however, is relatively large despite its small area. Considering that 95% of former wetlands are now diked, prehistoric marsh production must have far exceeded that of the open waters.

7.2 FACTORS CONTROLLING PRIMARY PRODUCTION

The factors which control overall production in the marsh are the same as those which affect the elevational distribution of plants: light, salinity, tidal flow, and nutrients. Much of this information is discussed in chapter 5 and only data pertinent to production are reviewed here.

Pearcy et al. (1981) measured photosynthesis under varying light intensities for several salt and brackish marsh species (Figure 40). At the highest light intensities measured (equivalent to fall sunlight levels), Pacific cordgrass had the highest CO_2 uptake, followed by alkali bulrush (Scirpus robustus), pickleweed and brass buttons (Cotula coronopifolia). As light intensity was reduced (as within a marsh canopy), pickleweed reached a compensation point (no net CO_2 uptake) at a higher light intensity than either Pacific cordgrass or alkali bulrush. At 1/4 full daytime light intensity (500 µein/m²/sec = 0.5 mmol/m²/sec), the photosynthetic rate for the latter two species was twice that of pickleweed. Pickleweed is, therefore, more sensitive to shading. Most of the photosynthetic tissue of pickleweed is located in the upper branches as compared to Pacific cordgrass, in which leaves are found at all heights in the canopy. Even at light intensities near full sunlight (2000 µein/m²/sec), CO_2 uptake by pickleweed is only two-thirds that of Pacific cordgrass. If light were the only controlling factor, one would expect the taller Pacific cordgrass to dominate tidal marshes.

Salinity, especially the seasonal range, has an important influence on photosynthesis and growth of individual species. Zedler et al. (1980) showed that reduction of hypersaline conditions in southern California marshes significantly enhanced Pacific cordgrass production. Hypersaline conditions are not frequently observed in bay tidal marshes; however, changes in sediment salinity can reverse the relative photosnthetic rates of marsh plants. Pearcy et al. (1981) found that CO_2 uptake in alkali bulrush and Pacific cordgrass declined above 20 ppt while that in pickleweed increased (Figure 41). At 30 ppt, pickleweed had the highest photosynthetic rate of all species tested. On a relative basis, pickleweed exceeded Pacific cordgrass at approximately 24 ppt, remarkably similar to the field salinity observed by Mahall and Park (1976a) in the ecotone between Pacific cordgrass and pickleweed.

In their two-year field study in San Pablo Bay, Pearcy et al. (1981) observed that reduced salinities in the spring did stimulate the growth of brackish water species in salt marsh habitats. Alkali bulrush grew most rapidly in the spring when Pacific cordgrass and pickleweed were growing at relatively slower rates. This period of rapid growth allowed alkali bulrush to exceed the other species in height, and therefore, shade its competitors in the summer when higher salinities reduced its own growth. On the other hand,

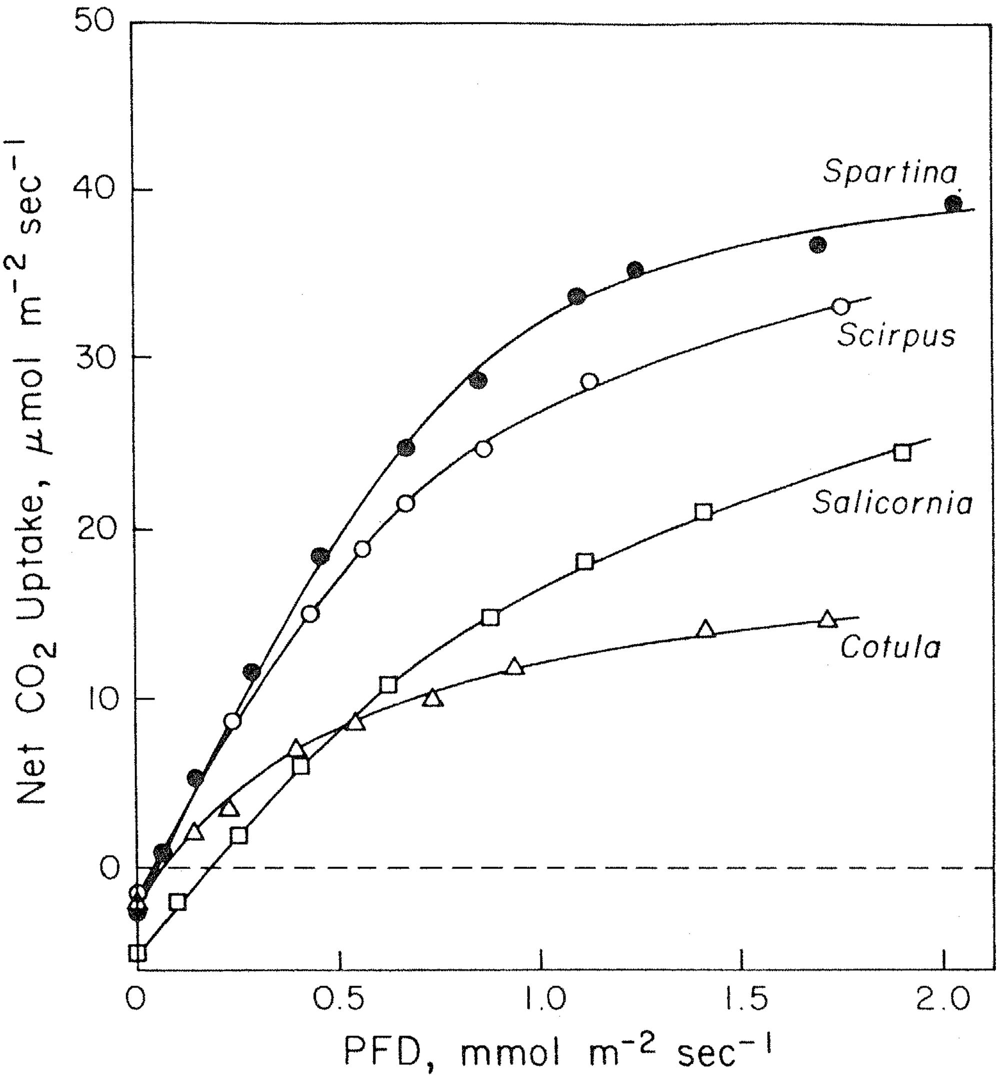

Figure 40. Photosynthetic CO_2 uptake as a function of light intensity. Measured at 30° C leaf temperatures, 320 μbar CO_2 pressures, and a vapor pressure differential of 5-10 ubar (from Pearcy et al. 1981).

if sediment salinities are not lowered in the spring (as during drought or reduced delta outflow), Pacific cordgrass and pickleweed will dominate.

Location within the marsh with respect to channels can also influence production. Balling and Resh (1983b) found that in the Petaluma marshes, annual above-ground production of pickleweed near watercourses was higher by 40% than in the open marsh. They also noticed that the plants were more robust and the canopy denser adjacent to the channel. They attributed the higher production to greater flushing of sediments near the channel. They were able to show that groundwater recharge occurred during every tide cycle in the areas within 1 m from the channel edge. There was also a reduction in groundwater salinity near the channel edge. The central marsh sites showed no lowering of the water table during tidal cycles and salinities were higher than near the channel. Spicher (unpubl) observed similar enhancement of standing biomass adjacent to dredged channels in the Muzzi Marsh restoration project in Corte Madera.

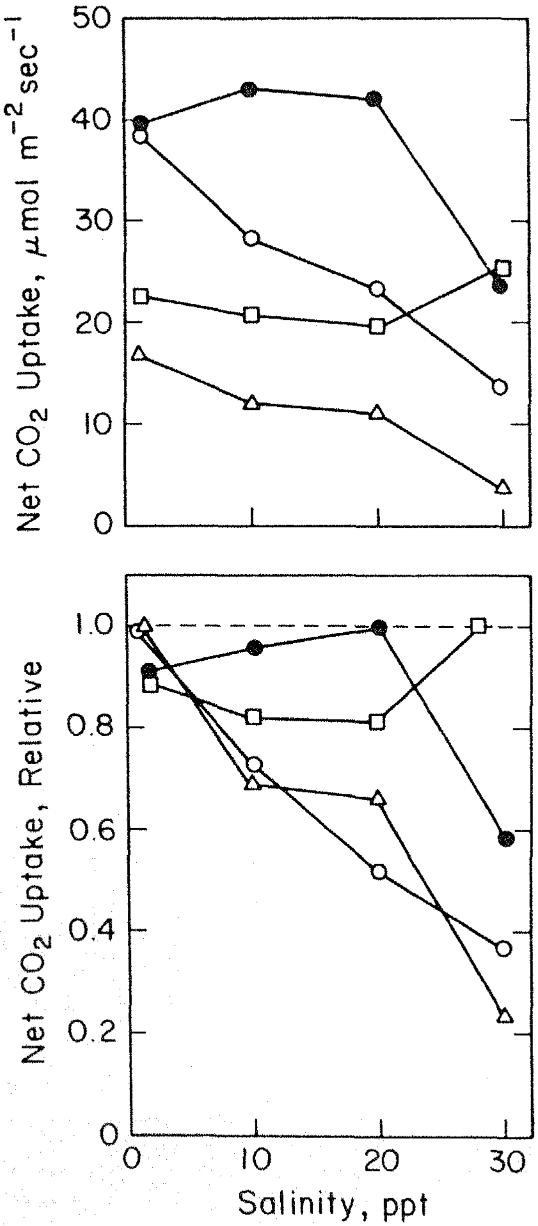

Figure 41. TOP: Effect of salinity on mean CO_2 uptake for various marsh plants. Filled circle = Pacific cordgrass; open circle = alkali bulrush; open square = pickleweed; open triangle = brass buttons. BOTTOM: Relative photosynthetic CO_2 uptake as a function of salinity. Rates plotted relative to the maximum rate for each species. Measurements made at 320 µbars CO_2 pressure, photon flux densities of 1.7-2.0 mmol/m^2/sec, leaf temperatures of 30°C and VPD of 5-10 mbar. Each point represents mean of 2-8 leaves. From Pearcy <u>et al</u>. 1981.

The effects of nutrients on tidal marsh production have not been measured for Pacific coast wetlands. For Atlantic coast marshes, Valiela and Teal (1974) have shown that direct addition of nitrogen does enhance above-ground biomass and productivity in smooth cordgrass, especially the short form. No increase was observed with additions of phosphorus alone suggesting that smooth cordgrass growth is limited by nitrogen. In a San Francisco Bay marsh restoration, Newcombe and Pride (1976) applied single doses of fertilizer containing unspecified amounts of nitrogen and phosphorus to Pacific cordgrass seedlings and observed no effect on survival, growth, or height form. Some enhancement in above-ground dry weight was observed for pickleweed. Studies using continuous or long-term application of nutrients to Pacific coast wetlands are needed to compare to the results of Valiela and Teal (1974).

Indirect measurements of nutrient uptake have been made from tidal flux studies. Winfield (1980) calculated a net import of ammonium for a tidal wetland in southern California. He estimated that 6% of the nitrogen needed for vascular plant production was imported during tidal cycles. Buchholz (1982) also observed an import of nitrogen for a salt marsh mudflat in San Francisco Bay. No vascular plants were present at the site and he attributed the nitrogen removal to geochemical (adsorption to clay particles) and microbial processes. Two important microbial processes appeared to be denitrification and benthic microalgal uptake. Without direct measurements of nutrient removal by marsh plants, it is unlikely that firm conclusions can be reached at this point on the role of nutrients in bay tidal marsh production.

7.3 UTILIZATION OF PRIMARY PRODUCTION

Pomeroy and Wiegert (1981) provide an excellent discussion of the utilization of marsh primary production for salt marshes in Georgia, based on 20 years of research. The data base for Pacific coast wetlands, including San Francisco Bay, does not approach this time span in intensity nor completeness. Zedler (1982) suggests that microbial utilization represents a major sink for marsh primary production in southern California wetlands. High microalgal production may also support an importantalgae-herbivore food web, which is not as well developed in Atlantic coast wetland systems. Much work remains to test these hypotheses to avoid making generalizations on marsh function which later prove to be unsupportable (Nixon 1980). In the discussion below, utilization of primary production is grouped into three catagories: direct grazing, microbial-detrital utilization within the marsh, and export to the estuary.

Direct grazing

Direct grazing is usually assumed to represent a small percentage of total production (Pfeiffer and Wiegert 1981). However, because marsh productivity is high, herbivore production (especially insect herbivores) can exceed that observed for terrestrial grassland systems. Insect grazers in bay tidal marshes can reach large population numbers and many species graze directly on vascular plant material (i.e. leaves, flowers, seeds, and plant sap) (Cameron 1972). Herbivore abundance and diversity are usually directly correlated with aboveground standing crop; however, no estimates of total consumption are available. Qualitative observations usually indicate minimal impact from insect grazers. Grazing on benthic algae by epifaunal invertebrates is hypothesized to represent a more important food web in southern California wetlands (Zedler 1982). Algal material forms a major portion of the diets of gastropods and deposit feeders within the marsh. The numbers of mudsnails (Ilyanassa obsoleta) in tidal channels can exceed 1000/m^2 and their tracks are apparent as cleared areas in the algal mat. Other direct grazers in tidal marshes are the filter feeders. They feed on phytoplankton and benthic microalgae suspended in the tidal channels. The ribbed mussel (Ischadium demissum) feeds partially on vascular plant detritus and phytoplankton (Montague et al. 1981). Finally, direct grazing by vertebrates probably has some minor impact on the vegetation, particularly its reproductive capacity. Waterfowl graze heavily on seeds of alkali bulrush and brass buttons (Cotula coronopifolia). Many small birds and mammals also include seeds in their diet. The impact of seed eaters may be more important to plants such as Pacific cordgrass, which frequently do not produce abundant viable seed.

Microbial-detrital utilization

Microbial metabolism is the major link in the mineralization and transformation of organic matter in salt marshes. The organic matter is subsequently utilized by detritivores or deposited as fossil material in the build-up of marsh sediments. The microbial processes occurring in the marsh are generic to all regions: decomposition, sulfate reduction, denitrification, nitrification, nitrogen fixation, and methanogenesis. However, the rates of these processes can vary with climatic factors, substrates, and oxygen availability. Only a few measurements are available for bay marshes.

Murray and Horne (1979) estimated rates of nitrogen fixation and sulfate reduction in an isolated (diked) wetland in the central bay (Richmond). Rates of nitrogen fixation based on acetylene reduction ranged between 0.0 to 1.9 μl ethylene/g wet wt sediment. Assuming a moisture content of 45%, a bulk density of approximately 1.00, and a constant rate throughout the year, nitrogen fixation can be estimated at between 0 and 52 g N/m^2/yr which is equivalent to that observed in smooth cordgrass (Spartina alterniflora) marshes (Whitney et al. 1981). Glucose addition stimulated acetylene reduction indicating that nitrogen fixation is limited by available carbon sources. Murray and Horne (1979) estimated the thiobacilli (sulfate reducers) in the marsh soils as between 10^2 to 10^6 bacteria/g wet wt sediment. Higher numbers were found in isolated, acidic portions of the marsh. Unfortunately, few generalizations from these analyses can be made for all bay tidal marshes.

Detritivore food webs are also poorly known, although organisms known to include large amounts of detritus in their diets are common to tidal marshes. Deposit feeders (polychaetes, bivalves) are especially abundant in mudflats and tidal sloughs whereas litter shredders and grazers (amphipods and insects) are prevalent in the high marsh where detrital material accumulates. Because their population numbers are only poorly known, quantitative models would be difficult to develop at this point.

Export

Export from the marsh to the estuary represents another means by which tidal marsh productivity can be utilized. Although many estimates of material flux are available, methodological difficulties abound, and most sites have specific attributes which make comparisons tenuous (Nixon 1980). Several categories of material flux must be considered: chemical flux, dissolved and small particulate carbon flux, and macro-detrital flux.

Winfield (1980) measured a net influx of nitrogen to southern California marshes in the bulk water column. Buchholz (1982) measured the flux of inorganic, organic, and particulate nitrogen between San Francisco Bay and a salt marsh mudflat. He calculated fluxes based on discrete samples multiplied by the estimated volumes of water entering or leaving the marsh. He determined that the mudflat was a nitrogen sink, removing up to 25% of the flood phase dissolved inorganic nitrogen, primarily ammonium. An adjacent sewage effluent outfall may have contributed a significant portion of the nitrogen observed in his study. Seasonal variability was attributed to microbial activity and microalgal (diatom) uptake. Chan et al. (1981) report uptake of inorganic nitrogen in stormwater retention basins which contain pickleweed, in addition to settling of suspended sediments and removal of some pollutants. In general, Nixon (1980) concluded that marshes act as nitrogen transformers by importing dissolved oxidized forms of inorganic nitrogen and exporting dissolved and particulate reduced forms. It is apparent that more information on microbial processes in marsh sediments is needed to evaluate their role in net nutrient fluxes in bay wetlands.

Trace metal uptake is a function frequently attributed to bay marshes, often without sufficient experimental measurements. Lion and Leckie (1982) found the opposite for a tidal marsh in the south bay: three trace metals (Cd, Cu, and Pb) were exported to the bay. Metal flux differed between the surface microlayer and the bulk water column; net import was observed for metals in the surface microlayer and export was measured in the water column. The greater volume of the water column weighted the net flux as export.

Both dissolved and particulate carbon flux can vary between marshes and seasons. Recent research has focused on the use of stable carbon isotopes to estimate organic carbon sources. Plants differ significantly in the relative amounts of ^{13}C and ^{12}C taken up, based on sources of carbon and metabolic pathways. Haines (1979) has challenged previous assumptions about carbon flux from marshes to near-shore areas as a result of an analysis of stable isotope ratios. Her study indicates that phytoplankton production is a more important carbon source for near-shore waters and that vascular plant production is utilized primarily within the marsh. Spiker and Schemel (1979) reached a similar conclusion for San Francisco Bay. They found that stable isotope ratios supported the hypothesis that phytoplankton are the most significant carbon source to bay consumers. They were unable to identify any carbon input by Pacific cordgrass to the estuary. Pacific cordgrass has a very distinctive stable carbon ratio because it is a C-4 plant (based on its method of carbon fixation) whereas pickleweed, a C-3 plant, has a ratio similar to terrestrial plants. Pacific cordgrass is only a minor component of the tidal marsh system compared to pickleweed. Any input from pickleweed might be masked by terrestrial sources. Nevertheless, terrestrial (and possibly pickleweed) carbon contributed only 10%-20% of the total bay particulate organic carbon.

Macrodetrital flux is evident in winter and spring months. Very often the amount of marsh debris observed within the bay can be correlated with extreme high tides and winter storms. In addition, debris containing marsh plants is also transported to higher portions of the marsh and deposited in extensive wrack lines (Figure 42). The significance of either wrack deposition or export is dependent on the morphology of the tidal marsh. Open marshes generally are

Figure 42. Winter wrack line in developing salt marsh. Litter contained many seeds which germinated in spring and rapidly colonized area.

exporters of debris whereas marshes with narrow openings tend to accumulate debris (Odum 1980).

In summary, the utilization of primary production in bay marshes generally follows that described in more detail for other regions. Differences are not in terms of processes, but in terms of rates and, of course, the individual species involved. As Zedler (1982) has emphasized, it is unwise to make blanket assumptions for Pacific coast wetlands based on research from Atlantic coast habitats. Figure 43 is an attempt to develop a conceptual model of San Francisco Bay tidal marsh function based on evidence from bay marshes and other regions (Pomeroy and Wiegert 1981, Zedler 1982). Sizes of boxes and arrows provide some estimate of relative standing crop and magnitude of transfer. Habitats in which these processes occur are also indicated. Brackish habitats are similar in function except that the bulrushes and cattails replace Pacific cordgrass and pickleweed. It is likely that further research will modify these concepts of marsh function.

7.4 RELATIONSHIPS WITH DIKED WETLANDS

Recent emphasis has been placed on the ecological values of diked wetlands and salt ponds (BCDC 1976, 1982). Many functions analogous to those placed on tidal wetlands have been attributed to these habitats. Yet, even less research has been conducted in these habitats than in their tidal counterparts. The studies completed have focused primarily on bird utilization.

Salt ponds cover over 160 km^2 of former wetland, primarily in Alameda, Santa Clara, and San Mateo Counties in the south bay. The USFWS includes many of these ponds in their management responsibilities for the San Francisco Bay

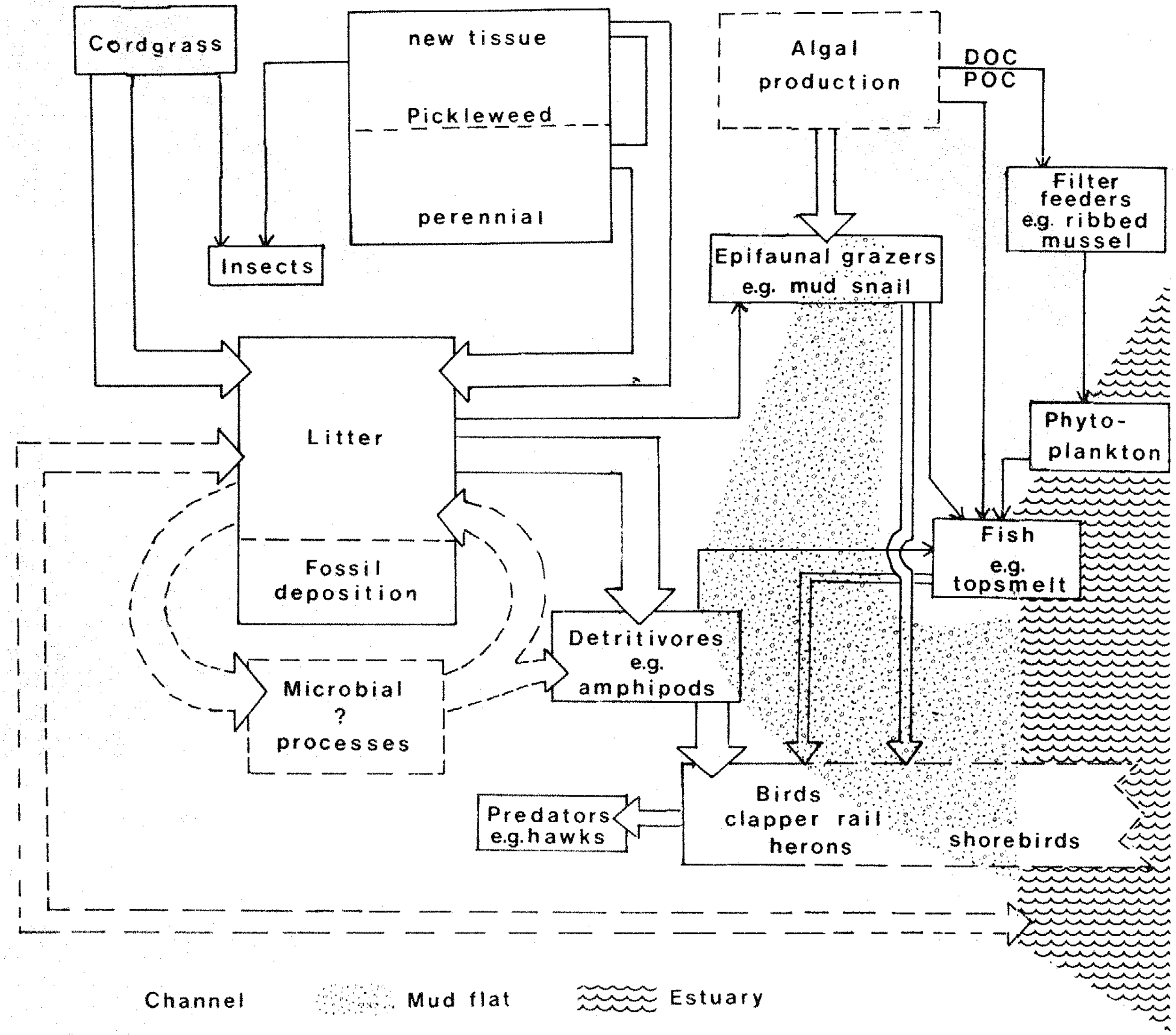

Figure 43. Conceptual model of energy fluxes in tidal marshes of San Francisco Bay. Relative size of state variable (box) indicates biomass. Relative size of flux (width of arrow) indicates energy flow. Dotted lines suggest that limits of biomass or energy flow are completely unknown.

National Wildlife Refuge. Salt pond salinities vary in concentration from those similar to bay waters to highly concentrated, saturated brines. The distribution of organisms in the ponds is dependent on their response to the physical stresses present, as well as on available food and shelter. The ponds tend to be dominated by a few organisms such as the alga *Dunaliella salina*, brine shrimp (*Artemia salina*), water boatman beetles (*Trichocorixa reticulata*), brine flies (*Ephydra cineria*), and the topsmelt (*Atherinops affinis*)(Anderson 1970). Some enter the pond system as larvae or juveniles which are entrained from the bay during the first stage of the salt evaporation cycle. Others are only found in salt ponds, upon which their life cycles are dependent. Most species are found in salt marshes, but are not dominants there. Dispersal mechanisms bring them to salt ponds where they flourish in the unique environmental conditions and in the absence of competitors. Their presence in salt ponds usually has little impact on adjacent tidal marshes except to provide food sources to birds. A number of species of waterfowl and shorebirds feed in both tidal marshes and salt ponds. Some, such as the earred grebes (Podiceps nigricollis) and Bonaparte's gulls (Larus philadelphia) feed almost exclusively in salt ponds. Although diversity of prey items is low in salt ponds, the organisms are usually plentiful and attract large numbers of birds. Anderson (1970) observed 55 species of birds in south bay salt ponds, many of which are common to bay tidal marshes. The birds may be supplementing their diet, foraging in the salt ponds when the outer tide flats are covered, or seeking reduced competitive pressure for available prey. The ponds may, therefore, support bird populations which would otherwise be limited by lack of tidal marsh. A few species, such as the Caspian tern (Hydroprogne caspia), prefer the habitat offered by the salt ponds and surrounding dikes and are not found in tidal marshes.

Suisun Marsh represents another type of diked habitat: the managed wetland. The management program is directed towards encouraging wetland vegetation which attracts waterfowl. Specific methods have been developed to manage salinity levels in the diked wetlands through alternate flushing and drying of the wetland sediments (Rollins 1973). The resulting wetland vegetation attracts numerous waterfowl and may serve as a refuge for birds otherwise excluded from tidal marshes. Certainly fish and invertebrates taken into the diked wetlands may also thrive here and later be pumped back into the tidal slough system. The magnitude of these interactions is unknown and deserves much closer attention towards improving management techniques.

Finally, diked agricultural land provides an important roosting and feeding area for birds, especially during high tides. In many cases, agricultural land may support extensive bird populations in winter and spring when flooded by heavy rains.

CHAPTER 8

MANAGEMENT OF TIDAL MARSHES AND THEIR RESTORATION

The human impacts on San Francisco Bay tidal marshes are many and long lasting. The term "pristine" is often used to describe the remaining tidal marshes, yet even these areas have been invaded by introduced species, affected by pollutants and pesticides, and seen the last of some species. Few, if any, of these impacts can be reversed or changed and management plans must take into account the new parameters forced on the tidal marsh habitat.

The isolated nature of remaining tidal marshes adds another difficulty to their management. Each site must be evaluated in relation to its specific needs due to the unique conditions which surround it, i.e. urbanization, diked wetlands, industrial activity. In most cases, only portions of the total habitat remain because transition habitats have been lost to development and the Pacific cordgrass (Spartina foliosa) zone has been eroded by wave and isopod damage. Habitat quality and size requirements are known for only a few species, leaving managers with little guidance as to which habitats to emphasize in the restricted areas available to them. Finally, pressures to provide public access to wetlands for viewing and education add further complications in managing these isolated parcels. The purpose of this chapter is to review some widespread management problems and the efforts underway to restore former marshes to tidal action.

8.1 MANAGEMENT PROBLEMS

Sedimentation and erosion are the most serious problems affecting tidal marshes. In most cases, upland sources of sediment have been eliminated due to dikes surrounding wetlands. Most local rivers and streams enter directly into the bay and are held within their beds by flood control levees. The sediment which does accumulate within the river bed is often dredged and placed in deep portions of the bay. The major portion of sediment which accumulates in marshes is derived from suspended material transported to the bay via the Sacramento-San Joaquin system. Krone (1979) estimates a net annual deposition of 4.2 x 10^6 m^3, although no estimate is available for the portion deposited in marshes.

Under natural conditions, marsh development proceeds landward in bay tidal marshes (Krone 1982). Sediments are deposited on the marsh surface raising the elevation to keep pace with rising sea level. Sea level is now increasing about 18 cm/century and in the absence of land uplifting, will continue to inundate more land. Erosion and submergence of the outer edge of the tidal marsh restricts its spread bayward. Only during periods of excess sediment supply do marshes extend outward, as during the period of hydraulic mining. Atwater et al. (1979) mapped historic changes in tidal marsh shorelines for the periods during and after hydraulic mining. The shoreline exhibited considerable accretion in Suisun, San Pablo, and south bays during the period of greatest input of hydraulic mining sediments. As this supply of sediment was reduced, retreat or stabilization of the shoreline occurred in south bay and San Pablo Bay.

At the same time sea level is rising, land surfaces in many parts of the bay are subsiding. Poland (1971) cited groundwater withdrawal as the reason for subsidence in Palo Alto, and Atwater et al. (1977) attributed the general subsidence observed in south bay to tectonic crustal movements. The lowering of surface elevation can result in community change from pickleweed to cordgrass or mudflat.

The problem confronting managers of tidal marshes is the reduced amount of sediment in bay waters and the inability of marshes to expand landward due to dikes and upland development. Neither problem can be alleviated, but sedimentation in marshes can be encouraged by proper shoreline protection. One suggested means of shoreline protection is the planting of Pacific cordgrass (Spartina foliosa) on the outer edge of the marsh. Newcombe et al. (1979) found that Pacific cordgrass did not stabilize sediments as well or as rapidly as smooth cordgrass (Spartina alterniflora). In areas of long fetch (and resulting frequent wind wave erosion), Pacific cordgrass transplants were not successful, even when combined with ribbed mussels (Ischadium demissum). Plantings for erosion control will probably require temporary or permanent breakwaters in order to stabilize the outer shoreline. Small, elongated offshore islands might provide both valuable nesting habitat and increase sedimentation. An alternate approach may be to deposit dredge spoils in shallow water to provide a sediment source to tidal wetlands. Extensive documentation is available on techniques to enhance beach nourishment (US Army Coastal Engineering Research Center 1977), and appropriate methods may be available to manage fine muds in the bay. Thin layers of dredge material might even be directly deposited over marsh surfaces to raise their elevation. This technique has been applied to east coast wetlands with some success (Dr. H. Smith, COE, Wetlands Expt. Stat., pers. comm.), but needs much more work to analyze the impacts on the marsh community.

Water management must also be considered in maintaining the original community structure of the tidal marsh. Additional water will be diverted from the estuary for export and local domestic use. Treated domestic and industrial effluents are discharged by deep water diffusers into the bay and ocean. As a result, the water budget for many tidal marshes is shifting towards a more saline condition. Extensive plans are underway to protect the diked wetlands of Suisun Marsh from excess salt (Calif. DWR 1982). These water control facilities should also provide some protection to the tidal water marshes. In the salt marshes of the bay, longer periods of saltier conditions should not change the community structure substantially, but may reduce productivity. Rerouting treated sewage effluent to marshes or using other reclaimed water is receiving increased attention, primarily for restoration purposes (Demgen 1981). Wakeman (1982) recommended that freshwater and brackish marshes be given priority in restoration activities within the bay. Overall, these goals will increase habitat diversity and should be encouraged if the impacts of localized freshwater discharge do not affect existing tidal marsh community structure.

Hydrologic changes are also induced through ditching activities to decrease mosquito larval habitat. Early efforts on the Atlantic coast involved digging a system of deep, parallel ditches to purposely lower the marsh water table. This method had serious impacts on the salt marsh plant composition, and more recently, shallow ditch systems have been used to increase tidal circulation in channels and ponds (Provost 1977)(Figure 44). In San Fracisco Bay, local mosquito abatement districts use an all-terrain vehicle to dig and maintain these ditches. Resh and Balling (1983a) recently reported on the results of a five-year study on the impact of ditching in bay marshes. They examined the impacts on plant species composition, insect community structure, fish utilization, and bird usage of ditched and unditched marshes. In general, they found that increased tidal circulation due to ditching enhanced or had minimal impact on the biota of the marsh. They concluded that ditches caused less environmental disturbance than insecticidal applications.

Ditching, however, must be done under careful management criteria. Monitoring studies of potential breeding areas should be done prior to ditching to avoid unnecessary draining of nonproducing ponds. Balling and Resh (1983a) recommend a one-year sampling program and suggest managers not react prematurely to small larval numbers on a single sampling date.

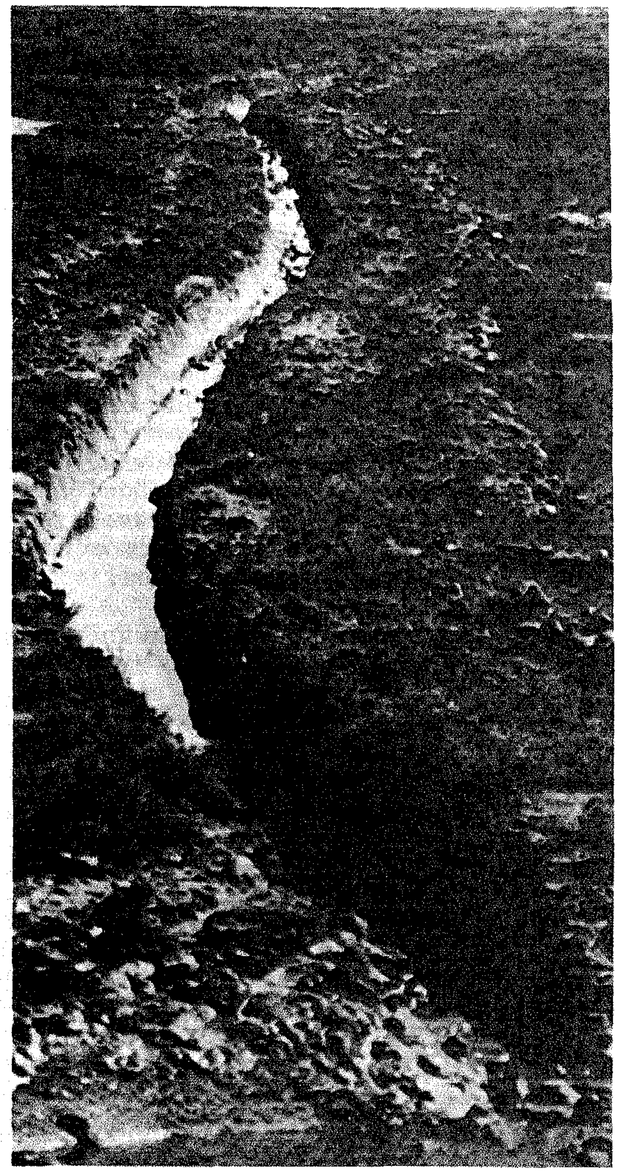

Figure 44. Recent mosquito control ditch dug within pickleweed marsh to enhance circulation. Note spoils deposited by trencher on either side.

For the most part, ponds and potholes located below MHW are sufficiently flushed by natural tidal action to reduce or eliminate mosquito problems. Ponds above MHW may produce mosquitos, particularly if they are less than 100 m^2 or if they are greater than 100 m^2 and contain more than 30% emergent vegetation in the pond basin. The primary deterrent to larval occurrence is tidal flushing and/or surface wave action which disrupts surface breathing by larvae. Resh and Balling (1983) further recommend against ditching marshes with sandy, porous soils as this will lower the water table too much and change the plant community structure. Finally, ditches should be designed as shallow as possible to reduce the amount of spoil material placed on the marsh surface.

A critical habitat often neglected in management plans is the transition zone from marsh to upland. This habitat is extremely important as a high-tide refuge to many marsh inhabitants. Diking and filling activities usually extend up to and into the pickleweed zone. The transition zone is then limited to a steep slope along the dike. Management of the transition zone requires strong and prompt enforcement of penalities for illegal fill. Loss of this region during a short period of extreme high tides might cause the demise of salt marsh harvest mice or California clapper rails unable to find refuge from predators. Recolonization may take years given their slow dispersal rate. If development is planned near a tidal marsh, upland slopes should be gradualand protected from human or feral animal intrusion. Tall, dense vegetation should be planted to provide cover to animals retreating during high tides.

The size or width of the transition habitat is important in reducing disturbance to marsh fauna, especially birds. Onuf (1979) recommended that only low intensity uses be allowed near the habitats of highest value and that buffers be established according to the sensitivity of the most readily disturbed species. Natural barriers such as bluffs, channels, and small hills should be utilized to minimize human impacts. Birds are usually studied in relation to buffer width and only limited data are available on flushing distances. Perhaps more important is the distance at which bird activity is modified or distracted from normal feeding or nesting. Jungius and Hirsh (1979) studied a group of marine birds in the Galapagos Island which were accustomed to human approach and found that the bird's heart rate increased two to four times the normal rate as people approached within 18 m. The increase in heart rate occurred prior to any obvious change in behavior.

The California Coastal Commission (1981) established the following criteria for buffers between wetlands and upland development: (1) the widest and most protective buffer zone feasible with a minimum width of 30 m, (2) the buffer should begin at the landward edge of the wetland, and (3) the width of the buffer should be based on the distance necessary to ensure that the most sensitive species will not be significantly disturbed. These recommendations need further biological verification to be applied to management issues in San Francisco Bay.

The philosophy to "let nature take its course" is often applied to tidal marshes. Certainly, they are not static or permanent habitats and can be expected to grow, decline, and disappear. The problem is that nature can no longer "take its course," as so many restrictions have been placed on the environment. Tidal marshes need management to survive the rapid onslaught of changes brought in the last 130 years by European settlers. The marsh community is resilient and if properly cared for, can respond to its new environment.

8.2 RESTORATION OF TIDAL MARSHES

Restoration of former marshland to tidal conditions has been actively pursued in the bay area. Over 2.4 km^2 have been returned to tidal action with the objective to create tidal marsh (Josselyn and Buchholz 1982)(Table 28). Many other projects have partially restored tidal wetlands, are being initiated, or are in the planning stages. Only a few have been monitored to determine the success of meeting their original objectives, but most are not assessed. Those monitoring studies that have been done are usually too short in duration to determine if and when planned objectives are met. Race and Christie (1982) found little evidence available to conclude that man-made marshes function like or provide the important values of natural marshes. They warn against accepting restoration as a quick means to meet mitigation requirements. In San Francisco Bay, Race (1983) found that mitigation requiring the creation or restoration of marsh habitats was placed on 17 out of 36 wetland development permits issued by BCDC between 1977 and 1982. She determined that many projects were unsuccessful in meeting the stated restoration or mitigation goals. In addition, she felt that many planners and wetland managers may be misled by the listing of wetland projects without any indication of their successful completion. She concluded that more rigorous standards need to be applied to restoration objectives and monitoring of projects. Zedler

Table 28. Restoration in San Francisco Bay with tidal marsh creation as an objective. Does not include experimental plantings or projects in which open water is primary objective. Does not include planned or recently initiated projects (from Josselyn and Buchholz 1982). Present status refers to observations of vegetated portions.

Site	Date	Area (km^2)	Site conditions	Present status
Faber tract, Palo Alto	1968-71	0.38	Dredge spoil disposal	Revegetated by pickleweed
Pond 3, Hayward	1975	0.44	Dredge spoil disposal	Partially restored
Muzzi, Corte Madera	1975-81	0.51	Dredge spoil disposal	Mostly restored
Creekside Park, Kentfield	1978	0.06	Dredge spoil disposal	Partially restored
Benicia Marina	1978	0.08	Regraded marsh	Mostly restored
Hayward Regional Shoreline	1980	0.91	Regraded salt evaporator	No planting yet

et al. (1982) also comment on the experimental nature of marsh restoration projects. They give a number of goals for wetland vegetation establishment and recommend several areas of research to better define these goals.

Guidelines for marsh restoration are given in Harvey et al. (1982) and Zedler (1982). The guidelines provide both general objectives and specific requirements of various species. Both conclude that successful restorations require careful consideration of hydrology and elevation. Most diked areas have undergone subsidence due to clay compaction, and therefore, sediment must be added either through dredge spoil deposition or natural processes. In the former case, circulation channels must often be excavated following disposal to provide proper tidal flushing (Josselyn and Atwater 1982). Another alternative is to excavate channels first and use the material to create higher surfaces for marsh plant colonization, as was done at the Hayward Regional Shoreline (Figure 45). Natural sedimentation can also increase elevations once tidal action is returned. Circulation and sedimentation models are necessary to estimate the length of time necessary to reach equilibrium elevations suitable for natural recolonization or planting (Williams and Harvey 1982). When spoil disposal or natural siltation cannot be used, tidal control structures are necessary to reduce the tidal extremes to allow vegetation establishment. Zedler et al. (1982), Sorenson (1982), and Harvey et al. (1982) provide detailed steps to follow

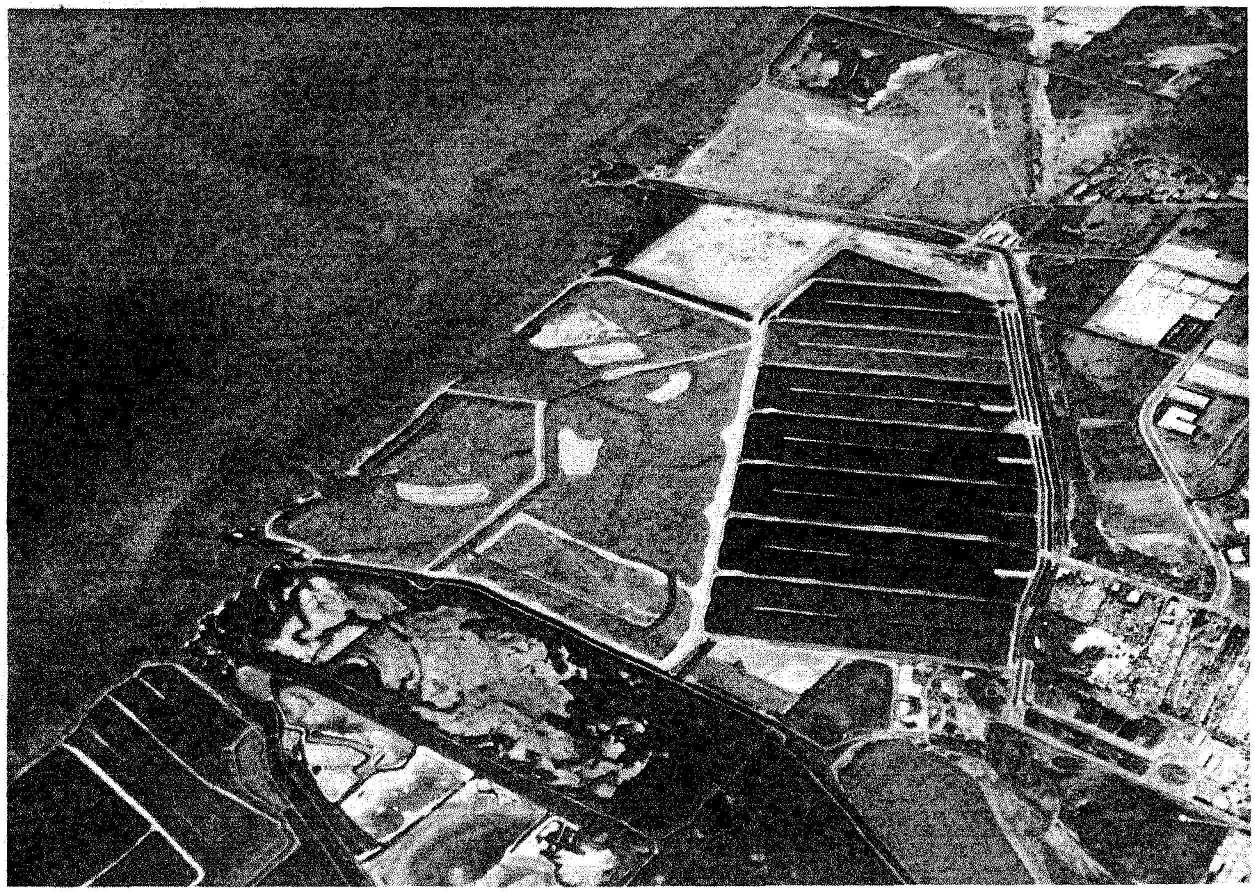

Figure 45. Hayward Regional Shoreline marsh restoration project in center (1981). Area was former salt evaporation pond system. Channels and ponds were excavated and material used to create islands. Site now colonized by pickleweed along upper margins and cordgrass in patches on lower mudflat. Sewage oxidation ponds on right.

when planning, undertaking, and monitoring marsh restorations.

8.3 EXPECTATIONS FOR WETLAND RESTORATION

The creation of tidal marshes is frequently framed in very broad objectives. The objectives or goals are based on published literature, personal observations, and agency perspectives, with little analysis of the ability of the habitat to meet these expectations. Zentner (1982) reviewed the most frequent goals expressed for California coastal wetlands: high primary productivity, shoreline protection, wildlife habitat, preservation of endangered or rare species, water purification, groundwater recharge, flood protection, nursery ground for commercially important fish and shellfish, and cultural values. A similar, though less comprehensive, listing has been given for bay diked wetlands (Madrone Assoc. et al. 1982). However, Zentner's (1982) analysis found that many values have been rejected by more recent studies. His conclusion was that wildlife habitat (including that for endangered species) and cultural uses (education ad recreation) were the best supported for California coastal wetlands, while other goals needed further documentation. Wakeman (1982), in setting restoration goals for San Francisco Bay wetlands, added the concept of diversity to the need for additional wildlife habitat. She especially noted the need for additional fresh and brackish marsh habitat due to their decline as a result of diversion and diking. In addition, a gradient of habitats is needed from low wet to dry upland areas, in order to support wildlife under all tidal conditions.

Setting specific goals for individual restoration projects requires more detailed data as listed by Harvey et al. (1982). Both an evaluation of the existing community and that of the planned habitat need to be made to assure the restored area will provide substantial improvement. Although habitat evaluation procedures (HEP) are available, they are difficult to apply to bay wetlands where quantitative data are lacking. Scientific research is developing more detailed information on habitat requirements for individual species, which can be useful in both HEP and restoration design planning (Table 29). Early involvement by scientists in the planning process can bring these research results and analyses to aid in determining habitat goals and needs (McCreary 1982). Recently, flow charts and organizational procedures have been proposed which define the process needed to undertake a successful restoration (Sorensen 1982, Smith 1983). The most difficult issue is usually a determination of which habitat alternative is most appropriate to the region. Site constraints do limit final choices, but habitat diversity and configuration can usually be manipulated to achieve several objectives. The final result must ultimately be based on the best scientific evidence available. The extent of that evidence has been presented here. The challenge is to expand not just the descriptive body of knowledge, but to provide the links necessary for an understanding of functional relationships. This is indispensible in formulating long-term management and restoration goals.

Table 29. Tidal marsh habitat requirements for selected plant and animal species reviewed in this profile.

Target species	Elevational zone/ habitat	Habitat characteristics
Pacific cordgrass (*Spartina foliosa*)	MTL-MHW	Tidal flushing; sediment salinities less than 25 ppt
Pickleweed (*Salicornia virginica*)	MHW-MHHW	Sediment salinities >10 ppt; well-drained areas between tidal cycles
Alkali bulrush (*Scirpus robustus*)	MHW-MHHW	Spring salinities close to zero; late summer salinities up to 26 ppt
California tule (*Scirpus californicus*)	MLLW-MTL	Freshwater conditions to slightly brackish in late summer
Narrow-leaved cattail (*Typha angustifolia*)		Saturated sediments or ponded conditions. Sediment salinity <5 ppt
Ribbed mussel (*Ischadium demissum*)	Bayward edge of Pacific cordgrass	Firm clay substrate; attachment to rhizomes
Hornsnail (*Cerithidea californica*)	High marsh pannes	Panne wetted by high tides; pickleweed along edges
Mosquito (*Aedes dorsalis* and *Aedes squamiger*)	High marsh potholes and ponds	Ponds higher than 1.6m above MLLW as referenced to Golden Gate; less than 100m^2 surface area; 30% emergent vegetation
Striped bass juveniles (*Morone saxatilis*)	Marsh sloughs	Brackish to freshwater in spring; channel edges vegetated
Mosquitofish (*Gambusia affinis*)	Marsh sloughs, channels, and ponds	Interconnecting system of channels spreading to high marsh ponds
Saltmarsh song sparrow (*Melospiza melodia*)	Channel edges vegetated with pickleweed	Pickleweed canopy over 50cm high along natural tidal channels. Presence of higher roosting vegetation
Black rail (*Laterallus jamaicenisis*)	Pickleweed marsh	90-97% cover by pickleweed; moderate penetrability; canopy height 29 cm; adjacent tall vegetation above MHW
California clapper rail (*Rallus longirostris obsoletus*)	Cordgrass-tall vegetation near channels	Tall salt marsh vegetation within 1.5m of moderate to small channels
Salt marsh harvest mouse (*Reithrodontomys raviventris*)	*Salicornia* marsh	100% cover, at least 60% pickleweed; canopy height 30-50cm. Connections 20m wide with 100% cover between habitat areas

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16. Abstract (Limit: 200 words)

San Francisco Bay, the largest estuary on the Pacific coast, historically contained an extensive contiguous system of salt and brackish tidal marshes. Urbanization has decreased tidal marshes by 95% and created a patchwork of remnant tidal marshes highly impacted by human activity. This document compiles available published and unpublished scientific literature to describe the current status and ecology of these remaining marshes.

Variation in river inflow (strongly seasonal) and individual species salinity tolerances result in gradual and overlapping distributional ranges. Saline marshes are usually dominated by two halophytes: Pacific cordgrass and pickleweed and brackish marshes by bulrushes: Scirpus spp and cattails.

Animals are distributed in relation to their salinity tolerances, vegetational habitat requirements, and tidal elevation within the marsh. Distribution of native species is complicated by competitive interactions and frequent dominance by introduced species.

The ecological role of tidal marshes are threefold: high plant productivity, important habitats for endangered and rare species, and the exchange of materials (nutrients and organic matter) with estuarine waters. Lack of quantitative studies, on microbial processes and food chain dynamics, provide a focus for future research.

Preservation of remaining marshes requires careful management. Habitat requirements for selected species can be incorporated into management practices as well as carefully planned and executed restoration projects.

17. Document Analysis a. Descriptors

Biological productivity, estuaries, animals

b. Identifiers/Open-Ended Terms
tidal marshes, salinity tolerance, cordgrass, pickleweed, bulrushes

c. COSATI Field/Group

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