Biological Services Program

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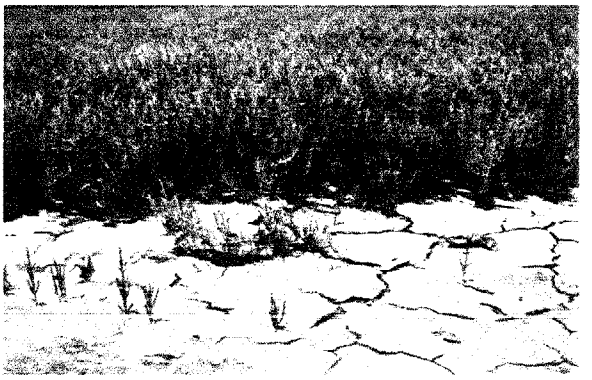
THE ECOLOGY OF SOUTHERN CALIFORNIA COASTAL SALT MARSHES: A Community Profile



Fish and Wildlife Service

U.S. Department of the Interior

The Biological Services Program was established within the U.S. Fish and Wildlife Service to supply scientific information and methodologies on key environmental issues that impact fish and wildlife resources and their supporting ecosystems. The mission of the program is as follows:

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ERRATA SHEET

Please note the following corrections to errors that either were overlooked or introduced in proofreading and are not the responsibility of the author.

1. Page 4, last line, left column: "5°C (41°F) warmer" should read "5°C (9°F) warmer." Page 6, left column, last paragraph, eighth line: "5°C (41°F) cooler" should be "5°C (9°F) cooler."

2. Page 16, Table 4: Malibu Creek should show the following species: Frankenia grandifolia, Distichlis spicata, Cuscuta salina, Jaumea carnosa, and Salicornia virginica.

3. Page 32, Figure 24: The caption should read "scale = 2 mm."

4. Page 68, bottom of right column: "Gillichthys mirabilis" should be underlined.

5. "Belding's savannah sparrow" should be "Belding's Savannah sparrow" in Figure 48, Table 16, Table 18, page 81 last paragraph, page 82 third paragraph, and elsewhere in the text.

6. Page 96, left column, third paragraph with bullet should begin "Where tidal flushing is impaired, breaching barriers is the usual first suggestion."

7. Page 100: The title of the J.S. Bradshaw 1968 reference should read "The biological and ecological relationships in the Los Penasquitos Lagoon and salt marsh area of the Torrey Pines State Reserve Park."

8. Page 110: "Winfield, F. 1980" should read "Winfield, T. 1980."

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THE ECOLOGY OF SOUTHERN CALIFORNIA COASTAL SALT MARSHES: A COMMUNITY PROFILE

by

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The findings in this report are not to be construed as an official U.S. Fish and Wildlife Service position unless so designated by other authorized documents.

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PREFACE

This community profile is part of a developing series of publications concerning coastal habitats. Its purpose is to describe the structure and functioning of coastal salt marshes of southern California. 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 euhaline to hypersaline, with occasional mixohaline conditions.

The profile brings together a wide range of information on coastal salt marshes, with emphasis on the vegetation which dominates the intertidal sediments. Several conceptual models are suggested as hypotheses of marsh dynamics, e.g. how vegetation becomes established on bare soils, the role that algal mats play in marsh food production, how food is transferred through consumers, and how nutrients and organic matter move back and forth between the marsh and its adjacent tidal creeks. These models should be viewed as tentative, and future research should test them rigorously.

The first chapter describes the physiographic setting of southern California coastal wetlands. Chapter 2 describes vascular plant vegetation; Chapter 3 summarizes the sparse information on soil algal communities, and Chapter 4 compares the functional roles of both plant types in overall salt-marsh functioning. Chapter 5 examines the marsh fauna, and the final chapter relates the ecological information to current management problems.

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

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This report is dedicated to Emily and Sarah, who encouraged me.

INTRODUCTION TO SOUTHERN CALIFORNIA COASTAL MARSHES

Southern California has a varied and attractive coastline, a warm climate, and a large human population. It is a region where cities have grown rapidly and where the natural landscape has been extensively modified to serve urban development, military uses, shipping and industrial needs, recreation, and tourism. Because of their flat topography and occurrence near waterways, coastal marshes have been prime targets for these modifications. And because disturbance is such a common feature in southern California wetlands, its effects must be considered in developing a profile of the marsh community. Ideally, the profile should summarize the natural characteristics of coastal marshes and discuss how various disturbances have altered them. But disturbance has occurred for so long, has been so pervasive, taken such different forms, and had such different results in each wetland, that sorting out natural and unnatural features is extremely difficult.

An early investigation provided some information about the numerous coastal marshes prior to the post-war construction boom along the southern California coast (Purer 1942). But urban expansion proceeded without regard for or information about the natural resources of coastal wetlands, and no pristine examples are left to reconstruct exactly what was destroyed or altered. Hence, this community profile relies heavily on what ecologists today believe to be more natural versus more disturbed, what is likely to be the normal situation versus what is probably the result of man's intervention, and what experimental studies and long-term observations can tell us about cause-effect relationships.

Southern California coastal wetlands are small and discrete. They are confined to narrow river valleys, and are separated by coastal hills and mountains (Figures 1, 2). Between the International Border with Mexico (32°N) and Point Conception (34-1/2°N lat.), there are about 30 wetlands. Their total area (less than 5000 ha [12,500 ac]) is estimated to be 25% of their area prior to the arrival of European man (Speth 1969a,b).

The marshes within these wetlands are not identical to one another. Some of the differences result from disturbance; others appear to correlate with characteristics of tidal flushing (whether continuous or intermittent). In general, the marshes occur on intertidal slopes or the tops of creek banks which grade rather quickly from mean sea level to extreme high water. A dozen or more halophytes (salt-tolerant plants) are found within this narrow band of habitat. Low-growing succulents (especially the pickleweed, *Salicornia virginica*) are abundant throughout most of the intertidal zone, while cordgrass (*Spartina foliosa*) is conspicuous only at the lower elevations in some, but not all, of the marshes. Tidal creeks dissect the marshes, and lead to larger channels or bays. Coastal dunes partially enclose the wetlands, and at times sand bars completely cut off oceanic circulation.

Because of the great contrast between these general features and the broad coastal plains elsewhere in the United States, the physiographic setting and geological history will be examined first. Then, a summary of the hydrological characteristics and climatic conditions will explain the hypersalinity of southern California marsh soils, which in turn will set the stage for discussing salt marsh vegetation. The role of marshes as habitats for a variety of birds, fish, and other wildlife will then lead to a discussion of management considerations and current attempts to restore and enhance southern California's coastal marshes.

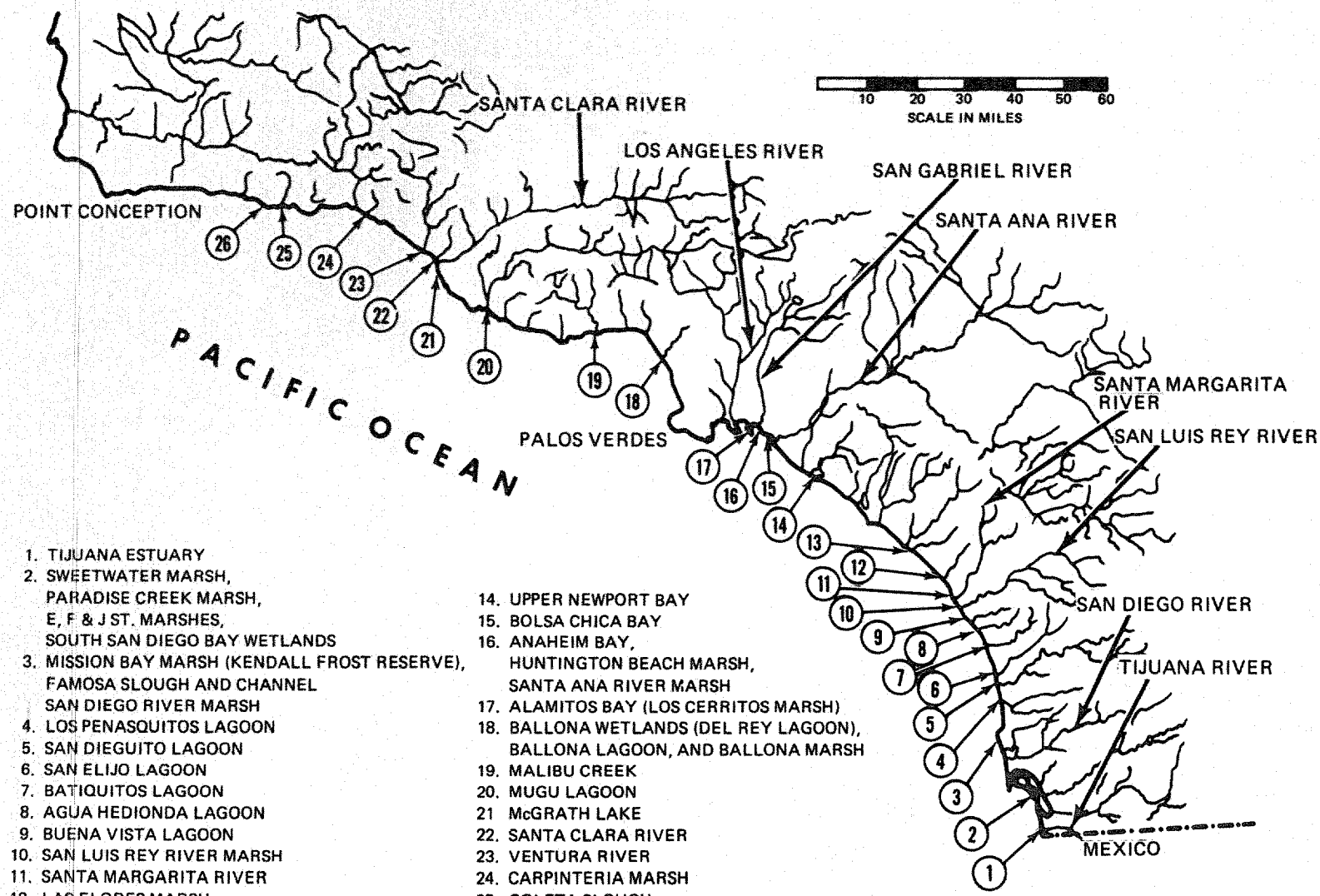


Figure 1. Location of southern California coastal wetlands and major rivers.

Figure 2. Marine and terrestrial topographic contours. Triangles indicate mountain peaks on the mainland.

CHAPTER 1

THE PHYSIOGRAPHIC SETTING

The Pacific coastline is noted for its nearby mountains and steep bluffs which provide overviews of rocky shores, sandy beaches, and occasional river outlets. The rugged topography that meets the Pacific Ocean contrasts sharply with the broad, flat coastal plains of the Atlantic and Gulf of Mexico coasts. Because of California's position on the leading edge of the continent, its history of recent uplift, and its continuing seismic activity, only limited areas of flat topography have formed to support bays, estuaries, lagoons, and marshes.

But the Pacific coastline is not uniform throughout its length. Several features make the southern California region unique. The coastal mountain ranges of California bend eastward near Point Conception (34-1/2°N lat.), forming the Transverse Ranges of southern California (Figure 2). The coastline likewise bends toward the southeast, where there are a number of submerged basins and troughs which parallel the various submerged mountain ridges. The submarine topography is as rugged as the exposed land and depths drop quickly to 500 m (1,640 ft), leaving a very narrow continental shelf. Isolated peaks to the west form the Channel Islands, where the topography is too steep to support marsh communities.

Point Conception has long been recognized as a transition area for marine biota, many of whose northern or southern boundaries coincide with this landmark and the nearby shifts in ocean currents and surface temperatures. Along northern and central California, the California Current parallels the shore. At Point Conception it continues southward and creates a countercurrent which curves back toward the north after becoming warmed along the coast of Mexico. The nearshore water off southern California is often 5°C (41°F) warmer than that of the California Current. While such a difference is expected to influence the distributions of marine organisms along the exposed coast, it may be much less important to marsh plants and associated animals found within protected embayments. The point is a convenient boundary for describing southern California marshes. While marshes between Mexico and Point Conception have many similarities with ones further north and south, a single "community profile" would not be valid for wetlands spanning such a broad latitude.

1.1 GEOLOGICAL HISTORY

Coastal areas of southern California have a dynamic geological history, and the area continues to be influenced by seismic activity, by subsidence, and by catastrophic flooding with its associated impacts of scouring and accretion of sediments. Intertidal organisms are very sensitive even to small changes in elevation; hence, it is important to consider how their habitat has changed in the past in order to interpret their modern distribution and composition. The relative instability of this coastline suggests that marsh habitats may have undergone quite recent changes and that current species distributions have not yet stabilized.

The present location of the southern California coastline is between the maximum and minimum elevations of sea level known for recent geological history (Figure 3). Thick marine deposits were laid down along the coast in the Pliocene and Pleistocene, when waters were at times several hundred meters deep over the present marsh habitats. More recently, sea level fell to about 120 m (400 ft) below the present level, reaching its minimum about 18,000 years ago (Vedder and

Howell 1980, Nardin et al. 1981). The subsequent rise in sea level averaged about 12 m (40 ft) per 1000 years until about 5000 years ago, when the level was perhaps within 5 m (16 ft) of its current elevation. In recent centuries, sea level appears to be relatively stable with respect to the land surface (Isaacs 1979). Topographic changes today are largely due to accretion and erosion of sediments, which are greatly influenced by activities of man.

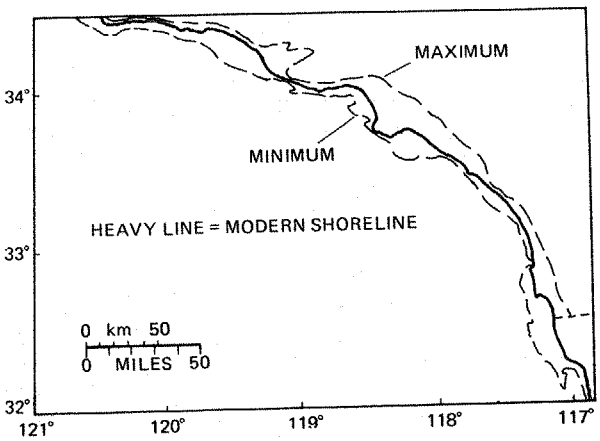


Figure 3. Changes in sea level (from Vedder and Howell 1980). Inner boundary is the maximum extent of the sea during the last half million years; outer boundary is the probable minimum, 17 to 18 thousand years ago.

Mudie and Byrne (1980) reviewed data from marsh cores which have been carbon dated and cores for which Foraminiferan assemblages have been analyzed. They estimated a sedimentation rate of 10 cm/100 years for the period from 2500 B. P. until the late 19th century. Then, based on pollen analysis (using introduced species as a marker for the arrival of European man), they concluded that accretion increased to 50 cm during the last century, following changes in agricultural practices which no doubt enhanced erosion. Their conclusions agree with Macdonald's (1969) statement that Mission Bay doubled its marsh acreage between 1859 and 1933 and with the conclusion that some present-day marshes are of quite recent origin. Lohmar et al. (1980) documented sedimentary filling of Goleta Slough following flooding in the 1860's and subsequent replacement of channels and intertidal flats by saltmarsh. Stevenson and Emery (1958) likewise concluded that the Newport Bay marsh was only 90 to 130 years old at the time of their study.

Some of the sedimentation may have slowed following the construction of upstream dams, however. Nordstrom and Inman (1973) estimated that 33% of incoming sediment loads are being trapped by 10 dams within the watersheds between San Clemente and La Jolla, while 72% of the sediment normally flowing down the Tijuana River was blocked behind its upstream dams. These decreased sediment inputs are widely visible as losses in sandy beaches along the southern California coast (Nordstrom and Inman 1973).

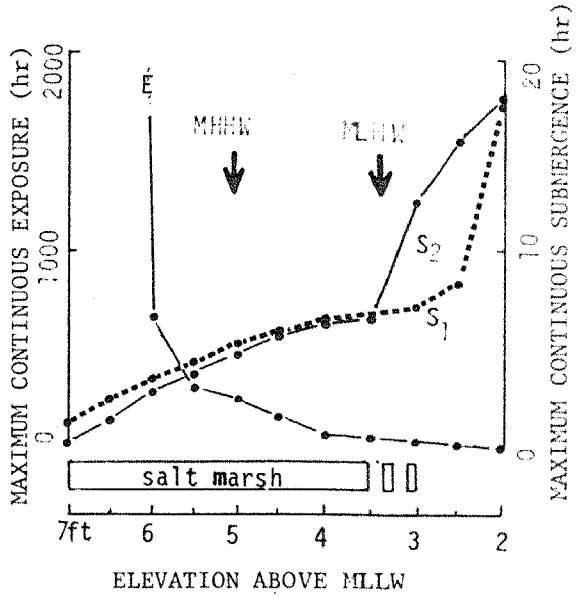
Still, local point sources of sediment can be seen next to slopes where prolonged disturbance occurs, such as near storm sewers draining housing developments (as at Los Penasquitos Lagoon) or next to agricultural fields (e.g. at Mugu Lagoon and also documented by Dickert et al. 1981 for Elkhorn Slough in central California). Observations during the flood years of 1978 to 1980 suggest that catastrophic sedimentation is limited to periods of unusual flooding, and that coastal marshes undergo alternating periods of stable elevation and accretion.

1.2 TIDAL CIRCULATION

Tidal circulation is extremely important to coastal marshes in southern California because of the low, seasonal precipitation, low runoff and frequent droughts. Sea water provides most of the soil moisture for intertidal wetlands. Southern California tides are of the mixed semidiurnal type, that is, the two daily high tides are of different height, as are the two daily low tides. The mean tidal

amplitude is about 1.1 m (3.6 ft) for most monitoring stations and the average amplitude of spring tides is generally over 1.6 m (5.2 ft; USC&GS 1978).

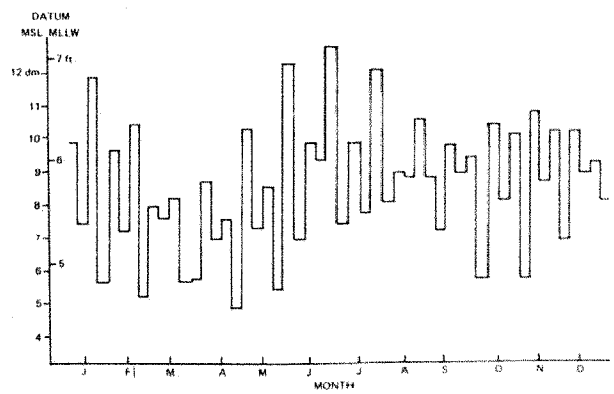
Extreme conditions are probably more important to marsh organisms than annual averages. Macdonald's (1977a) data on maximum submergence and exposure times for different elevations at Mission Bay Marsh indicate the broad range of environmental conditions found in the intertidal zone (Figure 4). Additional patterns occur during the year. Lowest low tides occur during the daytime in fall to winter and during nighttime in spring and summer. A seasonal progression of tidal characteristics can be seen by averaging the higher high tides for each week of the year (Figure 4). This analysis shows that upper marsh habitats go for long periods during spring without much tidal wetting. For years of low spring rainfall, desiccation of soils and vegetation, especially soil algae, may be severe (Zedler 1980).



Duration of maximum tidal exposure (E) and submersion (S_1=Nov. 1964; S_2=Jan. 1965) for Mission Bay Marsh. Adapted from Macdonald (1977a). MHHW = mean higher high water; MLHW = mean lower high water; MLLW = mean lower low water.

1.3 CLIMATE AND WEATHER

The southern California climate is termed Mediterranean because of the warm, dry summers and cool, moist winters which are similar to Mediterranean countries. Frost is rare along the coastline. Annual daily temperatures average from 15°C (59°F) at Santa Barbara to 21°C (70°F) at San Diego, with winters about 5°C (41°F) cooler than summer. Annual rainfall is quite low, averaging from 20 cm (8 in) at Chula Vista (near Tijuana Estuary) to 40 cm (16 in) at Santa Barbara (near Goleta Slough) (Table 1). However, annual averages do not satisfactorily describe the conditions to which coastal wetlands are subjected. Rainfall is usually concentrated in the winter months, but the timing of storm events and the total winter rainfall are both highly variable (e.g. San Diego rainfall, Figure 5). Two years of similar rainfall can lead to drastically different conditions if precipitation occurs in one or two storm periods instead of being distributed over several months.



Weekly mean high water predicted for San Diego in 1977 (from Zedler 1980). Data are in decimeters (dm) above mean sea level (MSL) as well as feet above mean lower low water (MLLW).

Figure 4. Tidal characteristics in southern California.

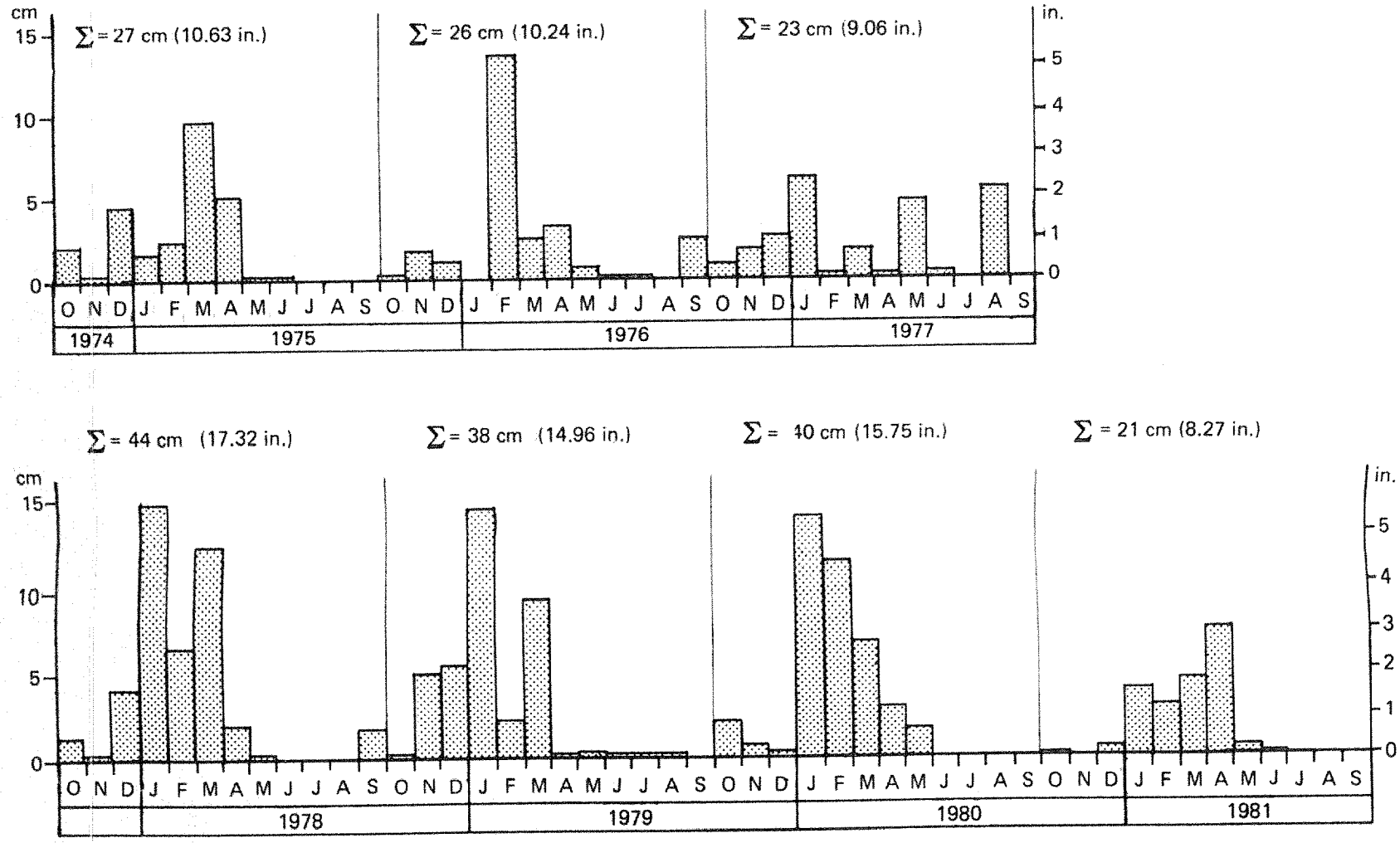


Figure 5. Rainfall data for San Diego (Lindbergh Field). Totals for the 1 October to 30 September water years are given. The years 1978 to 1980 were relatively wet. Rainfall in summer 1977 was unusual. The 30-year average rainfall is 24 cm at this station.

Whether or not rainfall has a major effect on marsh organisms depends in part on tidal conditions and the degree flooding. Rainfall during high tides may have no effect, while a storm during periods when tides rarely wet the middle or upper marsh elevations may substantially increase soil moisture, decrease salinity, and improve plant growing conditions. In contrast, lack of rainfall at such times results in extreme desiccation of marsh soils and soil algae, as was documented for Tijuana Estuary in April 1977 (Zedler 1980).

Table 1. Climate data for southern California coastal weather stations (from NOAA 1980).

Station, elevation (m) and location	Mean Daily Temp (°C)	Mean Annual Ppt (cm)
Chula Vista (2.7m) 32°36'N 117°06'W	15.7	20.4
San Diego (4.0) 32°44'N 117° 10'W	21.3	24.0
Long Beach (7.6) 33°49'N 118°09'W	17.4	26.0
Los Angeles (29.6) 33°56'N. 118°24'W	20.7	29.4
Santa Barbara (2.7) 34°26'N 119°50'W	14.9	39.5

Floods occur under a number of conditions in southern California. Heavy rainfall concentrated in a short period of time is likely to cause flooding of coastal wetlands. According to Climates of the States (NOAA 1980, p. 66),

> "The maximum intensity of precipitation for periods of 12 hours or longer which might be expected at intervals of 10 to 100 years is greater in portions of the San Gabriel and San Bernardino Mountains in Southern California than anywhere else in the continental United States."

Twenty inches of rain in 24 hours is not impossible! When one storm closely follows another, watershed soils may become supersaturated and result in flooding sufficient to inundate coastal marshes. Or, when water is released from upstream reservoirs, the volume may be sufficient to overflow the channels and tidal creeks.

Stream discharge data provide a better measure of flooding in coastal marshes than does annual rainfall along the coast. For example, Tijuana Estuary had severe flooding during 1980, even though rainfall was not much greater than in the previous two years. From 1978 to 1980, the coast had 1.5 to 2 times average rainfall, yet winter discharges from the Tijuana River ranged from average in 1979 to 28 times normal in 1980 (Table 2). At least two factors interacted to make 1980 a year of severe flooding at Tijuana Estuary--successive storm events in January and February and release of water from Rodriguez Dam upstream, as a flood protective measure for the city of Tijuana, Mexico. Reservoir releases can change the stream discharges both by altering peak flows (as at Tijuana River in 1980) or by changing the period of freshwater flow (as at San Diego River in 1980).

Drought is also a common occurrence in southern California, since evaporation usually exceeds precipitation during the summer and fall. Along the coast, the tidal cycle is such that upper marsh habitats are not inundated during the periods of greatest drought stress (i.e. late fall). The high spring tides, which occur in January and June (Figure 4), are primarily responsible for wetting the highest marsh habitats. Their absence in August and September leads to dry, cracked soils in the upper marsh. Late fall is also the time when hot, dry desert winds displace the usual moist marine air mass. The dry air, sometimes close to zero in

humidity, is very clear. The coastal haze, which usually reduces light penetration, is absent, and both evaporation and moisture stress become extreme.

Table 2. Stream discharge at the Tijuana River (Nestor gage). Watershed area drained by this gaging station = 4,390.

Water year (1 Oct-30 Sep)	Acre-ft/ water year	Acre-ft/ Jan-Mar	Floods
1975	50	19	no
1976	663	661	no
1977	96	88	no
1978	71,250	67,940	moderate
1979	40,700	20,620	minimal
1980	587,200*	506,008*	extreme
average, 1937-80:	21,080		

*Estimated from upstream since Nestor gage was destroyed by flood.

1.4 LAGOON CLOSURE

Because tides are so important in providing moisture for coastal marshes, any interruption in tidal circulation can have drastic effects on these communities. Many of southern California's coastal wetlands have a tendency to become closed to tidal flow through the formation of sand bars across their ocean connection. Longshore currents move sand along the southern California coast, so that entrances to estuaries and lagoons are not stable. Aerial photographs through time show that entrance locations migrate, and historical records document that many entrances close off entirely for variable periods of time. A typical sequence at Mugu Lagoon is for the sand bar to migrate south through the summer, eventually closing off the entrance. Stream discharges resulting from winter rain break the sand bar near the river channel, reinstating the pattern (Warme 1969a, Macdonald 1976b).

The cross-sectional area of lagoon entrances correlates with the tidal prism (i.e. the total volume of water moving in and out of the embayment) according to Inman and Frautschy (1966). As tidal prisms are reduced through sedimentation or filling for road construction or development, the likelihood of closure increases. Gravel, brought into the mouths of lagoons during winter periods when beaches are depleted of sand, may accumulate and block the ocean connection (W. Gayman, Oceanographer, Sea Science Services, San Diego, CA). In addition, restriction of lagoon entrances to a single location, as under bridges along the Pacific Coast Highway and railway, may further enhance closure.

The extent to which these embayments closed prior to changes brought about by man is difficult to determine, but local geologists seem to agree that closure of smaller lagoons was a natural phenomenon. Man's intervention has no doubt increased the tendency for closure as well as the persistance of the sand bar blockage. Study of Indian middens adjacent to three San Diego County wetlands (San Elijo Lagoon, Los Penasquitos Lagoon, Batiquitos Lagoon and Agua Hedionda Lagoon) record aboriginal use of molluscs which most likely grew in the lagoons (Miller 1966). Of these lagoons, only Agua Hedionda had a living molluscan fauna (74 species) during the study. The remaining three were closed to the ocean and did not support any living molluscs due to their brackish (San Elijo) or hypersaline (Los Penasquitos and Batiquitos) condition. Middens next to the three closed lagoons consisted of molluscs now found at the well-flushed Agua Hedionda Lagoon.

While open to tidal circulation, coastal marshes are ordinarily wetted by sea water (salinity ca. 34 ppt), since

rainfall and runoff are rare. The smaller lagoons are most likely to close. The enclosed lagoon water may become brackish, (<30 ppt) if rainfall or runoff accumulates, or hypersaline (>40 ppt), if evaporation exceeds freshwater input. The changes following closure have no doubt been modified by man. Urban and agricultural runoff, a result of irrigation by imported water, has the potential of reducing salinities, while upstream dams may have the opposite effect. Hence, the present salinity status of enclosed coastal lagoons may be very different from early historic and prehistoric systems. Whether man has substantially increased the range of salinities in enclosed lagoons or not, it is safe to say that such wetlands endure a much broader range of salinities than tidally flushed systems.

In addition to salinity, other physical and chemical features change following lagoon closure, including elevated temperatures and decreased oxygen. The surrounding marsh will be most influenced by the depth of the enclosed water and its salinity. Closure followed by runoff accumulation may subject the marsh to a long period of inundation by brackish water (Macdonald 1971). But if the closure is followed by a period of low runoff, the marsh will experience extended drought conditions. Observations at Los Penasquitos Lagoon (Chapter 2 and Zedler et al. 1980) document some of the consequences of lagoon closure on marsh vegetation.

Biological changes within the lagoon water also occur and make the enclosed lagoon esthetically unappealing. Floating algal mats flourish, then die, decay and emit offensive odors. Mosquitos and midges reach pest densities. Hence, various measures to reopen lagoons have been attempted (see Chapter 6).

1.5 INTERTIDAL SOIL SALINITY

Two characteristics of southern California marsh soils stand out when these wetlands are compared to coastal marshes elsewhere in the United States. The soils have an extremely broad range of salinities, and long periods of hypersalinity occur. Unfortunately, no widespread system for recording marsh soil salinities has been developed. The generalization that southern California wetlands are usually hypersaline is based on detailed, long-term observation of Tijuana Estuary and scattered information from other wetlands (Table 3). However, the conclusion is consistent with records of water salinities within lagoons, which are more readily available, and with predictions based on the previous information about tidal circulation and climatic conditions because most of the soil water derives from tidal sea water and because evaporation usually exceeds precipitation, salts accumulate in the soils.

The specific annual and long-term patterns are less easily predicted. Measurements of soil salinity in the lower marsh of Tijuana Estuary, where cordgrass (Spartina foliosa) is the dominant, record how variable the salt conditions are for the upper 10 cm of substrate (Figure 6). Salinities decreased slightly following the winter rains of 1979, dropped dramatically following the extensive flooding of 1980, but remained hypersaline throughout the dry year of 1981. The rapid return to hypersaline conditions in 1979 and 1980 occurred because of the predominating influence of tides in this low marsh habitat.

Lagoon closure can result in large changes in soil salinity, as the impounded water either accelerates or prevents the leaching of salts. Closure followed by the accumulation of runoff or urban effluent can result in a brackish water lagoon. For example, Buena Vista Lagoon (Figure 7) received fresh water throughout Carpelan's (1969) study. Water levels were maintained by a weir, and the lagoon's meter-deep water was consistently under 5 ppt in 1958-59. San Elijo Lagoon and San Dieguito Lagoon were also closed to tidal flow, but freshwater input was

Table 3. Summary of intertidal soil salinity data in several southern California marshes.

Data in Salt Concentrations

Purer (1942) sampled within the marsh at 1 location (habitat not given) once a month for 12 mo. during 1939-1940 (a relatively wet period). Data are ppt, obtained by collecting water from soil pits.

Wetland	Min.	Max.
Tijuana Estuary	5	44
Sweetwater Marsh	23	42
Mission Bay	18	53
Los Penasquitos Lagoon	5	37
San Dieguito Lagoon	10	43
San Elijo Lagoon	5	145
Batiquitos Lagoon	5	55
Agua Hedionda Lagoon	2	22
Buena Vista Lagoon	1	45
Loma Alta	2	145
San Luis Rey	2	30
Santa Margarita	3	53

(Maxima are from summer & fall)

Eilers (1981) sampled several stations with the marsh 7 times between fall 1977 and summer 1978. Data are ppt, from refractometer readings of interstitial water in the upper 5 cm of soil.

Wetland	Min.	Max.
Sweetwater Marsh	20	121
Los Penasquitos Lagoon	8	125
Upper Newport Bay	9	90
Bolsa Chica (non-tidal)	7	54

(Maxima are from summer except for Los Penasquitos where max. values occurred prior to lagoon closure caused by a sand bar.)

Data in Conductivity Units[1]

McIntyre (1977) sampled with the *Salicornia virginica* marsh at the San Diego River from winter through summer 1976. Data are soil paste conductives from the top 15 cm of soil, expressed as mmhos/cm.

Season and depth of core		Average in control plots
Winter	1-15 cm	12.9
Spring	1-5 cm	15.8
	6-15 cm	10.8
Summer	1-5 cm	39.3
	6-15 cm	28.2

Zedler (1977) sampled 3 transects across the elevation gradient at Tijuana Estuary marsh in winter and late summer 1974. Data are soil paste conductivities from the top 10 cm of soil, expressed as mmhos/cm.

Season	Range
Winter	0.8-24.5
Summer	14.9-38.8

(The higher summer values were from the lower elevations.)

[1] Soil salininity data in mmho/cm are not converted to ppt, because water is added to dry soils in preparing soil pastes for conductivity measurements. A useful reference point is 15 mmho/cm, which approximates a soil saturated with sea water (34 ppt) (see Zedler 1977).

more dependent on rainfall. Salinities decreased during winter storms and increased in response to evaporation or, in the case of San Elijo Lagoon, to overflow of storm tides into the lagoon (Figure 7).

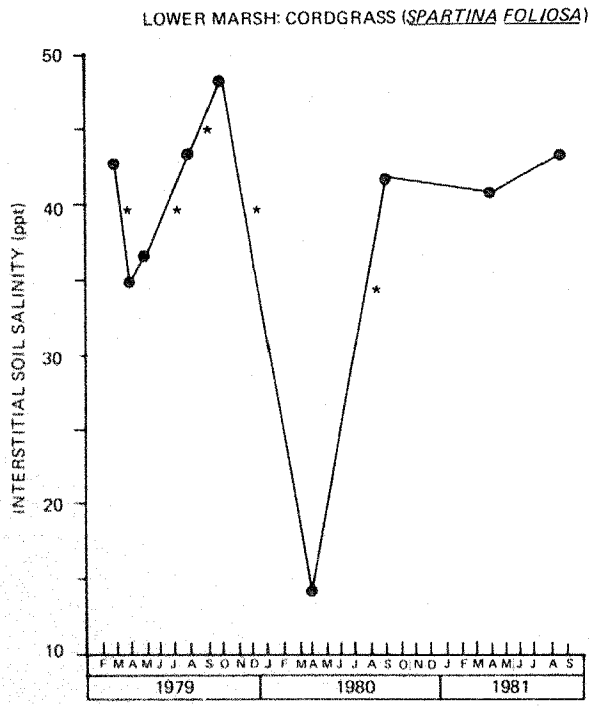


Figure 6. Interstitial soil salinities in the lower marsh (elevation averaging about 7 dm above MSL) at Tijuana Estuary, where Spartina foliosa is dominant. Asterisks indicate significant differences ($p < 0.05$) between sampling dates. Data from Zedler (unpub. ms.b).

When water levels of closed lagoons are high enough to flood the marsh, soil salinities can be expected to change in proportion to the length of inundation periods. Long periods of reduced tidal influence at Los Penasquitos Lagoon followed by heavy rainfall in 1978 seem to be responsible for the persistent brackish soils found by Zedler et al. (1980) and Eilers (1981). The influence of heavy rainfall on tidal estuaries and non-tidal lagoons is summarized in Figure 8.

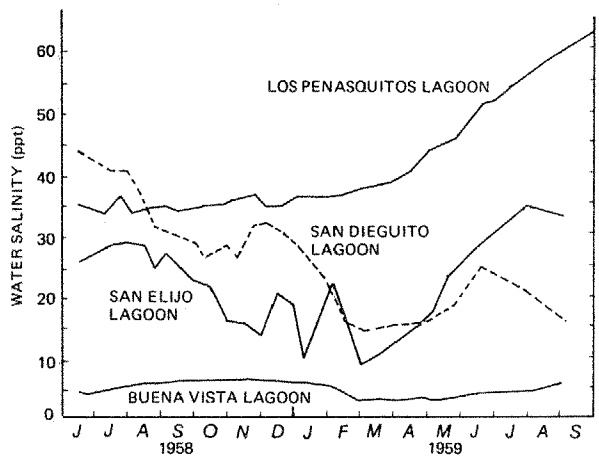


Figure 7. Seasonal changes in water salinity of four lagoons (from Carpelan 1969). Los Penasquitos Lagoon became closed to tidal circulation during December 1958 and remained closed for the rest of the study.

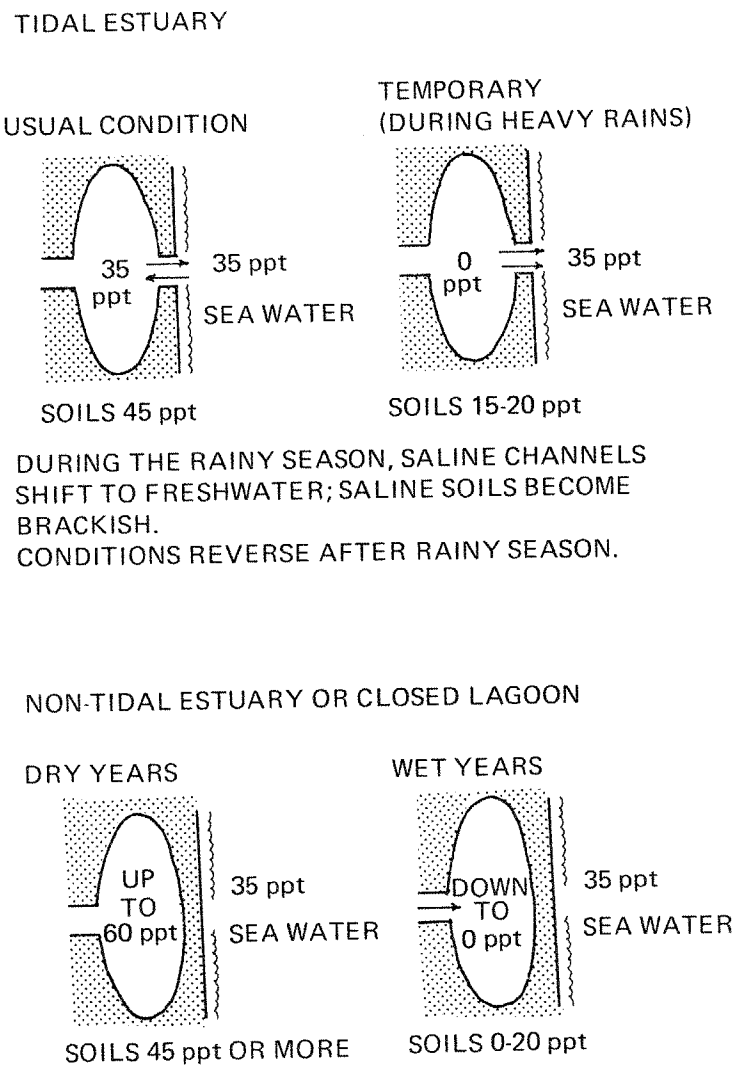


Figure 8. Effects of heavy rainfall on the channel water and intertidal marsh soils of tidal estuaries and closed lagoons.

1.6 SUMMARY OF CHAPTER 1

Southern California coastal marshes are confined to narrow stream outlets along a coastline of rugged topography and continuing geological activity. The Mediterranean climate of the region provides little rainfall, on the average, so that tidal sea water is the major source of moisture throughout all but the brief winter wet season.

Sand, deposited by longshore currents, tends to build up along the ocean inlets, and wetlands with small tidal prisms are likely to become completely closed to tidal circulation. Various land use practices reduce tidal prisms, which in turn increase the probability and duration of lagoon closure.

Extreme variations in intertidal soil salinities occur between years of flooding and drought. Lagoon closures cause additional variability in salinity. Large areas of southern California marsh habitat are hypersaline throughout the spring to fall growing season. The wide-ranging salinities and long periods of hypersaline conditions contrast greatly with brackish tidal marshes elsewhere in the United States.

CHAPTER 2

VASCULAR PLANT VEGETATION

Given the relatively short list of species known to tolerate saline conditions worldwide and realizing that even these species grow best in environments less saline than the intertidal zone, one might predict a rather limited flora and highly stressed community for hypersaline marshes. This appears to be the case. Up to 17 halophytes (mostly succulents) are common in the areas of greatest tidal influence (Table 4). They intermix to produce a low-growing, relatively open canopy of vegetation which readily responds to decreased salinities by becoming taller and more dense.

Despite the short list of species found in southern California marshes, there is wide variation in vegetation structure and functioning from marsh to marsh, as well as within individual wetlands. At the smaller scale, compositional differences relate to position over the intertidal elevational range and to patterns of establishment, followed by vegetative expansion. At a larger scale, many of the structural patterns relate to the size of the wetland and its history of tidal circulation and other disturbances. Functional patterns, especially differences in primary productivity, show strong correlations with soil salinities. Plant growth differs both spatially and from year to year, increasing in areas of brackish soils and during years of heavy rainfall.

This description of marsh vegetation begins with the patterns of composition which occur from low to high intertidal position. Factors controlling the distribution of the more common halophytes are discussed, and changes in species composition following various types of disturbances are documented. Together, the observations of spatial and temporal patterns of composition suggest a conceptual model of marsh community development. Plant productivity data are summarized and the relationships between plant growth and freshwater influence are demonstrated.

Although a thorough understanding of what controls marsh structure and functioning awaits experimental tests of the ideas put forth here, we can conclude with certainty that southern California marshses are highly dynamic communities which readily respond to both natural and man-caused environmental changes.

2.1 COMPOSITION AND INTERTIDAL POSITION

While this profile of marsh structure does not include all of the variation within southern California, it summarizes present knowledge, indicates what ecologists have determined to be the most likely characterization of undisturbed marsh vegetation, and provides a model for restoration and enhancement of degraded systems.

Distributional changes of species with elevation can be described at the small-scale or individual-marsh level. Because most of the halophytes rely on vegetative reproduction (rather than seedling establishment) for areal spread, discrete patches and boundaries can be seen in the marsh. In fact, patches seem to be the rule rather than the exception, suggesting that species distributions are commonly in a state of change. Also, since heights of a few species, such as cordgrass (*Spartina foliosa*) and spiny rush (*Juncus acutus*), greatly exceed those of the low-growing succulents, a marsh may display discrete boundaries where the upper or lower limits of such species occur. However, averaging occurrences or cover values over the full elevational range of a marsh shows that (1) most

Table 4. Check list of species within salt marshes of southern California wetlands. Data are cumulative lists from a variety of sources, including observations of W. Ferrens (UCSB Herbarium) and J. Zedler. Wetlands with a history of good tidal flushing are boxed on the right-hand column below.

HIGHER MARSH - LOWER MARSH

Wetland	Juncus acutus	Frankenia palmeri	Lasthenia glabrata	Cressa truxillensis	Atriplex watsonii	Salicornia subterminalis	Cordylanthus maritimus	Limonium californicum	Monanthochloe littoralis	Frankenia grandifolia	Triglochin concinnum	Suaeda californica	Distichlis spicata	Cuscuta salina	Jaumea carnosa	Batis maritima	Salicornia bigelovii	Salicornia virginica	Spartina foliosa
Tijuana Estuary	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Sweetwater Marsh	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Mission Bay Marsh						●		●	●	●	●	●	●	●	●	●	●	●	●
Penasquitos Lagoon	●		●	●		●	●	●	●	●		●	●	●	●			●	
San Dieguito Lagoon	●		●	●		●		●	●	●		●	●		●			●	
San Elijo Lagoon				●		●				●			●		●			●	
Batiquitos Lagoon	●		●	●		●		●	●	●			●		●			●	
Agua Hedionda Lagoon	●			●		●			●	●		●	●	●	●			●	
San Luis Rey River Marsh	●									●			●		●			●	
Santa Margarita River Marsh	●		●	●	●	●		●		●		●	●	●	●			●	
Las Flores Marsh						●				●			●		●			●	
San Mateo Marsh										●			●	●	●				
Upper Newport Bay Marsh	●				●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Bolsa Chica Marsh	●				●	●		●	●	●		●	●		●	●	●	●	●
Anaheim Bay Marsh	●			●	●	●		●	●	●	●	●	●	●	●	●	●	●	●
Ballona Wetland				●		●				●		●	●		●			●	
Malibu Creek																			
Mugu Lagoon	●		●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
McGrath Lake	●									●			●		●			●	
Santa Clara River	●									●			●					●	
Carpinteria Marsh			●	●	●	●	●	●	●	●	●	●	●	●	●			●	
Goleta Slough			●	●	●	●		●	●	●	●	●	●	●	●			●	
Deveraux Lagoon				●						●			●	●	●			●	

species have rather broad ranges of distribution and (2) a high degree of overlap occurs (Vogl 1966, Zedler 1977) (Figure 9).

The most detailed vegetation surveys have been conducted at Tijuana Estuary, where species occurrences and cover were recorded along with elevation, soil conductivity, and other environmental characteristics at 357 sampling points (Zedler 1977). Summary of these data (Figure 9) illustrates the changes which occur with elevation. Distributions of species at Tijuana Estuary are similar to other large marshes, such as Sweetwater Marsh (Mudie 1970), Mission Bay (Macdonald 1967), Upper Newport Bay (Vogl 1966, Massey and Zembal 1979), Anaheim Bay (Massey and Zembal 1979), and Mugu Lagoon (Onuf, unpub. data), with one major exception. The lower elevations of all except the marsh at Mugu Lagoon are dominated by cordgrass (Spartina foliosa). The limited occurrence of cordgrass at Mugu Lagoon may be due to habitat elimination resulting from past dredging activities. Most of the evidence suggests that cordgrass was the typical low marsh dominant in tidally flushed marshes of southern California. It has disappeared from Los Penasquitos Lagoon where it was once abundant (Purer 1942), and this too is probably due to disturbance of tidal flushing (Zedler et al. 1980).

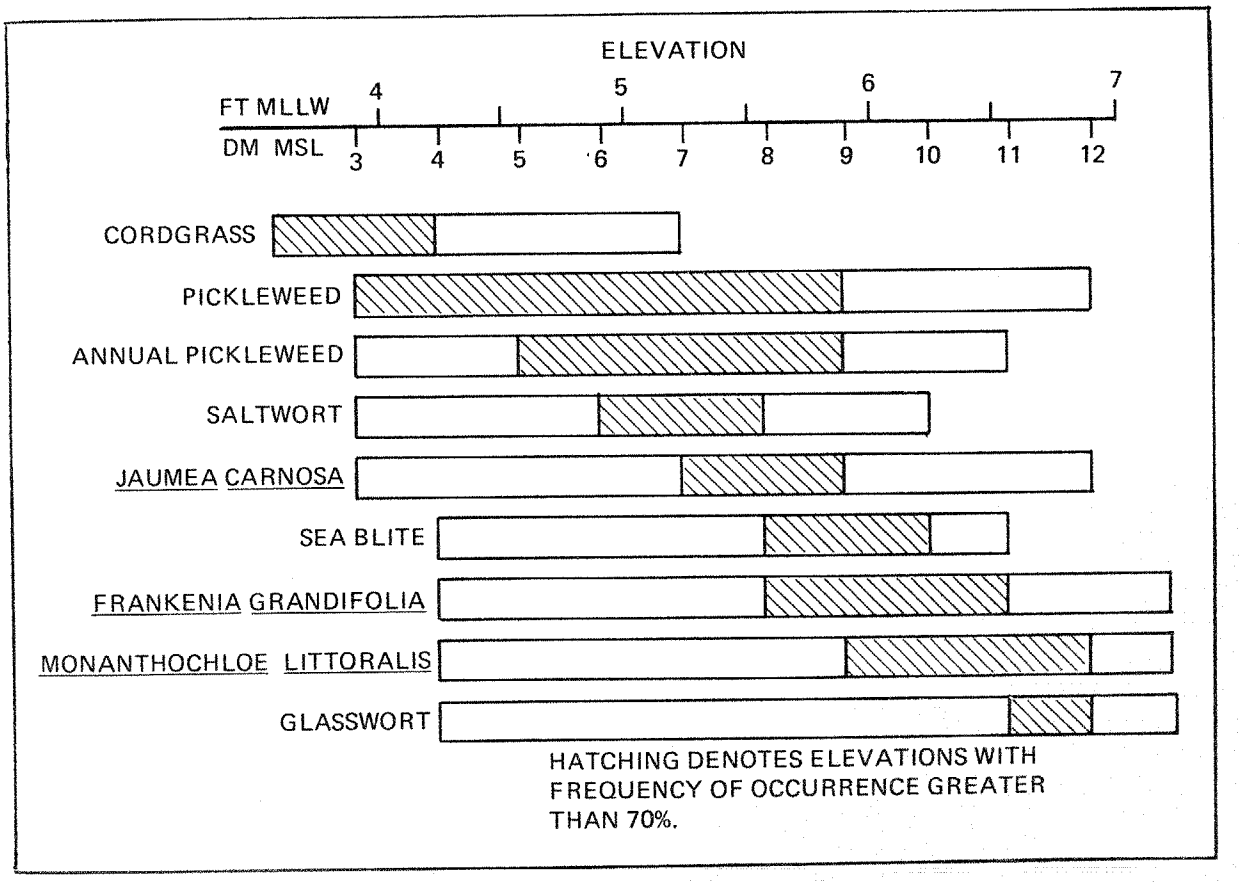


Figure 9. Distribution of the most common halophytes by elevation, at Tijuana Estuary (Zedler 1977). Data from Anaheim Bay (Massey and Zembal 1979) were used to extend the ranges of species beyond the 3- to 12-dm MSL range observed at Tijuana Estuary.

Change in species composition with elevation has been attributed to differences in inundation tolerance, differences in salinity tolerance, and competitive interactions of species (Purer 1942). Little experimental work has been done to test these ideas which were put forth nearly 40 years ago. But, we do have a better data base for the physical features which change with elevation and some indication of the importance of competition between certain marsh species.

Inundation is obviously more frequent and of longer continuous duration at the lower elevations. Macdonald's (1969) measurements of submergence at Mission Bay show that the lower marsh boundary coincides with MLHW (about 3.5 ft MLLW) and with a sharp change in hours of continuous submergence noted in January 1965 (Figure 5). Above this boundary, maximum continuous submersion decreased gradually to zero at 2.1 m (7 ft) MLLW (mean lower low water).

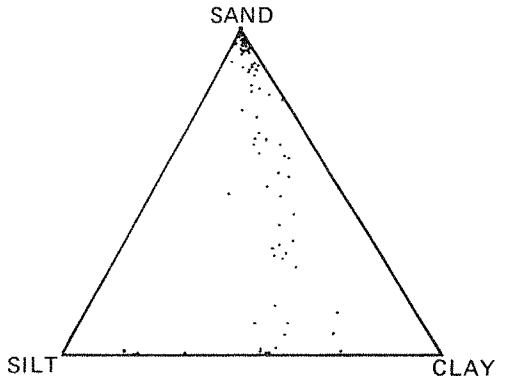
Soil organic matter content is often lower in the upper marsh (Table 5) and soils are sandier there as well (Figure 10). Together, these factors reduce the water-retaining capacity of upper marsh soils and cause the higher bulk densities (dry wt/volume) of upper marsh soils noted at Tijuana Estuary (Zedler 1977).

These three environmental features, marsh elevation, organic content and percent sand, are unlikely to change greatly from year to year and hence cannot explain the variations in species distribution which occur from year to year.

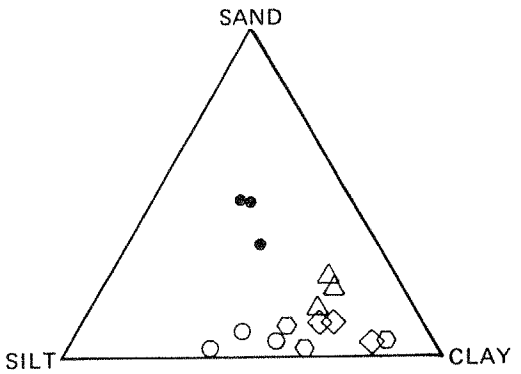
Soil salinity does change with time, and this may well be the most important physical variable which influences marsh vegetation. Macdonald (1977a) suggested a simple model of soil salinity differences with elevation for California marshes, namely that "soil salinities increase landward to a maximum around MHW (i.e. the low marsh-high marsh ecotone) and then gradually decline" (Macdonald 1977a, p. 271). But since salinity extremes are more likely to influence plant distribution than are average conditions, a more detailed description of soil salinities is necessary. Data from a transect at Tijuana Estuary (Figure 11) illustrate the usual hypersalinity of southern California wetlands and reveal several patterns: (1) soil salinity is relatively constant at low elevations where cordgrass dominates; (2) soils in the middle and upper marsh elevations become leached of salts following rainfall events; (3) on the average, upper marsh soils are less saline than lower marsh soils; (4) the variability of soil salinity, and hence its unpredictability, increases with elevation. These last two points are made clearer by plotting averages and standard errors of soil salinity against elevation (Figure 12). These results are consistent with Macdonald's (1977a) model of increasing salinity towards MHW, and decreasing salinity thereafter, but inclusion of the variability term (standard error) shows the necessity of frequent salinity measurement in order to characterize the marsh soil environment. If this transect

Table 5. Soil organic matter content (%) determined by loss on ignition. Data are for the Tijuana Estuary, at stations where vascular plant productivity was measured by Winfield (1980).

Elevation (dm MSL) & vegetation	depth of core (cm)	$\bar{x}$	S.E.	n
low (4-6)	0-10	25	4.5	7
Spartina foliosa	10-20	26	4.3	6
middle (6-8)	0-10	32	4.9	10
various succulents	10-20	18	2.1	10
high (8-11)	0-10	19	5.2	6
Monanthochloe littoralis & *Salicornia subterminalis*	10-20	18	1.5	2



SURFACE SEDIMENTS OF MUGU LAGOON (n=79). MANY HABITATS ARE INCLUDED. ADAPTED FROM WARME (1969B).



SURFACE SEDIMENTS FROM TIJUANA ESTUARY MARSH HABITATS: LOW=OPEN CIRCLES; MIDDLE=HEXAGONS; HIGH=SOLID CIRCLES; AND FROM LOS PENASQUITOS LAGOON: LOWER MARSH=OPEN SQUARES; UPPER MARSH=OPEN TRIANGLES.

Figure 10. Soil texture data for two tidal wetlands. Tijuana Estuary data are from Zedler et al. (1980).

were measured only in September or February, very different results would be obtained (c.f. Figure 11). Because salinity is decreased only following rainfall events, the best times to assess salinity are at the end of the dry season (to obtain maxima) and after each major storm. Wet years should produce longer periods of brackish soils, as well as greater leaching of salts. Hence species relying on fresh water for seed germination would have a higher probability of population expansion during such years, while populations might fail during dry years. The higher a species occurs in the intertidal zone, the more unpredictable its soil salinity environment will be. Again, if an annual species occurs in the higher marsh habitat, reproduction may not be assured from year to year, and seeds would have to remain viable for more than a year to prevent extinction.

Perhaps the instability of soil salinity at middle and high elevations, together with the requirement of fresh water for seed germination (Waisel 1972), explains why most marsh plants rely on vegetative reproduction. Perhaps also the variability of soil salinity explains why the annual pickleweed (Salicornia bigelovii) is widespread and successful at Tijuana Estuary, while salt marsh bird's beak (Cordylanthus maritimus, ssp. maritimus), an annual of high elevation, is rare and patchy, both in space and time. Clearly, there is need for a more detailed examination of population changes with soil salinity patterns.

The extent to which physical factors control the distributional limits of perennial species is uncertain. Laboratory tests of inundation and salinity tolerance have been done only for cordgrass (Spartina foliosa) and pickleweed (Salicornia virginica) utilizing San Francisco Bay populations (Mahall and Park 1976a,b,c). Dominance of low elevations by cordgrass is consistent with Mahall and Park's finding that cordgrass has greater inundation tolerance than pickleweed. Likewise, the shift from dominance by cordgrass to pickleweed and other succulents could be explained by their finding that pickleweed is more tolerant of high salinity. Higher salinities at about MHHW (mean higher high water) could restrict the landward extension of this species, at least during dry years. However, it is more likely that a combination of factors is involved.

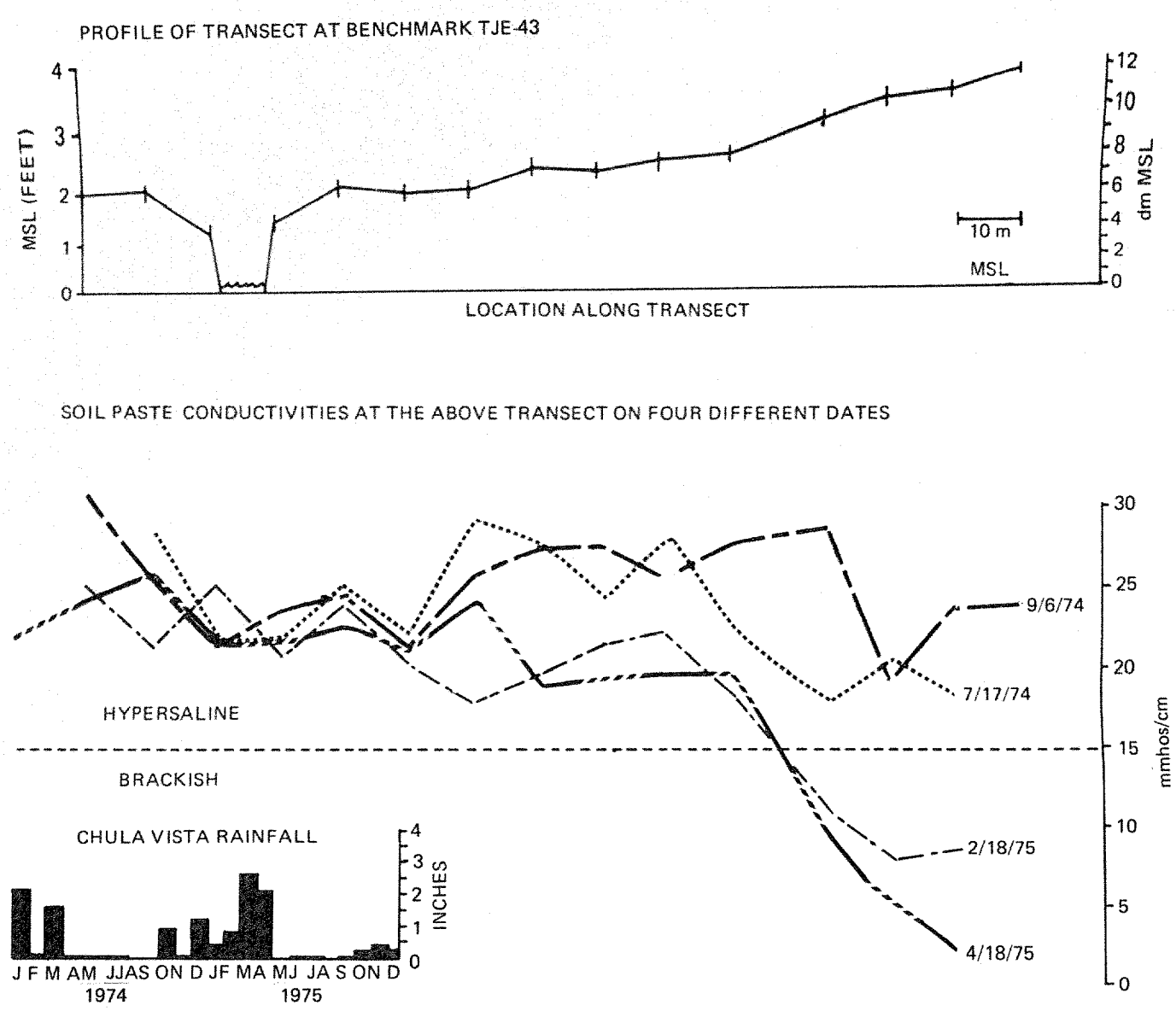


Figure 11. Soil salinity changes in relation to (A) elevation, (B) time of year and (C) rainfall. Data for Tijuana Estuary (Zedler, unpub. ms.b). See footnote of Table 3 for interpretation of mmho/cm.

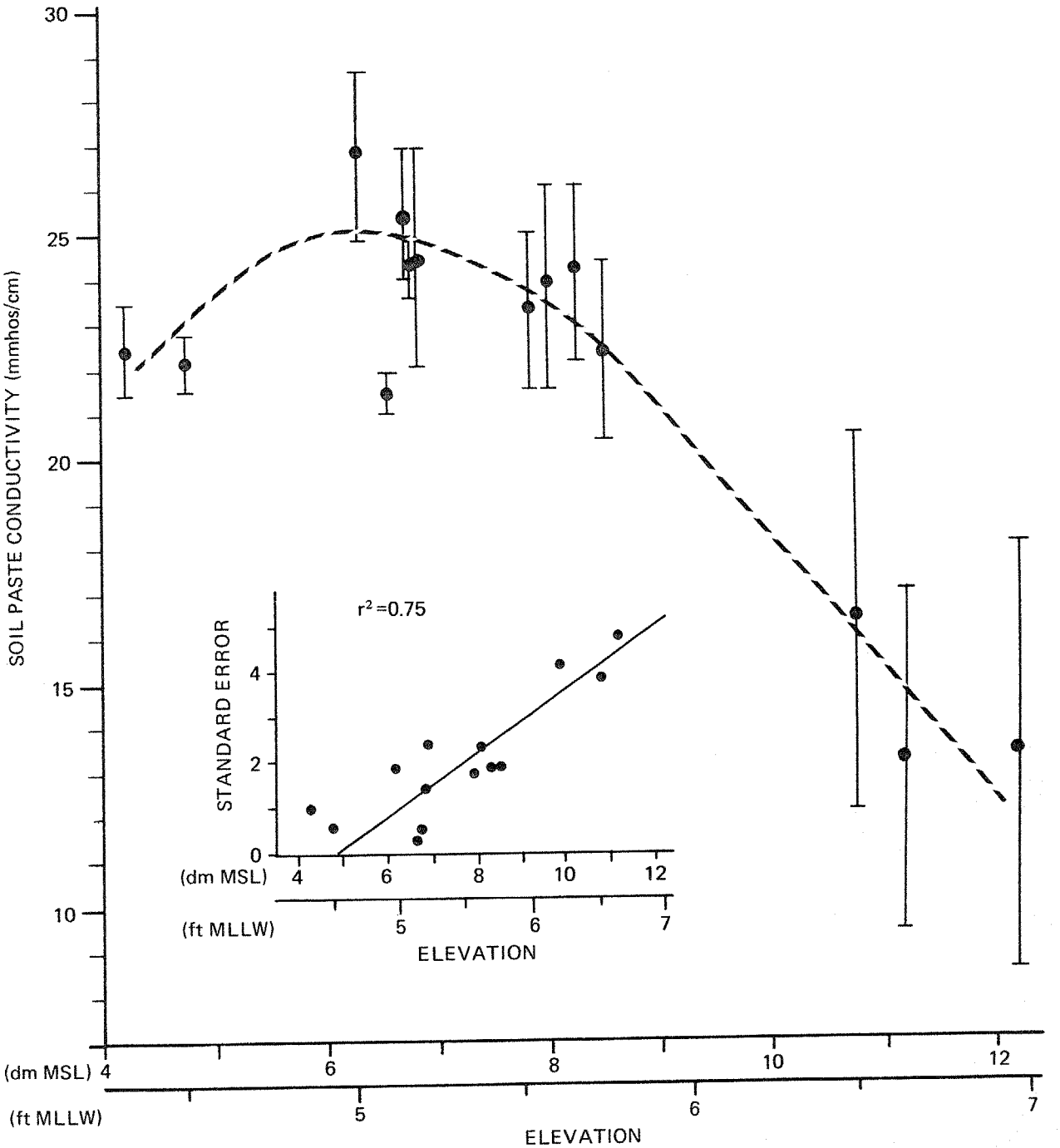


Figure 12. Average soil paste conductivity across one transect (see Figure 11) at Tijuana Estuary. Data are means of four observations through the year; vertical bars are ± S.E. Inset shows that variability (S.E.) increases with elevation. See footnote of Table 3 for interpretation of mmhos/cm.

Recent evidence suggests that this boundary is unstable and that competition with pickleweed restricts the abundance of cordgrass at its landward boundary. To determine if distributional limits were stable, Chris Nordby examined eight areas along the upper boundary of cordgrass at Tijuana Estuary (Zedler, Nordby and Williams 1979). The study was done in fall of 1979, following two wet years (Chula Vista's rainfall was 39 cm in 1978 and 36 cm in 1979, compared to a 23-cm average). Comparing numbers of live and dead stems, Nordby found that cordgrass was expanding in five of the areas, temporarily stable in one location and receding in only two areas. Instability was the rule; stability, the exception.

The role that competition plays in the abundance of cordgrass in this ecotone was indicated in a 1981 field experiment carried out near three of Nordby's study plots. Removal of pickleweed from plots which averaged 65 cordgrass stems/m^2 in February resulted in nearly a 3-fold increase in numbers of cordgrass stems and a 1.7-fold increase in biomass (Table 6). The two species probably compete for both light and nutrients. Differential tolerance to salinities could shift the competitive advantage toward pickleweed during years of high salinity stress (i.e. drought years); the upper limit of cordgrass should recede in response to high salinities, as well as reduced competitive ability. During wet years, both species would do well and cordgrass's rapid spring growth would allow expansion. Additional features of these two southern California marsh dominants are given in the following section.

Since the speculations of Edith Purer, some forty years ago, we have progressed relatively little in explaining the distributional limits of species across the intertidal zone. Future research should recognize the dynamic aspects of both the soil's environment and species distributions, and it must consider the importance of species interactions under a variety of changing conditions. Experiments to determine the competitive advantage of cordgrass and pickleweed over a range of salinity and inundation regimes are badly needed. Likewise, experiments to assess the establishment ability of annuals during short- and long-term periods of wet, brackish soils are needed. These experiments would be complex and difficult to carry out because both the timing and duration of freshwater influence would have to be manipulated.

2.2 COMMON SPECIES

Macdonald (1977a) has summarized autecological features of seven common California halophytes, and the anatomical descriptions given by Purer (1942) have yet to be improved upon. Hence this discussion will emphasize recent information about the most common southern California marsh plants, proceeding from low to high marsh.

Cordgrass (*Spartina foliosa*) (Figure 13) forms robust stands in the lowest elevations of most tidally flushed wetlands. At Tijuana Estuary densities averaged 60 stems/m^2; heights averaged 0.8 to 1.5 m; and August standing crops were 1.0 to 1.4 kg/m^2 in 1980. All values are for n=100 plots between 3 and 6 dm MSL (decimeters above mean sea level) (Zedler unpub. ms.) and represent growth under unusually good conditions.

Because of the importance of cordgrass as habitat (Jorgensen 1975) for the endangered light-footed clapper rail (*Rallus longrirostris levipes*), considerable attention has been given to the artificial propagation of this species. Although Phleger (1971) was unable to germinate its seeds, Seneca (1974) and Mason (1980) achieved success with seeds from San Francisco Bay populations; and several populations have yielded viable seed in San Diego County (Zedler 1981a). Seedlings are extremely rare in nature, however, and most of the spread of the species is vegetative. Transplantation has been successful in expanding the species' local distribution, suggesting

Table 6. Effects of competition with pickleweed (*Salicornia virginica*) and other succulents on the abundance of cordgrass (*Spartina foliosa*) at Tijuana Estuary.

	1981 Sampling Date		
	27 Feb	6 July	5 Oct
Soil salinity in ppt: $\bar{x}$ (S.E.)	37 (0.5)	46 (0.5)	44 (2.4)
Spartina density number per m^2	65	+Sv: 31	+Sv: 53
		-Sv: 81	-Sv: 152
			*
Live biomass of *Spartina* g dry weight/m^2	56[1]	+Sv: 240	+Sv: *
		-Sv: 417	-Sv:

+Sv quadrats were unaltered until 5 Oct; -Sv quadrats had all plants (ave. = 1,085 g dry wt/m^2) except *Spartina foliosa* removed on 27 Feb. Resprouts of other species were removed 3 times, and their total dry weight (ave. = 216 g/m^2) indicates that nutrient competition was not completely eliminated. However, shading effects were removed, and the response of *Spartina foliosa* was probably due to increased light as well as some nutrient release.

[1]Live biomass at the start was determined from quadrats where all vegetation was removed.

*Significantly different ($p<0.05$).

Figure 13. Pure stand of cordgrass (Spartina foliosa) at Tijuana Estuary. Photo by C. Nordby.

that additional habitats are suitable for growth but some factor limits seedling establishment in southern California. Substantial increases in its abundance surrounding abandoned sewage lagoons at Tijuana Estuary coincided with brackish soils after the 1980 floods. From this we suggest that episodic events are extremely important in controlling the spread of cordgrass and perhaps other southern California halophytes which require reduced salinities for germination and early growth.

Pickleweed (Salicornia virginica, Figure 14) has the broadest distribution of any southern California salt marsh plant. It occurs throughout most of the elevational range of cordgrass as well as the middle and high marsh habitats. It even dominates saline dredge spoil deposits well above the intertidal zone at the Ballona Wetland in Los Angeles. Presumably it is able to grow in saline areas without tidal influence if seasonal rainfall accumulates long enough to allow seed germination and seedling establishment or if moisture is available from runoff or subterranean sources. Pickleweed is abundant in the lower and middle elevations of well-flushed marshes and in lagoons closed to tidal circulation. Also, it appears to be an opportunistic invader which is capable of becoming established on disturbed soils. Reproduction in situ is primarily vegetative, but seedlings readily appear in bare spots.

Not only is pickleweed variable in the habitats it occupies, it also is variable in its growth form. At Tijuana Estuary, individuals in the lower marsh are decumbent and elongate, while middle and higher elevations are more upright and bushy. The middle elevations at Mission Bay marsh support very short individuals which contrast sharply with taller plants both below and above this zone. While there have been many speculations about the causes of these variations, from genetic to environmental differences, including waterfowl grazing, the experimental tests (e.g. transplantation, grazing exclosures, etc.) have not been done.

The biomass and growth characteristics of pickleweed have been measured in painstaking detail by Chris Onuf (unpub. ms.) at Mugu Lagoon. By tagging and measuring all branches of 25 or more plants each month in 1977, he determined that (1) pickleweed grows all year long, with new shoots being produced in every month; (2) most new shoots appear in March and July; and (3) annual productivity was estimated to be 240 g dry weight/m^2/yr. Concurrent monthly measures of pickleweed standing crops showed that (1) dry weight of green, succulent branches increased gradually from February to a peak in August; (2) live woody stem parts (brown in color) averaged over 300 g/m^2 in April, but about 100 g/m^2 in July and November, indicating that losses occur through the growing season; and (3) much (perhaps two-thirds) of the growth of

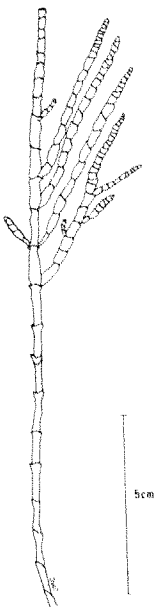


Figure 14. Pickleweed (Salicornia virginica). Photo by C. Nordby; illustration by J. DeWald. Scale = 5 cm.

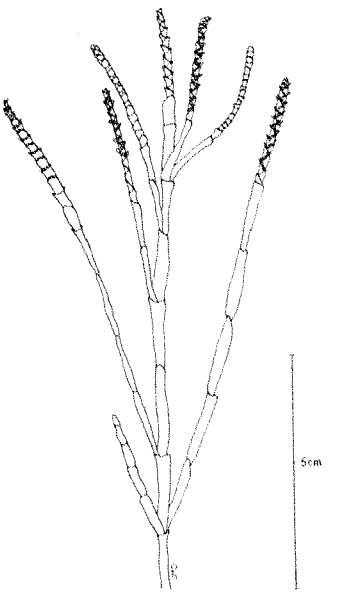
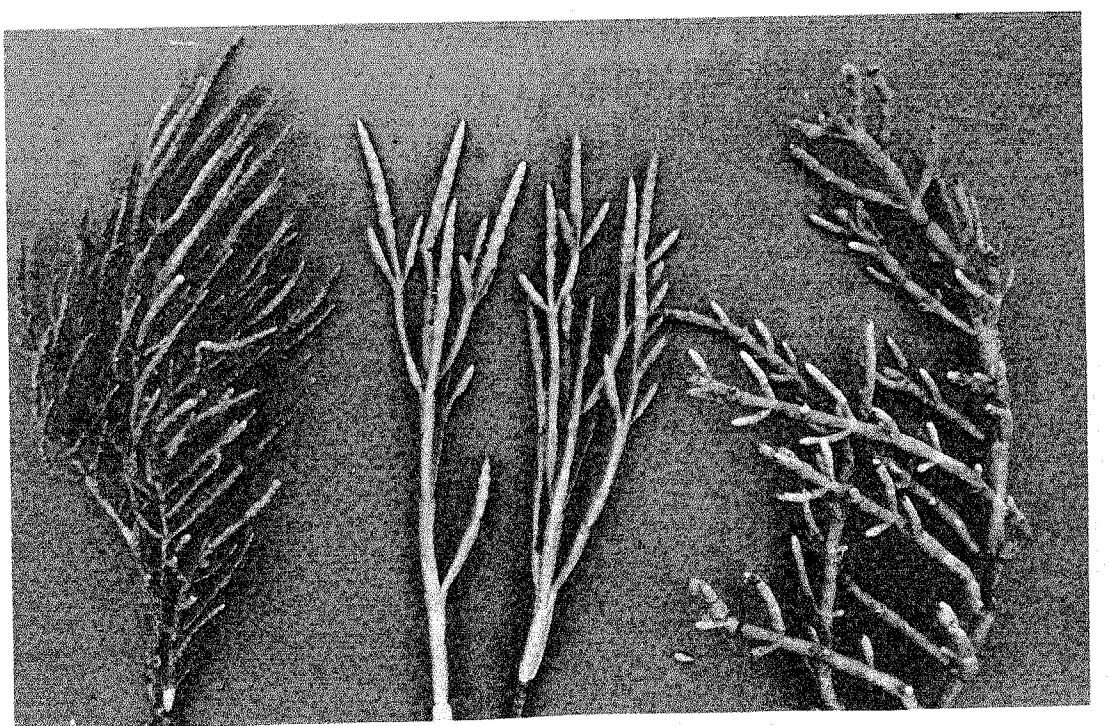


Figure 15. Annual pickleweed (Salicornia bigelovii). Illustration by J. DeWald. Scale = 5 cm.



The three species of Salicornia are sometimes difficult to distinguish. Salicornia subterminalis, on the left, is heavily branched; annual pickleweed (S. bigelovii), center, is sparingly branched, and pickleweed (S. virginica), right, is usually intermediate in branchings and more bluegreen in color. Photo by P. Zedler.

pickleweed cannot be measured by the harvest method because of losses to herbivores and export. Percent cover of pickleweed, measured by the point method, was 41% and bare space 58% in the lower marsh, compared to 25% cover and 35% bare space in the middle marsh, where other species co-occurred. Additional data (Onuf pers. comm.) provide average August standing crops (above ground) for pickleweed of 0.33 to 0.55 kg/m^2 during the years 1978 to 1981, with a high degree of variability between and among sampling transects.

At Los Penasquitos Lagoon, pickleweed forms pure stands in the lower marsh elevations. An especially lush stand developed during conditions of brackish soils after heavy rainfall in 1978. A dense canopy, nearly 1 m tall, measured 2.5 kg/m^2 (dry weight of live biomass) in August (Zedler et al. 1980).

The species usually reproduces vegetatively. Onuf (unpub. ms.) never saw a seedling during his intensive study of pickleweed. Seedlings are likewise rare at Tijuana Estuary. However, at the San Diego River, seedlings appear in open areas following winter rainfall.

Annual pickleweed (Salicornia bigelovii, Figure 15) is one of the few annuals found in California marshes, and its distribution is not extensive (Macdonald 1977). It often coexists with saltwort (Batis maritima) in areas of poor drainage and occurs on creek banks where other species provide only sparse canopies. I have censused densities up to 2,500/m^2 in August at Tijuana Estuary (Zedler 1975) and the species' success here makes it difficult to understand its absence in other nearby marshes (c.f. Table 4). Both annual pickleweed and saltwort reach their northern distributional limits near Point Conception.

Saltwort (Batis maritima, Figure 16) is a trailing succulent, which reaches lengths of a meter or more, but rarely gets taller than 0.3 m. Its decumbent branches root upon contact with the soil and vegetative spread can be very rapid. But they rarely produce dense cover and the open, spreading growth form allows annual pickleweed to coexist. Attempts to test this experimentally failed, however, because of the difficulty of keeping either species out of exclusion plots (Zedler unpub. data)! Annual pickleweed continued to germinate through August 1975, while saltwort sprouted rapidly from underground tissues.

Jaumea carnosa (Figure 17), like saltwort, is a low growing, vegetatively spreading succulent. The two are easily confused until the leaf bases are compared or the bright yellow flowers of Jaumea are contrasted with the fleshy but far-from-showy fruiting structures of saltwort. Pure patches occur, resulting from vegetative growth, but seedlings are occasionally seen. Further north in Elkhorn Slough (121°46'N, 36°50'W), Dr. John Oliver (pers. comm.; Moss Landing Marine Lab, Moss Landing, CA) has shown that Jaumea invades clearings which result from drift deposits or experimental removal of previous marsh canopies. While seedlings of Jaumea occur in well developed canopies such as at Tijuana Estuary, it is not known how often they grow to maturity.

Sea-blite (Suaeda californica, Figure 18) is a short-lived perennial which does not spread vegetatively (Purer 1942). Seedlings of this species are common at Tijuana Estuary. Its ability to establish from seed allows sea-blite to invade bare intertidal soils, but prevents it from forming dense stands in an otherwise vegetatively reproducing marsh vegetation.

The succulent arrow grass (Figure 19), is sometimes reported as Triglochin maritima (e.g. Zedler 1977) and sometimes as T. concinnum (e.g. Winfield 1980). Taxonomic keys distinguish the species on the basis of rhizome and ligule characteristics, so that close inspection is necessary to separate the two in the field. Winfield suggests that T. concinnum is the proper term for arrow

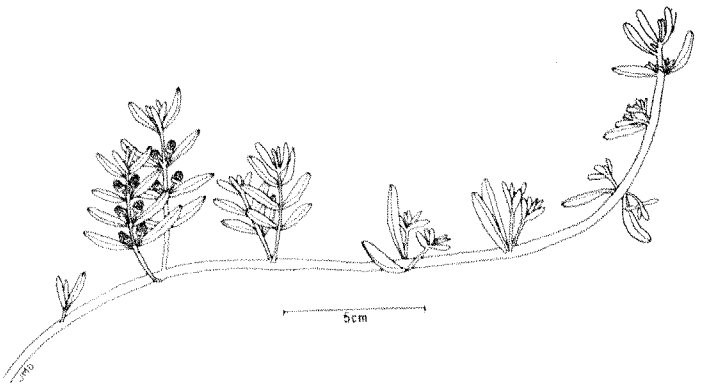
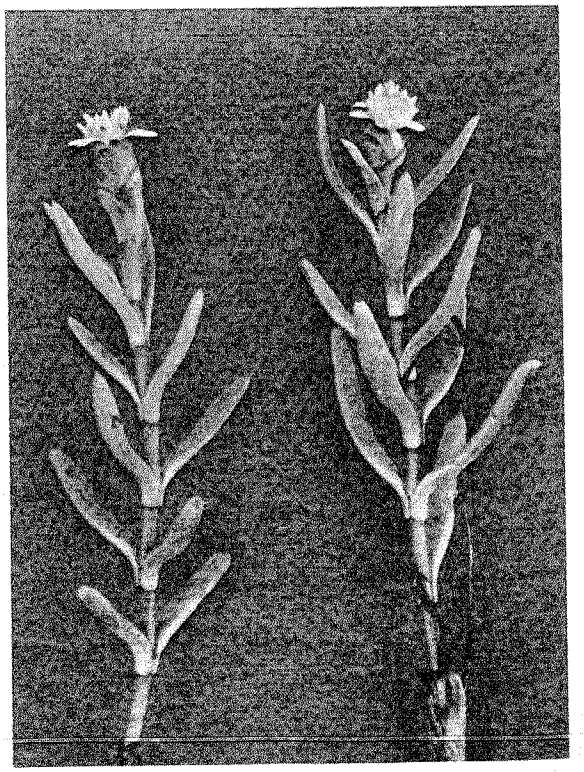


Figure 16. Saltwort (Batis maritima). Photo by C. Nordby; illustration by J. DeWald. Scale = 5 cm.



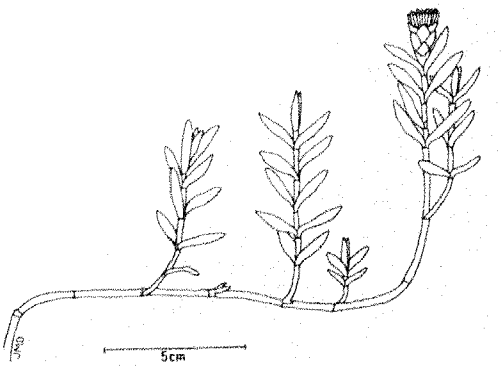


Figure 17. Jaumea carnosa. Photo by P. Zedler; illustration by J. DeWald. Scale = 5 cm.

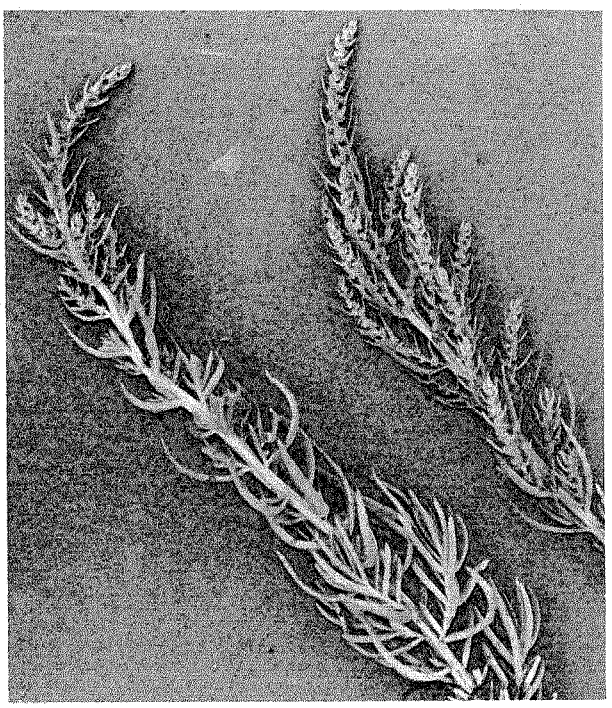


Figure 18. Sea-blite (Suaeda californica) surrounded by pickleweed at Tijuana Estuary. Photo by J. Zedler. Close-up photo by P. Zedler.

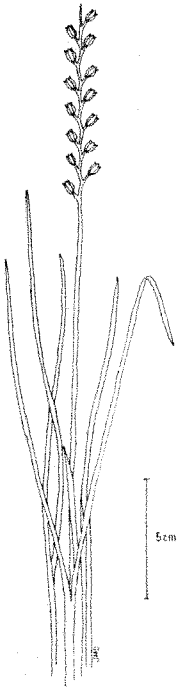
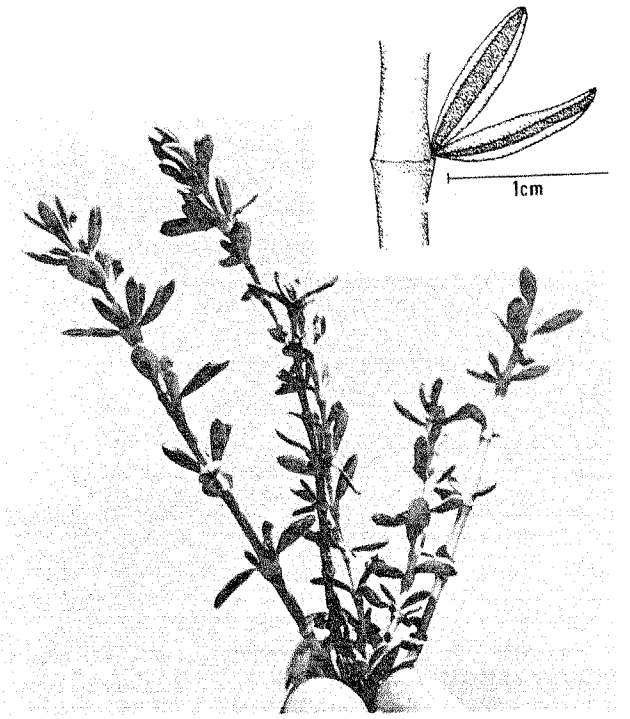


Figure 19. Arrow grass (Triglochin concinnum). Photo by D. Fink; illustration by J. DeWald. Scale = 5 cm.

grass at Tijuana Estuary, pending proof that T. maritima actually occurs there. Arrow grass is the earliest growing species in southern California marshes. It usually sprouts, flowers, and dies to the ground while other marsh plants are just initiating growth. Perhaps its early timing is in response to cool, rainy conditions, while other species are cued to longer daylengths or warmer weather. Patchy distributions are characteristic of the vegetatively reproducing species, while its absence at marshes such as the San Diego River suggest that it has limited establishment ability.

Frankenia grandifolia (Figure 20), a broad-leaved plant, offers some relief from the monotony of succulents in southern California marshes. However, when its small lavender flowers are absent or dry, or when saline conditions have caused its leaves to fold, it too blends in with the pickleweed, saltwort, and Jaumea. The species appears to be somewhat more salt tolerant than drought tolerant, as suggested by its recent decline in the upper marsh of Los Penasquitos Lagoon. It was abundant, along with saltgrass (Distichlis spicata), during the late 1970's, but has nearly disappeared from the higher elevations under conditions of brackish, dry soils. It persists, however, in the adjacent lower marsh, where soils are becoming hypersaline but remain moist.

Saltgrass (Distichlis spicata, Figure 21), enjoys a broad distribution, both ecologically and geographically. In southern California it occurs in dunes, in middle to high marsh elevations, and is sometimes abundant in adjacent salt flats which are entirely cut off from tidal circulation. Its success in the upper marsh at Los Penasquitos and other locations (e.g. Upper Newport Bay, Stevenson and Emery 1958) may be due to its greater drought tolerance than other potential competitors. Within the intertidal marshes, it rarely forms dense patches, but it can achieve nearly pure stands and high biomass (4 to 6 kg/m^2 in



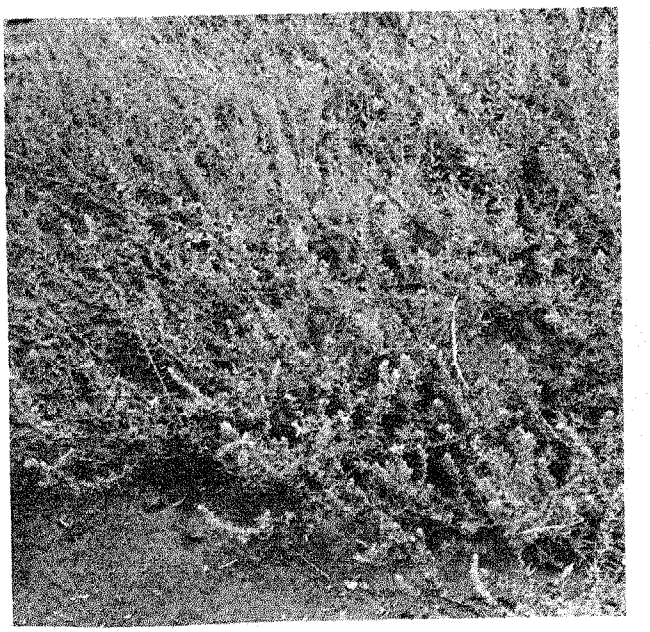


Figure 20. Frankenia grandifolia. Top photo by D. Fink; close-up illustration by J. DeWald (scale = 1 cm); bottom photo by J. Zedler.

August 1981 at Los Penasquitos Lagoon, Zedler unpub. data). Flowering was notably common in 1981 and future observations are needed to determine if good seed crops are sporadic.

Shoregrass (Monanthochloe littoralis, Figure 22) is another subtropical species whose northern limit of distribution is near Point Conception. The prostrate grass readily expands vegetatively and forms dense mats in the upper marsh habitats of many southern California marshes (Zedler 1977, Vogl 1966). It is rarely seen flowering or fruiting and I have never seen a seedling.

Salt marsh bird's beak (Cordylanthus maritimus ssp. maritimus, Figure 23) was once a common plant of the upper marsh (Purer 1942) but it is now on the Federal Endangered Species List. It occurs in patches at Tijuana Estuary (Dunn unpub.), Mugu Lagoon (H. Ferguson, U.S. Navy), and Upper Newport Bay (Eilers 1981). This annual germinates best after seeds have had a cold treatment (Dunn unpub. data) and is densest in or near open habitats. It is a facultative parasite; its roots can draw resources from a number of potential hosts.

Salicornia subterminalis (Figure 24) is common at the highest intertidal marsh habitats at both Tijuana Estuary and Mugu Lagoon but does not occur in marshes north of Morro Bay (35°22'N). It appears to be both salt tolerant and drought tolerant; it occurs adjacent to salt pans and in areas above extreme high water or behind dikes which prevent tidal inundation. Although it resembles S. virginica and commonly occurs with it, S. subterminalis can be recognized by its narrower branches and darker green color. Although the name refers to the occasional subterminal location of its flowers, it is more common to see terminal flowers as on S. virginica. S. subterminalis more often forms dense, upright bushes than its congener and extends higher along the elevation gradient than S. virginica.

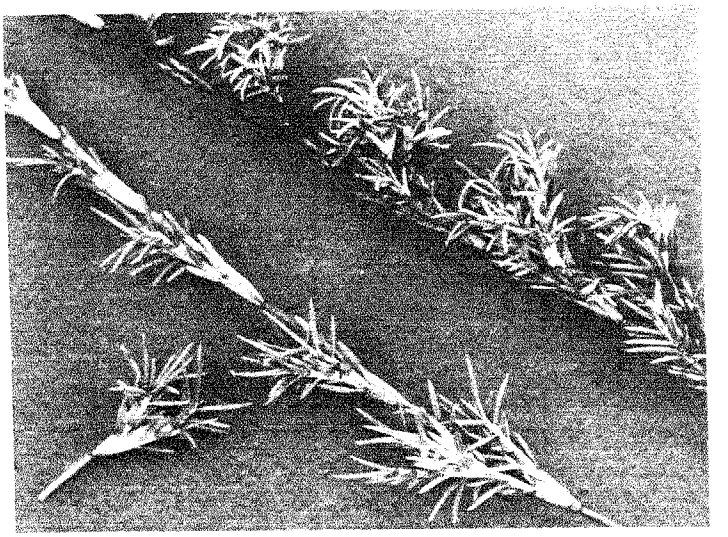
Sea lavender (Limonium californicum, Figure 25) is the showiest of the southern California halophytes. Inflorescences up to a meter tall rise from a basal rosette of broad, spatulate leaves. Hundreds of tiny lavender flowers appear and dry on the stalks, much like its ornamental relative Statice. Of the species which actively secrete salt (see Waisel 1972), sea lavender is perhaps the most conspicuous. There is usually a crust of salt crystals on the undersides of the leaves, and at times whole leaves are white from the dried brine. Sea lavender reproduces both vegetatively and by seed, and given sufficient time, can become abundant along artificial dikes or bare ridges.

Alkali weed (Cressa truxillensis, Figure 26) is a small, pale plant which is easily overlooked in most southern California marshes. However, its recent increase in abundance at the upper marsh of Los Penasquitos Lagoon and its obvious expansion following disturbance at the Ballona Wetland (in this case after plowing of seasonally wet pickleweed habitats) have stimulated interest in its ecological requirements. Whether it is an indicator of changing environmental conditions or of upper marsh boundaries remains to be seen; but it may prove useful in delimiting areas which could support salt marsh vegetation, provided disturbance were reduced or eliminated.

One obligate parasite, known as dodder (Cuscuta salina, Figure 27), occurs in southern California marshes, covering a number of hosts with bright orange stems and small white flowers. It can be very dense, but the effect on the host plants does not seem to be severe. It is an annual plant whose dispersal and establishment characteristics are unstudied.

Spike rush (Juncus acutus) may have formed a conspicuous band around the upper marsh of pre-1900 wetlands, but only remnant populations are now found in southern California. Its clump of long, sharp, stiff leaves and tall, dark,

Saltgrass (Distichlis spicata). Illustration by J. DeWald; scale = 5 cm.



Shoregrass (Monanthochloe littoralis). Photo by J. Zedler.

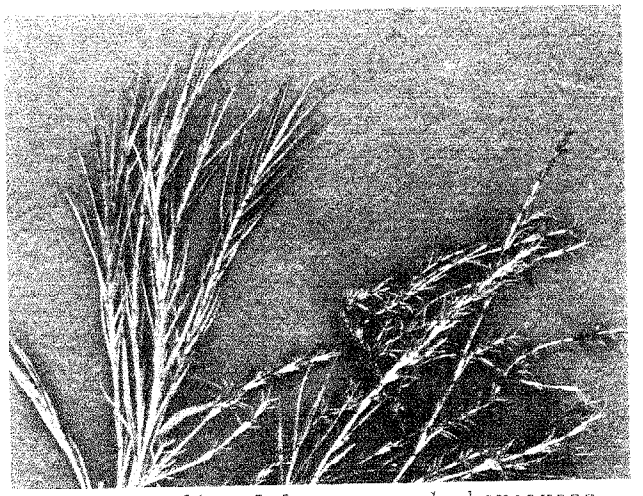


Figure 21. Saltgrass and shoregrass can be distinguished by the longer leaves of saltgrass and bunched leaves of shoregrass. Photo by P. Zedler.

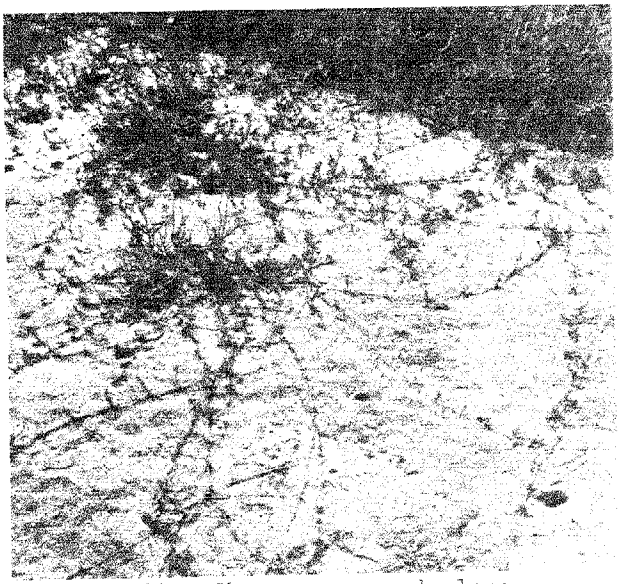


Figure 22. Shoregrass sends long runners over the surface of a salt flat. Photo by J. Zedler.

Figure 23. Salt marsh bird's beak (Cordylanthus maritimus ssp. maritimus). Photo by C. Nordby.

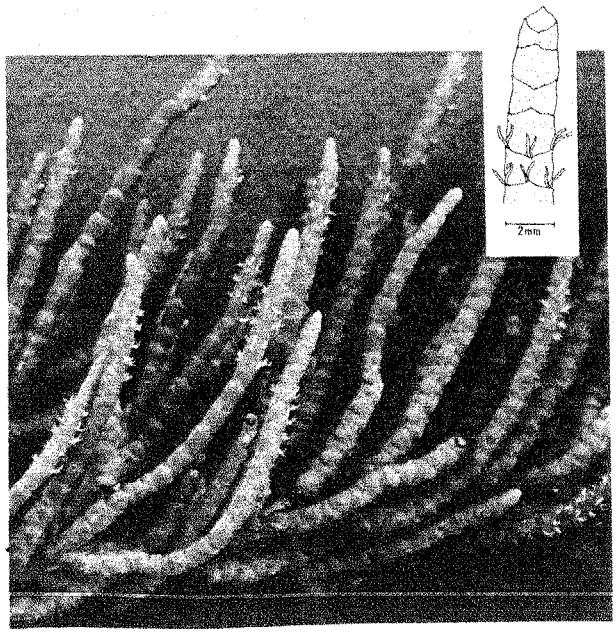


Figure 24. Salicornia subterminalis. Flowers are sometimes subterminal (see close-up illustration by J. DeWald; scale = 1 cm). Photo by P. Zedler.

Figure 25. Sea lavender (Limonium californicum). Photo by P. Zedler.

Figure 26. Alkali weed (Cressa truxillensis). Photo by P. Zedler.

Figure 27. Dodder (Cuscuta salina), parasitic on pickleweed. Photo by J. DeWald.

flowering stalks are unmistakable features of the species. Its distribution may correspond with lower soil salinities, though ecological studies are lacking.

2.3 TRANSITIONAL HABITATS

Habitats between the higher salt marsh and coastal scrub or dune vegetation have undergone so much disturbance that their communities are difficult to characterize. Perhaps the best understanding of their former composition can be obtained by extrapolation from the marshes at Bahia de San Quintin. Neuenschwander et al. (1979) identified the transitional zone as the area inland of the highest debris line. Marsh species had lower abundance and several desert and coastal upland species were present. Dominant species, both on the basis of frequency and cover, were Monanthochloe littoralis, Salicornia subterminalis, and Frankenia palmeri. The latter species is known only from San Diego Bay in the U.S., where it is rare. Lycium brevipes and Atriplex julacea were occasional, and Euphorbia mesera, Distichlis spicata, Allenrolfea occidentalis, Dudleya brittonii, Haplopappus venetus, and three cacti were relatively rare in the transition zone.

Transitional areas at Tijuana Estuary are likewise distinguishable by the appearance of a large variety of species not common to lower elevations. The main difference is that many of them are introduced weeds. They grow among the Salicornia subterminalis and shoregrass (Monanthochloe littoralis) wherever soils are low in salinity.

2.4 SIMILARITIES WITH OTHER PACIFIC COASTAL SALT MARSHES

Macdonald (1977a) separates the California marshes into three groups (northern, San Francisco Bay, and southern marshes) on the basis of species composition. Information on soil salinities is sparse, but higher rainfall

spread over the year should produce less saline soils, which probably affect plant growth rates, if not species composition.

The composition of marshes to the north of Point Conception differs in the absence of southern species (Salicornia bigelovii, S. subterminalis, Monanthochloe littoralis, Batis maritima). Pickleweed (Salicornia virginica) and cordgrass (Spartina foliosa) are important in the upper and lower elevations, respectively, except that cordgrass is absent from Elkhorn Slough, Tomales Bay and Bodega Bay (Macdonald 1977b). Disturbances have played important roles in the history of these wetlands as well, notably salt works and urban development surrounding San Francisco Bay, logging and urban development at Humboldt Bay, and dredging to enhance navigation at Elkhorn Slough.

South of Tijuana Estuary are the wetlands of Baja California, which are just now facing the prospect of intensive development. The marshes of Bahia de San Quintin (30°31'N, 116°0'W) are the most well studied (Neuenschwander et al. 1979). These marshes are of special interest because so little disturbance has occurred. Thorsted (1972) did not measure soil salinities in the intertidal marsh, but the low rainfall (5 to 10 cm/yr) strongly suggests hypersaline soils even with the moderating influence of frequent fog cover. Seven marshes within the Bahia were sampled for frequency and occurrence in the same manner as Vogl's (1966) study of Upper Newport Bay. I calculated percent similarities (Whittaker 1975) of about 70% between the lower, middle and upper marsh zones for these two widely separated (nearly 500 km [310 mi]) bays. The high similarity of species lists for Bahia de San Quintin, Tijuana Estuary, Mission Bay, Upper Newport Bay, Anaheim Bay, and Mugu Lagoon suggests that the northern Baja California marshes belong to the southern California regional group.

2.5 EFFECTS OF DISTURBANCE ON MARSH COMMUNITY STRUCTURE

Disturbance takes many forms in southern California wetlands. Some disturbances are natural; most are man-caused. Some are chronic; others are catastrophic. The first response of vegetation to disturbance will normally be change in the functional attributes of the plants, i.e. their rate of growth may increase or decrease. Changes in species composition of the vegetation, i.e. the invasion of new species or elimination of previously occurring species, generally take longer. This discussion will emphasize changes in species composition which result from the catastrophic disturbances of altered tidal circulation and of flooding. Changes which result from chronic disturbances, such as fertilization from adjacent agricultural runoff, are much more difficult to document. However, the effects of reduced tidal circulation, natural flooding, and artificially augmented flooding are becoming clear; and most of the species compositional changes can be explained on the basis of the changing soil salinities which are associated with these disturbances.

Reduced Tidal Circulation

As discussed in Chapter 1, closure of a wetland can result either in more brackish or more saline soils. Wetlands which undergo an annual cycle of closure, or which remain closed for several years at a time most certainly experience a broader range of soil salinities and soil moisture than marshes which are continually under the influence of tides. Given that halophytes have upper limits for salinity and drought stress, one might expect that sensitive species would be eliminated from habitats or from entire wetlands where tidal circulation is unpredictable. Furthermore, one would expect widely tolerant species to dominate under these disturbance conditions.

The smaller wetlands more frequently lose their tidal connection, unless

entrances have been stabilized by dredging and jetty construction. Fewer species of salt marsh plants tend to be found in such areas (Table 4). Cordgrass (Spartina foliosa) is usually absent from wetlands which are frequently closed to tidal circulation, and it has become eliminated from Los Penasquitos Lagoon since Purer's 1939-40 observations. A 1980 transplant of 40 cordgrass sprigs to the pickleweed-dominated lower marsh of Los Penasquitos Lagoon resulted in one survivor through the well-circulated 1980 growing season. However, it too died during 1981 when the lagoon was closed much of the year (Williams and Zedler, unpub. data). Eilers (1980) found that cordgrass remained behind a dike at Bolsa Chica marsh, even though regular tidal circulation had been lacking for almost 80 years. It had, however, migrated to elevations which would normally be too low for this species. Soils where cordgrass occurred were moist (65 to 89%) and their salinity varied from brackish to hypersaline during Eilers' 1977-78 study period, suggesting that seepage was occurring despite the closure of this marsh to tidal circulation. Hence it may not be access to tides that is required for cordgrass's persistence, but protection from extremes which usually occur after closure, i.e. long periods of high salinity and/or drought and competition with pickleweed.

Monotypic stands of pickleweed (Salicornia virginica) are often found in marshes with reduced tidal circulation. The occurrence of pickleweed in marshes of wide-ranging salinities and moisture conditions and its broad range at Tijuana Estuary (Figure 9) both document that this species has a broad tolerance to environmental conditions. The laboratory experiments of Mahall and Park (1976b,c) also showed that pickleweed from San Francisco Bay tolerated a wider range of salinities than cordgrass.

Reduced tidal circulation may also affect species composition of the upper marsh by reducing soil moisture. Although experimental evidence is lacking, the elimination of Frankenia grandifolia (but not saltgrass [Distichlis spicata]) from the upper marsh at Los Penasquitos Lagoon during dry periods has been documented (92% frequency and 1429 g/m^2 in August 1977, compared to 38% frequency and 7 g/m^2 in 1981) (Zedler et al., unpub. data). Salinities were brackish during much of the three-year period, but soils were very dry in 1981. Although Frankenia declined substantially in the upper marsh, it remained robust ($\bar{x}$=347 g/m^2 in August 1981) in the adjacent lower marsh, suggesting that plant disease or grazing were not the cause. Competition with saltgrass could have contributed to its demise, but the biomass of saltgrass also declined. Only alkali weed (Cressa truxillensis) increased in August biomass (from 7 g/m^2 in 1977 to 15 g/m^2 in 1981).

Natural Flooding

Flooding and reductions in soil salinity have dramatic effects on local species distributions, thereby altering marsh community composition. Cordgrass appears to be especially sensitive to freshwater input; it showed substantially greater ability to become established outside its usual boundaries following the 1980 flood at Tijuana Estuary (Zedler, unpub. ms.b). The observations which follow suggest strongly that flood events play an important role in allowing halophytes to invade new habitats.

At Tijuana Estuary, there are two abandoned sewage lagoons which received effluent from the city of Imperial Beach up until the early 1960's. The periphery of the lagoons is ringed with vegetation dominated by pickleweed (Salicornia virginica), but 33 discrete patches of cordgrass were located and their diameters measured in 1979. A recensus after the 1980 flood revealed 103 patches, most of which were very small and of recent origin (Figure 28). Those which were near old patches may well have established vegetatively, but a few of the new patches were several meters away from the nearest vegetative source. Excavations of two new

Figure 28. Patches of cordgrass have invaded a pickleweed marsh which surrounds an abandoned sewage lagoon at Tijuana Estuary. Patches increased in size and in number more during the wet year of 1980 than in previous or subsequent growing seasons. Photo by J. Zedler.

Figure 29. Prolonged flooding of the San Diego River marsh, caused by reservoir drawdown, leached soils of their salts and allowed freshwater marsh plants (e.g. cattails) to invade the former salt marsh. Pickleweed, shown here as dead understory plants, probably died from long periods of inundation. Photo by J. Zedler.

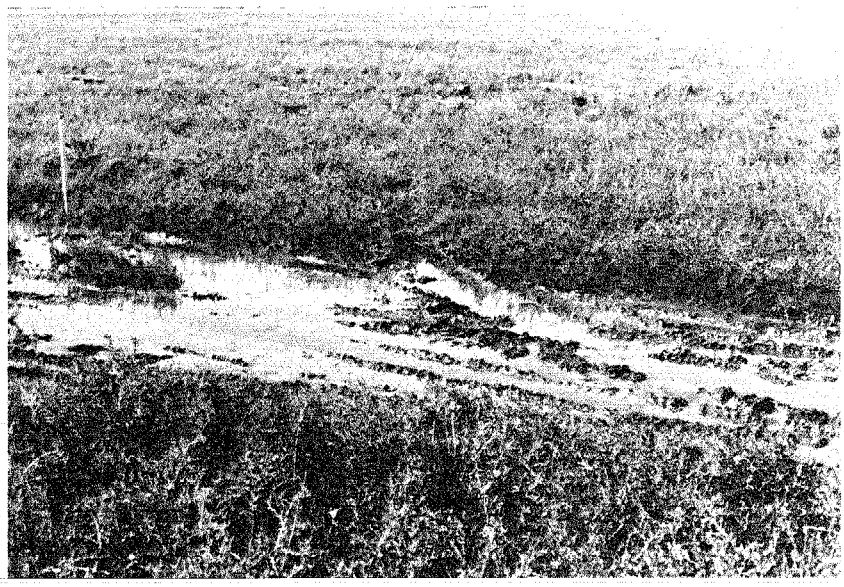


Figure 30. Off-road vehicle activities denude the salt marsh, compact soils, and alter drainage patterns. Photo by J. Zedler.

clones failed to reveal rhizomal connections outside the clone. Hence, at least some of the new cordgrass patches originated as seedlings. Prior to the 1980 flood there had been no record of Spartina foliosa establishment by seed despite several years' observation of other species' seedlings at Tijuana Estuary.

In addition, the original patches expanded in diameter significantly more in 1980 ($\bar{x}$=2.4 m) than during the 1979 growing season ($\bar{x}$=1.1 m) (Zedler, unpubl. ms.b). This expansion appeared to be entirely vegetative, which is consistent with the measured increases in density in the nearby Tijuana Estuary marsh. As further evidence that the flooding was responsible for the expansion of cordgrass, patches were again censused in 1981, a year of little rainfall and high soil salinities throughout the growing season. The original patches of cordgrass had their lowest expansion rates, indicating significantly poorer growing conditions. Several new patches were located, but the rate of establishment was clearly below that of 1980. To date, the evidence strongly suggests that flooding is a stimulant for major expansion of cordgrass.

Prolonged Excessive Freshwater Input

Small pockets of freshwater marsh have often been observed to develop next to storm drains or other areas of continuous freshwater input to salt marsh habitats, but it is rare to witness large-scale replacement of salt marsh by freshwater marsh. However, exactly that occurred in southern California (Zedler 1981b,c). Vegetation at the mouth of the San Diego River shifted from dominance by pickleweed (Salicornia virginica) to dominance by cattails (Typha dominguensis) when the natural floods of 1980 were followed by the deliberate release of water from El Capitan Reservoir. A two-month period of inundation early in the growing season killed large areas of pickleweed-dominated salt marsh vegetation at the seaward end of the river. Leaching reduced soil salinities to 0 ppt in many parts of the marsh, and seeds of freshwater marsh species, brought downstream by the floodwaters, germinated rapidly. Cattails developed a nearly continuous, tall, robust canopy within two to three months after flooding. The rapid shift in species composition demonstrates that pickleweed is sensitive to inundation and that mudflat habitats are readily colonized by opportunistic species (Figure 29).

Dominance by freshwater species was short lived, however, because the freshwater input ceased and tides resumed their role as the major water source. By July 1981 nearly all the cattails had died and the marsh was a nearly uniform canopy of standing dead vegetation. At this time, a few patches of salt marsh vegetation were visible; some of these were patches of cordgrass which had survived inundation and subsequent competition with cattails. (Many had been planted as part of the author's marsh restoration project.) Other patches were Jaumea carnosa or saltwort (Batis maritima) which either survived the floods or germinated shortly after. All three species began expanding vegetatively following the demise of the cattails, and may produce a dense canopy before pickleweed is able to re-invade by seed and dominate the area.

Chance events, such as the survival or establishment of small patches of halophytes, may have profound influence on the species composition of a marsh. Historical features such as local patches of mortality and establishment may explain some of the differences in species composition among southern California's coastal salt marshes. Even if identical habitats are available for salt marsh growth, one need not expect the ultimate species lists to be identical, let alone their respective abundances.

Other Disturbances

Denudation of marsh vegetation by vehicle abuse is one of the most visible

types of disturbance to marsh structure. Areas of dense vegetation become completely eliminated wherever traffic persists (Figure 30). Since most drivers steer clear of the muddier habitats, their damage is usually most visible in the high marsh and transitional communities. The impact on vegetation composition is two-fold. Species restricted to these habitats are eliminated, and opportunistic, weedy annuals invade during the rainy season when vehicle use is sparse.

Salt marsh bird's beak (Cordylanthus maritimus ssp. maritimus) most likely owes its endangered status to disturbance of this type. Marsh vegetation is notably sensitive to mechanical damage (McIntyre 1977) and the bird's beak is especially easy to break off (Dunn 1981). The latter is restricted to a narrow elevational range (less than 30 cm at Tijuana Estuary) at the upper limit of tidal influence near areas used by off-road vehicles.

Introduced species often invade native communities following disturbance, and some become a common part of that community even when disturbance is peripheral. Two ice plants, Gasoul crystallinum and G. nodiflorum, germinate readily in roadways at the upper marsh boundary, while brass-buttons (Cotula coronopifolia) has become a common member of southern California coastal marshes. All three species are native to South Africa. Two European grasses, Parapholis incurva and Polypogon monspeliensis, are sometimes abundant in upper marsh habitats.

Rarely does one see exotic species in lower marsh habitats, although smooth cordgrass (Spartina alterniflora) has been successfully introduced from the Atlantic coast to the State of Washington (Frey and Basan 1978). In southern California, there is one case of low marsh invasion, which still puzzles ecologists. A New Zealand mangrove (Avicennia sp.) was deliberately planted in Mission Bay to provide live material for physiological study. It subsequently spread and became a dominant feature of the marsh, occupying the channel banks and lower parts of cordgrass's distribution. Finally, concerned that the tall (2-3 m) plants would attract predators of the endangered light-footed clapper rail, the Clapper Rail Recovery Team called for the mangrove's removal. The puzzle? If exotic mangroves can occupy the tidal creeks at this latitude, why haven't native mangroves from Baja California migrated north or other vascular plant species developed tolerance to these low elevations?

2.6 A CONCEPTUAL MODEL OF MARSH COMMUNITY DEVELOPMENT

Observations of species compositional changes in southern California marshes can be combined to develop a conceptual model of community development. Since most observations deal with pickleweed (Salicornia virginica) and cordgrass (Spartina foliosa), these two dominants and their interactions are emphasized. But first a word of caution. Conceptual models are useful in summarizing ideas and clarifying questions which need to be approached experimentally. Until such models have withstood repeated attempts to disprove them, they should not be accepted as fact. Rather, they should be viewed as a set of hypotheses and discarded when better explanations come along.

The following model (Figure 31) suggests a likely progression of events which is predicted from observations of establishment ability and competitive interactions for pickleweed and cordgrass.

2.7 VASCULAR PLANT PRODUCTIVITY

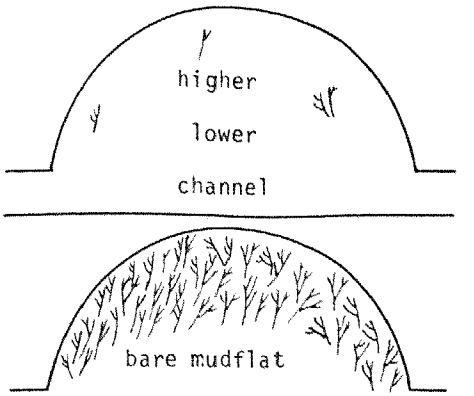
Across the nation coastal marshes have been acclaimed as highly productive natural ecosystems. The cordgrass (Spartina alterniflora) marshes of Georgia and Louisiana are particularly well-studied and estimates of up to 3 $kg/m^2/yr$ above-ground productivity are on record (see review of Turner 1976, Kirby and

USUAL CONDITIONS = HYPERSALINE SOILS

Habitat becomes available for colonization.

Opportunistic species invade by seed (*Salicornia virginica*, *S. bigelovii*, *Suaeda californica*).

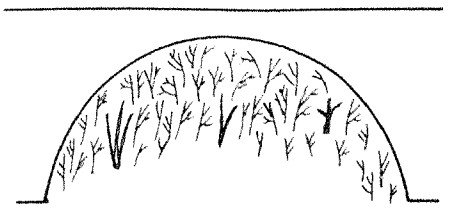
Salicornia virginica achieves early dominance due to
- --high growth rates under saline conditions
- --vegetative spread
- --perennial growth



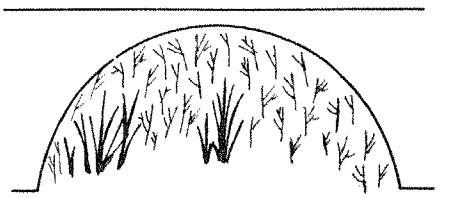
FLOODS OR HEAVY RAINFALL EVENTUALLY OCCUR

Germination of halophytes is stimulated.

Spartina foliosa may establish patches if a nearby source is available.



Spartina foliosa may spread vegetatively, especially at lower elevations.



LONG PERIODS OF HYPERSALINITY FOLLOW, INTERRUPTED BY OCCASIONAL WET YEARS

Species distributions continue to shift in response to environmental changes; *Salicornia* retains competitive advantage under more saline conditions.

Spartina foliosa expands substantially during years of less saline conditions and at lower elevations.

A mixture of species results, with *Spartina foliosa* restricted to the lower marsh.

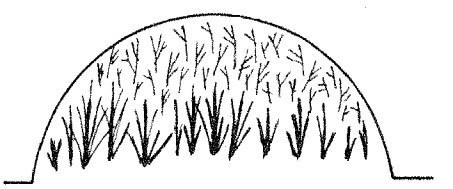


Figure 31. Conceptual model of species establishment and spread in southern California salt marshes.

Gosselink 1976, and Hopkinson et al. 1978).

Productivity studies have been carried out in several of the southern California wetlands (Table 7). All investigators calculate increases in biomass between periodic harvests of the vegetation, a technique which does not account for biomass lost to herbivores, decomposers or export from the marsh. Chris Onuf (unpub. ms) has also employed a plant tagging technique, which is perhaps the best means of estimating losses of plant biomass between harvests. According to his comparisons of harvest and tagging methods at Mugu Lagoon (Onuf et al. 1978), the harvest method underestimates productivity by a factor of 2.1 to 2.2 for pickleweed (Salicornia virginica), 3.7 for Jaumea carnosa, 1.8 for sea lavender (Limonium californicum), and 2.9 for saltwort (Batis maritima). It is not surprising that losses are high for the brittle-stemmed pickleweed; its branches are readily snapped off in trampling (McIntyre 1977) and presumably also by wildlife and tidal currents. Errors in harvest-derived productivity data clearly vary with the marsh species composition. Yet these are the most widely available data. For purposes of comparing marsh productivity from one marsh to another and one region to another, estimates based on periodic harvests must be relied upon.

Tijuana Estuary (Zedler et al. 1980, Winfield 1980) and Mugu Lagoon (Onuf et al. 1978) have net above-ground productivities of up to 1 kg/m^2 per year. The higher values tend to coincide with cordgrass's dominance. These values are probably representative of less disturbed, seasonally hypersaline marshes in southern California and they fall well below estimates for Atlantic and Gulf of Mexico marshes dominated by smooth cordgrass (Spartina alterniflora).

Eilers (1981) presents productivity data for two additional hypersaline marshes in southern California, the Sweetwater River marsh within San Diego Bay and Upper Newport Bay marsh. However, by calculating productivity on the basis of individual sampling stations (with one quadrat per sample date), he produces averages which are biased upward due to spatial variability (see Turner's [1976] discussion of error accumulation using the Smalley calculations). Re-analysis of Eilers' data, averaging biomass over all quadrats sampled at each date, gives results which are more in line with those of other studies (1.1 $kg/m^2/yr$ for Sweetwater River marsh and 0.7 for Upper Newport Bay marsh).

High soil salinity is probably the major limiting factor for vascular plant growth in southern California. Laboratory studies of Pacific Coast species (Barbour 1970, 1978; Barbour and Davis 1970; Phleger 1971) support the conclusion that fresh water enhances halophyte growth. Field experiments to vary soil salinity are less easily performed, and it becomes necessary to compare events associated with hypersaline and brackish conditions.

2.8 PRODUCTIVITY FOLLOWING FRESHWATER INPUT

Since flooding substantially reduced the soil salinity at Tijuana Estuary in spring 1980, one would predict an increase during that growing season. Although the monitoring of productivity has not continued, measurements of standing crop are made at the end of each growing season. The average live biomass in August correlates well with annual productivity ($r=0.9$, $n=11$ southern California marsh study sites), so that responses to changing soil salinity can be crudely measured by one harvest period.

The lower marsh vegetation at Tijuana Estuary had August standing crops of 0.9 to 1.1 kg/m^2 (live only) in years prior to the 1980 floods (Zedler et al. 1980). After the January-February floods and the brief period of brackish soils, the August 1980 standing crop was 1.4 kg/m^2. However, it dropped back to 1.1 kg/m^2 in 1981, when soils were hypersaline all year. Higher productivity in 1980 resulted from increases in both the

Table 7. Summary of vascular plant productivity in southern California's salt marshes. All values are kg of aboveground dry weight per square meter, estimated net annual productivity.

Wetland	Productivity		Reference
Tijuana Estuary	1976	1977	
Spartina foliosa-dominated low marsh	0.9	0.9	Zedler et al. (1980)
mixed succulents (middle elevations)	0.5	0.7	"
mixed species (upper elevations)	0.4	1.0	"
all elevations combined	0.7	0.9	Winfield (1980)
Sweetwater River marsh	1978		
all plots combined	1.1 1.1		Reanalysis of data in Eilers (1981)
San Diego River marsh			
Salicornia virginica dominant	0.6		Zedler et al. (1980)
Upper Newport Bay marsh			Reanalysis of data in Eilers (1981)
all plots combined	0.6		
Mugu Lagoon	1977		
low marsh	0.1		Onuf et al. (1978)
middle marsh	0.3		"

density (24%) and height (23%) of cordgrass (Zedler 1981c and unpub. ms. b).

At Mugu Lagoon, Onuf et al. (1981) reported stimulation of pickleweed growth following flooding and sedimentation in both 1978 and 1980, with a return to pre-flood conditions during 1979. The first response to flooding was a 71% increase in biomass of green growing tips at the time of the 1978 peak standing crop. The second response was a 31% increase in the same measurements (Onuf, pers. comm.).

These field responses to flooding support laboratory results that hypersalinity reduces salt marsh plant growth. And the range of values for cordgrass over recent years shows that one year's measurement is not sufficient to assess the "productivity" of southern California coastal marshes. There is a high degree of variability in both environmental characteristics and halophyte productivity.

2.9 DECOMPOSITION OF VASCULAR PLANTS

Determining what happens to the vascular plant material which is produced in the marsh is difficult. It may be consumed by animals, broken off and transported to some other area by winds or tides, or it may decompose or accumulate on the site. The latter process is easiest to follow, because portions of plants can be collected and known amounts placed in litter bags (usually these are mesh with 2-mm openings). Bags can be tethered in selected locations and reweighed later. As decomposition occurs, large pieces of plant material are gradually reduced in size by mechanical and biological forces, until the material moves out of the litter bag. Loss rates are usually exponential, that is, the greatest change occurs in the first few weeks, as soluble compounds leach from the plants and as consumers (fungi, bacteria and herbivores) utilize the most digestible portions. The remaining plant material is progressively less susceptible to digestion or leaching, and loss rates decline. Ultimately, with complete mineralization of the plant parts, the organic matter is converted back to carbon dioxide, water and nutrients, which are then available for reuse by other plants.

Several factors influence decomposition rates in southern California salt marshes. In a comparative study, Winfield (1980) found that plant type, location of litter bags, and type of decomposers all influence loss rates at Tijuana Estuary. Succulents and cordgrass (*Spartina foliosa*) leaves decomposed more rapidly (9%/mo) than the more fibrous cordgrass stems (7%/mo) when litter bags were placed at approximately mean high water. Litter bags placed in tidal creeks and middle marsh habitats all had higher decomposition rates than bags placed in the higher, drier habitats. The lowest rate (3%/mo) was for the fibrous shoregrass (*Monanthochloe littoralis*) placed in its usual high marsh location. The highest rate (33%/mo) was for dead leaves of cordgrass placed in a tidal creek, where several factors were conducive to decomposition. Moisture was usually high and nitrogen (especially ammonia) was available to enhance microbial growth. Crab larvae settled in the bags and their shredding and feeding activities further hastened plant losses.

From these results and the information on plant productivity, it becomes obvious that salt marsh functioning is strongly influenced by tidal circulation. The tides are responsible for physical, chemical and biological events which are important to the growth and decomposition of vascular plants and, as the next chapter shows, to the understory algal mats as well.

2.10 SUMMARY OF CHAPTER 2

Southern California coastal marshes are dynamic in both structure and productivity. The halophytes have broad ranges of tolerance for the conditions associated with the one meter intertidal

elevational range, and their distributions overlap considerably in most marshes. Small-scale boundaries between different dominants result from their vegetative mode of reproduction. Still, a pattern of compositional change with elevation can be seen, because the elevation of greatest abundance differs among the nine most common species (cf. Figure 9). Cordgrass (Spartina foliosa) dominates the lowest elevations; pickleweed (Salicornia virginica) is a major dominant through low and middle elevations; a number of other succulents and low-growing perennials become common in middle and high elevations. Transitions from intertidal marsh to coastal scrub vegetation are usually highly modified by disturbance and several introduced weeds intermix with the native halophytes.

Changes in the distribution of individual species within marshes are seen to be common events. Under conditions of local or whole-wetland disturbance from trampling or herbivory to elimination of tidal circulation, individual species may be reduced in area of distribution or eliminated from large patches. Events such as flooding may stimulate widespread expansion, particularly of cordgrass, provided a source of propagules is available. Most of the halophytes do not establish readily from seed; instead, they expand their distributions vegetatively. Only three native annuals, the annual pickleweed (Salicornia bigelovii), the endangered salt marsh bird's beak (Cordylanthus maritimus ssp. maritimus), and the parasitic dodder (Cuscuta salina) are found; all others are short-lived perennials. Two pickleweeds (Salicornia virginica and S. bigelovii) and sea-blite (Suaeda californica) appear to be the most opportunistic species. Once established in a newly exposed habitat, Salicornia virginica can probably outcompete other species, especially when soils are hypersaline. Freshwater input stimulates germination of most halophytes and flooding events appear to be important for establishment and expansion of species' distributions. Chance establishment after disturbance is no doubt an important factor in understanding the patchy distributions found in many southern California marshes.

The net annual productivity of the marsh vascular plants (above-ground only) tends to be under 1 $kg/m^2/yr$. In comparison with salt marshes of the Atlantic and Gulf of Mexico coasts, where soils are predominantly brackish, the southern California marshes have lower vascular plant productivity. That hypersaline soils are responsible for their relatively low productivity is demonstrated by increases in end-of-season live biomass following reduction of soil salinity by flooding and by higher productivity of marshes with brackish soils. Their relatively short, open canopies are evidence that the vegetation is usually under environmental stress. Both plant density and height increase after flooding.

CHAPTER 3

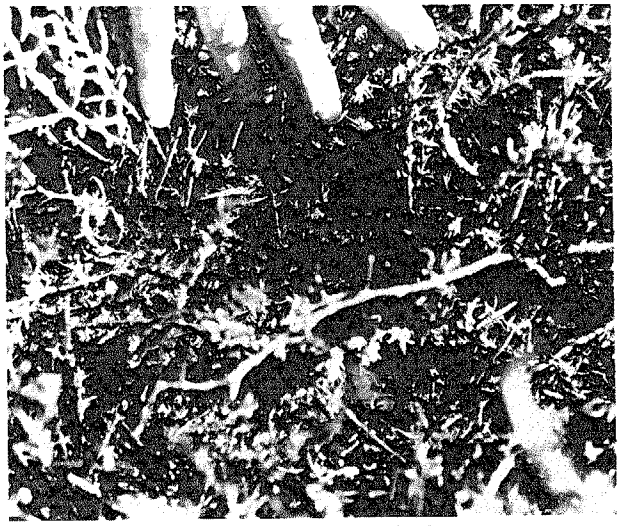
ALGAL MATS ON THE MARSH SOILS

3.1 ALGAL COMMUNITY STRUCTURE

The low-growing, open canopies of vascular plants in southern California marshes allow light penetration to the soil surface and subsequent development of lush algal mats. Filamentous bluegreen and green algae and dozens of species of diatoms form mats up to 1 cm thick on the moist soils and on the lower part of the halophyte stems (Figure 32). However, one cannot appreciate the beauty or complexity of these communities without a microscope (Figure 33). Unfortunately, the composition of these marsh algal mats has been studied only at Tijuana Estuary (Zedler 1980). Elsewhere in southern California, the mudflat algae (Riznyk et al. 1978) and subtidal epibenthic algae (Wilson 1980) have been examined. As a result of the paucity of information on species composition, it is uncertain whether the conclusions drawn from the Tijuana Estuary work would hold throughout the region.

Light penetration, temperature, and soil moisture are likely to be important factors for algal species distribution. These factors vary both seasonally and spatially over the elevation gradient of a marsh. Hence, in attempting to characterize the algal mat composition of Tijuana Estuary's marsh, sampling was carried out biweekly in four parts of the marsh chosen to allow comparisons with elevation (low, medium and high, differing in inundation, soil moisture, and salinity) and with different overstory canopies (at the same elevation, but with a short, open canopy of *Jaumea carnosa* and taller canopy of cordgrass [*Spartina foliosa*; Zedler, unpub. ms.b]).

The total species list which resulted from examining 1,680 wet-mounted microcores of the algal mats included 2 green algae, 7 bluegreen algae, and 74 diatoms. Of these, 38 species were considered common; they occurred in more than 5% of the microcores. The bluegreen and green algae form the matrix of the algal mats and probably contribute most of the biomass. However, their occurrence is patchy, perhaps due to herbivory and disturbance by crabs and snails. The species most commonly encountered are listed by algal group in order of decreasing frequency of occurrence for the marsh as a whole (Table 8). The habitat and season of greatest abundance are noted to indicate the general environmental conditions which seem to favor each species. All species except *Nitzschia obtusa v. nana* showed differential frequencies with sampling station (habitat), and all except *Amphora exigua* and *Rhopalodia musculus* differed with sampling season. Spatial and temporal patterns are the general rule for Tijuana Estuary marsh algae. Still, the sampling stations averaged 64% similarity, with the greatest difference in composition occurring between the highest and lowest stations sampled. These similarities are much greater than those for the overstory vegetation at the same sampling stations, and one can speculate that (1) algal communities have broader ranges of tolerance since algae readily go dormant and readily revive with favorable conditions, (2) that the environment for algae differs far less than that for vascular plants because of the ameliorating influence of the overstory canopy, or (3) that tides move the algae through the intertidal marsh and species are continually replenished at all habitats. Perhaps all are true. Much research remains to be done before a conceptual model can be suggested.



Above: bluegreen algae; below: green algae on pickleweed.

Figure 32. Luxuriant algal mats grow on the soil surface, underneath the vascular plant canopies and on intertidal mudflats. The bluegreen algae provide a matrix of filaments throughout which dozens of species of diatoms exist. Green algae become more conspicuous in winter. Photos by J. Zedler.

Table 8. Distribution of the 38 most frequently encountered algae of the Tijuana Estuary salt marsh. Numbers = occurrence rank; letters = habitat/season of greatest frequency (see codes below). Unpub. data of J. Zedler.

Green algae

12 Rhizoclonium riparium (Roth) Harvey: M/W
33 Enteromorpha clathrata v. crinita (Roth) J.Ag.: B/WSp

Bluegreen algae

3 Microcoleus lyngbyaceus (Kutz.) Cruoan: S/Su
13 Schizothrix mexicana Gom.: JBM/SpSuF
15 S. arenaria (Berk.) Gom.: B/Su
20 S. calcicola (Ag.) Gom.: M/Su

Diatoms

1 Trachyneis aspera (Ehr.) Cl.: JBM/WSpF
2 Denticula subtilis Grun.: MB/W
4 Nitzschia vermicularis (Kutz.) jrun: JS/Su
5 Diploneis smithii (Breb. ex W.Sm.) Cl.: JBM/W
6 Nitzschia incrustans Grun.: SJ/SpSu
7 Navicula ramosissima (Ag.) Cl.: BJ/SpSuF
8 Achnanthes sp. 1: BS/SpSu
9 Mastogloia exigua Lewis: B/SpSu
10 Nitzschia subtilis Grun.: J/SpSu
11 Amphora turgida Greg.: BJ/F
14 Gyrosigma obliquum (Grun.) Boyer: S/Su
16 Nitzschia obtusa v. nana Grun.: random/W
17 Surirella fastuosa (Ehr.) Kutz: M/W
18 Diploneis interrupta (Kutz.) Cl.: M/W
19 Navicula mollis (W. Sm.) Cl.: SBM/SpF
21 Ni. longissima (Breb. ex Kutz.) Ralfs: BS/Sp
22 Ni. punctata v. coarctata (Grun.) Hustedt: S/Sp
23 Achnanthes sp. 2: B/Sp
24 Nitzschia fonticola Grun.: B/FW
25 Achnanthes brevipes Ag.: M/F
26 Nitzschia fasciculata Grun.: J/Su
27 Caloneis westii (W. Sm.) Hendey: JB/F
28 Amphora exigua Greg.: M/random
29 Na. digito-radiata (Greg.) Ralfs: B/W
30 Rhopalodia musculus (Kutz.) O.Mull.: B/random
31 Nitzschia angularis W. Smith: JS/WSu
32 Amphora coffaeformis (Ag.) Kutz.: MB/W
34 Pinnularia ambigua Cl.: M/W
35 Ni. obtusa v. scapelliformis Grun.: MB/F
36 Diploneis bombus Ehr.: M/WSp
37 Nitzschia acuminata (W.Sm.) Grun.: B/W
38 Diploneis lineata (Donk.) Cl.: S/Sp

Habitat/Season codes are as follows:
S=dense Spartina canopy @ 7 dm MSL
J=open Jaumea canopy @ 7 dm MSL
B=open Batis canopy @ 8 dm MSL
M=open Monanthochloe canopy @ 9 dm MSL
random=no pattern using χ^2 test

W=winter
Sp=spring
Su=summer
F=fall

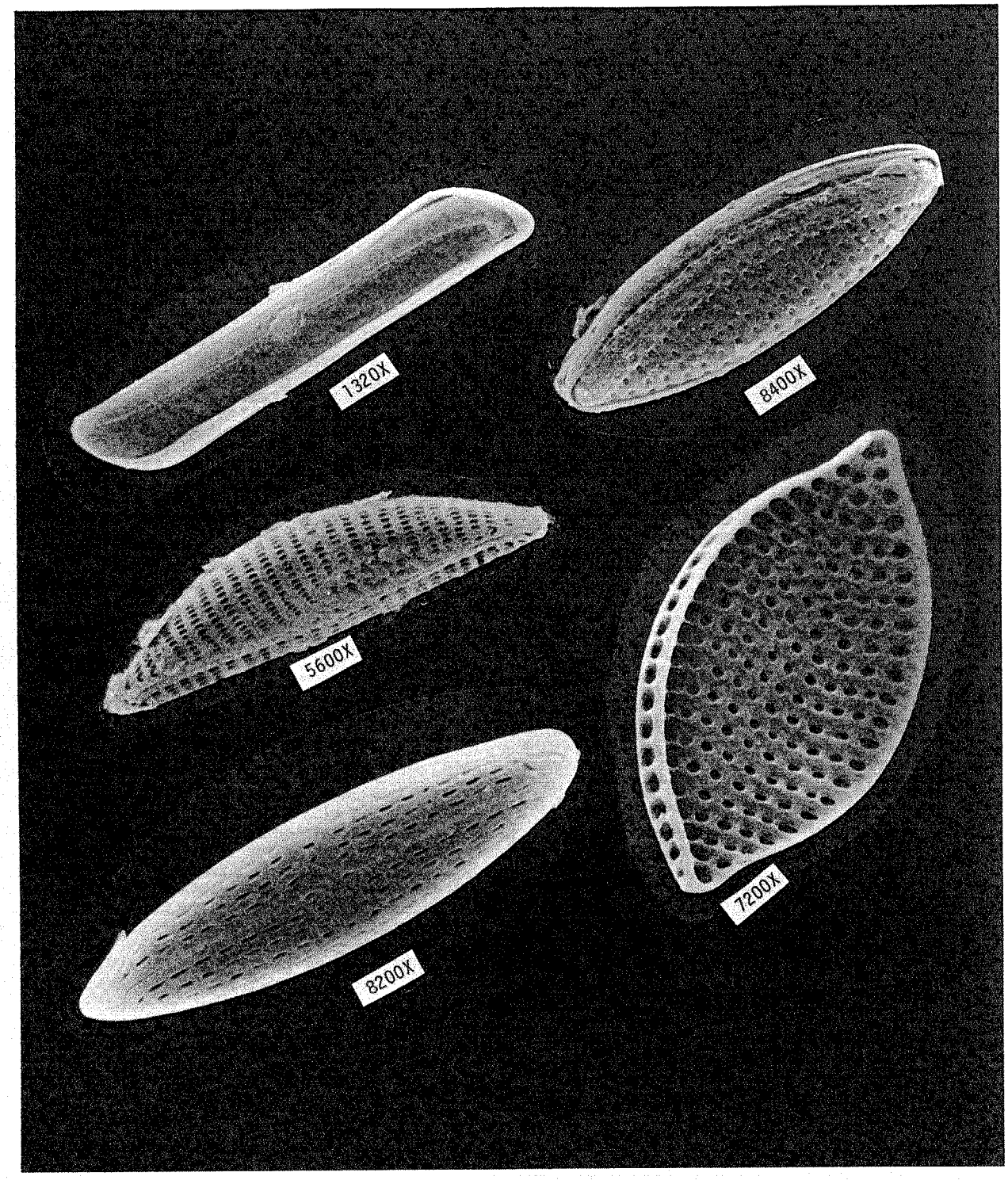


Figure 33. The beauty and diversity of salt-marsh diatoms are seen in these scanning electron microscope photos. Without a microscope, it is impossible to appreciate their structure; even with a light microscope it is difficult.

3.2 ALGAL MAT PRODUCTIVITY

Studies of intertidal algal productivity along Pacific Coastal marshes are more numerous than studies of algal composition. However, most of the work deals with mud- or sandflat algae (e.g. Pamatmat 1968, Riznyk et al. 1978, Onuf et al. 1978). Again, only the work at Tijuana Estuary (Zedler 1980) has dealt with soil algae found under a marsh canopy and general results are presented in order to suggest the role of algal mats in the productivity of southern California coastal marshes.

As with measurements of vascular plant productivity, there are different methods and assumptions for measuring and calculating annual algal productivity. Methods based on the measurement of oxygen produced do not give the same results as methods based on carbon dioxide uptake. The former method measures gross productivity (net productivity plus respiration), while the latter gives something closer to net productivity. Furthermore, assumptions must be made in extrapolating from hourly incubation measurements to daily and yearly estimates. Hence, annual algal productivity measurements are subject to large errors,and comparisons from study to study should be made with caution. Even comparisons made with the same methods can be faulty if different assumptions have gone into the annual calculations.

At Tijuana Estuary, it appeared that algal mats might be more productive, both on an absolute basis (more grams of carbon/m^2/yr) and on a relative basis (a larger proportion of the total marsh productivity), than in the eastern United States marshes. Hence, caution was used in making the assumptions necessary to convert short-term productivity measurements to annual net productivity (Zedler 1980).

Algal productivity was measured biweekly in the same four habitats for which compositional information was obtained, namely under canopies of cordgrass (Spartina foliosa), Jaumea carnosa, saltwort (Batis maritima), and shoregrass (Monanthochloe littoralis). Again, both seasonal and spatial patterns were found, with winter having the lowest values, followed by a spring peak in early March and a second low in April. The winter low was attributed to cool temperatures, while the April low coincided with a period of little tidal inundation, no rainfall, and dry algal mats. An April depression would not be expected in years of early spring rains. Values in late spring through fall were again high, in response to the long period of favorable temperatures.

Spatial differences in productivity (Figure 34) related to (1) elevation, with the higher, drier elevations being less productive than the low marsh habitats; and (2) the type of overstory canopy. The two sampling stations at low elevation differed significantly from one another, with mats under the tall, dense cordgrass canopy being less productive than those under the more open Jaumea canopy. Both desiccation and shading appear to be stresses for southern California marsh algae.

On an absolute basis, the annual productivity estimates for Tijuana Estuary marsh algae (net productivity up to 340 gC/m^2/yr) are among the highest recorded for epibenthic algae in soft sediments. What features of these marsh habitats would prove so favorable for algal growth? The year-round warm climate is no doubt one important factor in promoting algal growth, especially for the bluegreen algae. Substrate stability may well be another. Algal growths in the channels of Tijuana Estuary are never as persistent as within the marsh canopies (Zedler et al. 1978). Diatoms are abundant on the creek banks, but the few patches of bluegreen algae seem to be readily eliminated either through herbivore consumption or removal by currents. When tidal circulation is sluggish, large floating colonies of green algae (Ulva and Enteromorpha) develop and become entrained on the edges of the marsh, but these soon become desiccated.

The stabilizing features of the marsh vegetation, combined with the relatively open canopy which allows considerable light penetration throughout the year, seem to provide ideal conditions for algal growth.

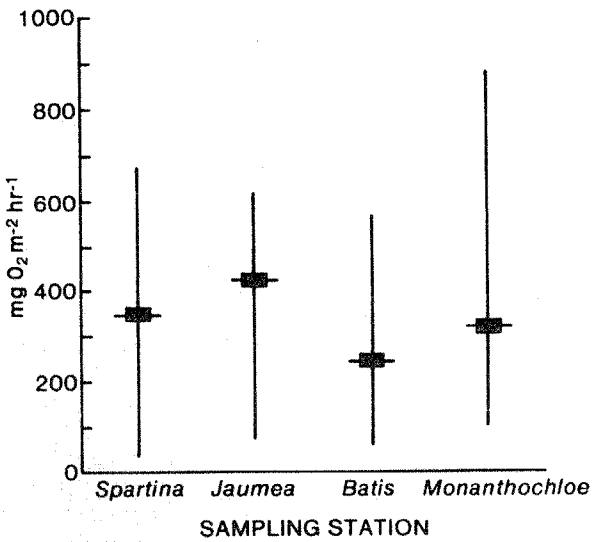


Figure 34. Estimated hourly gross primary productivity of algal mats under four different canopies at Tijuana Estuary; X = horizontal bar; ±S.E. = height of box; range = vertical bar. Data are summaries of biweekly measurements made in 1977 (Zedler 1980).

3.3 SUMMARY OF CHAPTER 3

The algal mats of Tijuana Estuary's salt marsh are diverse, conspicuous, and highly productive. Changes in both composition and productivity occur through the year, with bluegreen algae being most abundant and productive through the long, warm growing season. Diatoms and green algae are more important in the cool winter.

Whether or not algal mats at other southern California marshes are as productive is not known. However, it seems likely that the open canopies, warm climate, and stable soils should favor high algal productivity throughout the region.

CHAPTER 4

COMPARATIVE ROLES OF VASCULAR PLANTS AND ALGAL MATS

Vascular plants are large and conspicuous, while algal mats are generally ignored. Yet investigations of algal productivity and food value for marsh consumers suggest a functional role which is disproportionate to their size. Although information about the relative importance of these two primary producer groups is limited, the data available suggest that we should look much closer at the algal mats and identify more clearly how modifications of salt marshes affect them. Interactions between vascular plants and algal mats occur, and management practices which favor one group may hinder another.

4.1 RELATIVE PRIMARY PRODUCTIVITY

Both vascular plants and algal mats contribute to the food production of a salt marsh. Where productivity rates of each producer group have been measured, it is possible to assess their relative importance to the ecosystem's food base. However, such comparisons are not very precise, because measurements of productivity, and assumptions made in calculating annual rates, differ for the two groups of marsh plants. Only general conclusions can be drawn from such data bases.

On the Atlantic coast of the United States three studies have compared algal and above-ground vascular plant productivity. The proportion of annual productivity contributed by algal mats (mostly diatoms) was about 20% in Georgia (Teal 1962), about 25% in Delaware (Gallagher and Daiber 1974) and about 25% in Massachusetts (Van Raalte et al. 1976). From these results, it appears that algae provide less food for marsh consumers than vascular plants. Perhaps this is to be expected for marshes where the vascular plant canopy is tall and dense.

The study of the algal and vascular plant productivity at Tijuana Estuary suggests a contrasting situation for hypersaline marshes. Even the most conservative estimates indicate that algae are about as productive as the overstory plants (Zedler 1980). Proportions of total net carbon fixed by algae fell within 40% to 60%. The highest value was obtained in the low elevation Jaumea-dominated habitat, where both moisture and light were abundant. Evidence suggests that these algal mats are limited by light; productivity declined in winter and productivity was nearly always lower under dense compared to open canopies.

Generalizing the observations at Tijuana Estuary to the hypersaline marshes of southern California, a conceptual model of comparative productivity emerges (Figure 35). Soil salinity is seen as the major controlling factor. Where soils are hypersaline, vascular plant growth is reduced, canopies are open, and considerable light penetrates to the soil surface. Algal mats develop and contribute a major proportion of the marsh primary productivity. Brackish soils support denser vascular plant canopies, which in turn intercept more light, and soil algae are light limited.

While this model has not been tested by field experiment, our observations of other marshes under brackish conditions (at Los Penasquitos Lagoon and the San Diego River) suggest the same patterns. When canopies are densest, algal growth is sparse. With mortality in the overstory, algal mats are quick to develop.

The algal productivity takes on greater importance when the quality of the food produced is examined and the impact on food chains is explored.

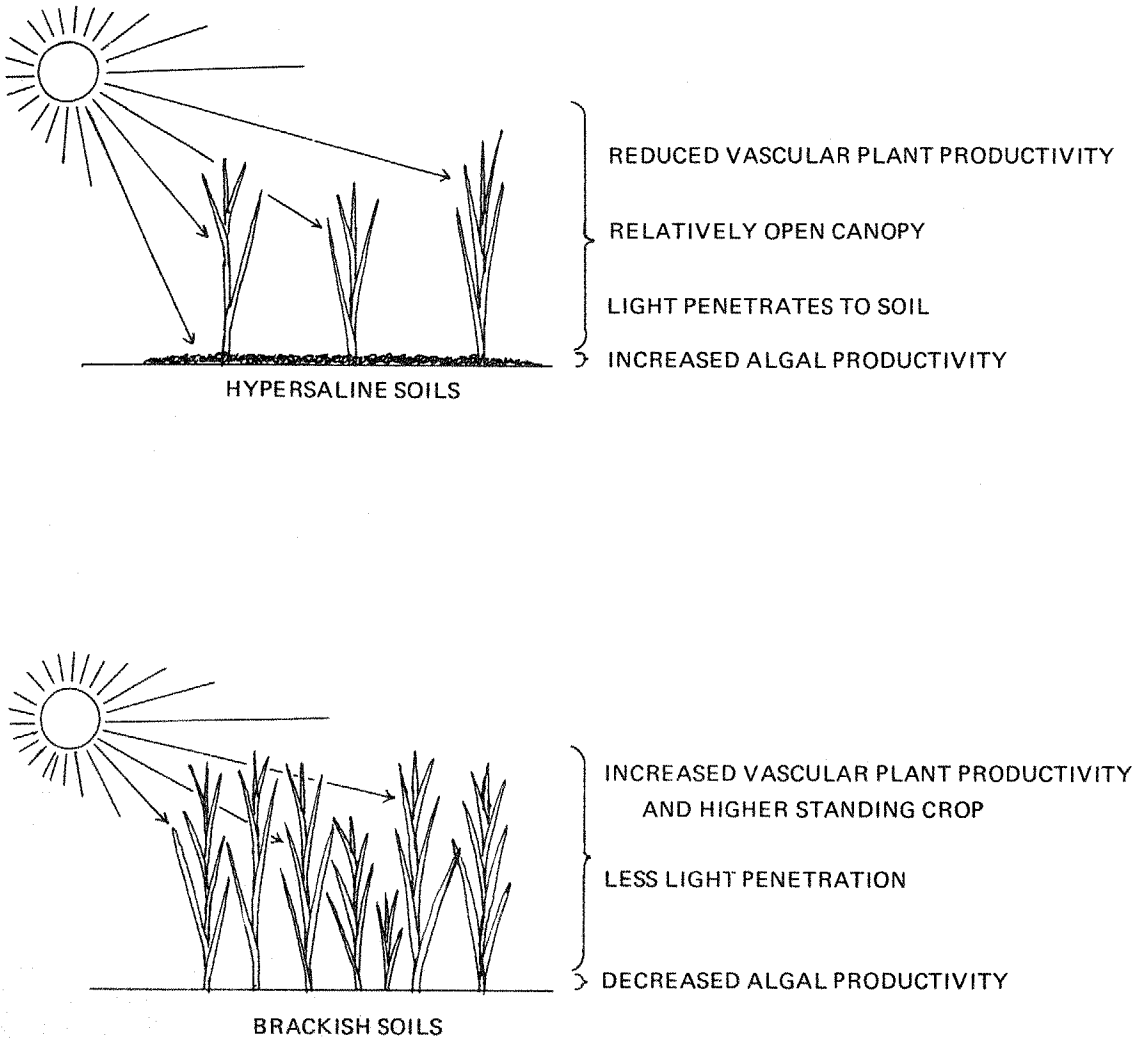


Figure 35. Effect of soil salinity on the relationship between vascular plant productivity and algal productivity: a conceptual model.

4.2 RELATIVE FOOD QUALITY

Vascular plants are generally recognized as having lower food value than algae (Crisp 1975). The percent protein content is higher in algae where there is less accumulation of non-proteinaceous structural compounds. The vascular tissue, thick cell walls, and lignified structural components make up a large proportion of the organic matter of marsh flowering plants. In addition, the structural components of vascular plants make them difficult for herbivores to digest. Caswell et al. (1973) suggested that plants with the C_4 mode of photosynthesis (their first products have 4-carbon molecules instead of the usual 3) are particularly problematic for consumers, since much of their protein-rich food is contained within thick-walled bundle sheath cells. Decomposition appears to be a prerequisite for use of vascular plants as food sources for many marsh consumers.

Are vascular plants utilized by southern California marsh animals? Williams (1981) examined the food value of two halophytes from Tijuana Estuary by preparing detritus and feeding it to young mussels (Mytilus edulis) under controlled laboratory conditions. Cordgrass (Spartina foliosa, a C_4 plant) and pickleweed (Salicornia virginica, a C_3 species were chosen to test the hypothesis that C_3 species provide better food for marsh consumers. Both types of detritus were poor food sources, however, even when detrital particles had been partially decomposed following a four-day aging process. Mussels lost weight when fed detritus alone. In contrast, mussels placed in channels of the Tijuana Estuary grew rapidly, indicating that other sources of organic matter were important in their nutrition.

A second factor which may make vascular plants less palatable for marsh grazers is high salt content. Winfield (1980) determined the carbon content of seven succulent and four non-succulent marsh plants to be from 19% to 35% of their dry weight, whereas Spartina alterniflora along the East Coast measures 38 to 47% carbon (Keefe 1972). Higher internal salt content would explain the lower carbon content for southern California marsh plants. In addition, the salt-excreting species (Spartina foliosa, Monanthochloe littoralis, Distichlis spicata, Limonium californicum, and Frankenia grandifolia) are all usually coated with salt crystals, which should make them less desirable to herbivores. In our outdoor laboratory at Mission Bay, we have witnessed more insect herbivory on cordgrass plants grown in fresh water than on plants grown in sea water (Boland, unpub. data), and it is tempting to hypothesize that salty plant tissues act to discourage herbivory.

Most of the marsh algae are single celled species or filaments of one cell thickness. Fibrous tissues are lacking. This suggests, but does not guarantee, that algae are palatable and digestible. Planktonic bluegreen algae are notorious for their unpalatability (Porter and Orcutt 1980). In part, this is attributed to their filamentous nature, which makes them difficult for zooplankton to ingest. In addition, many secrete toxic compounds which at least some zooplankton appear to be able to detect and thus avoid. Other consumers may be poisoned if toxins build up to high concentrations.

But the bluegreen algae of salt marsh muds apparently do not inhibit invertebrate feeding as do their planktonic relatives. On the contrary, the work of Brenner et al. (1976) shows that marsh algal mats dominated by bluegreen algae provide a high quality food source which is both palatable and digestible. Assimilation efficiencies (amount digested as a percent of amount ingested) of up to 67% were measured for salt-marsh amphipods in their Massachusetts marsh.

Diatoms are also palatable to marsh consumers. Whitlatch and Obrebski (1980) examined the feeding habits of two gastropods, Batillaria attramentaria

(introduced from Japan) and Cerithidea californica (native species), at three central California salt marshes. Diatoms accounted for most of the gut contents of both snails, and comparisons of chlorophyllose pigments in gut and fecal samples indicated that the diatoms were being digested.

4.3 CONCEPTUAL MODELS OF ENERGY FLOW

In the brackish marshes of Georgia, Teal (1962) described energy as moving predominantly through a vascular plant-decomposer-detritivore pathway. The highly productive Spartina alterniflora is little used by grazers (Smalley 1959). Most are first broken down by fungi and bacteria, which make the material more digestible and improve the nutritional quality of the detritus by adding organic nitrogen. Consumers feed on the resulting mixture of microbes and vascular plant fragments (Lopez et al. 1977).

Tremendous effort is required to quantify energy flow in marsh ecosystems and, unfortunately, work comparable to that reported in Teal (1962) has not been done in southern California. The concept which follows (Figure 36) is speculative, but is consistent with the observations of vascular plant and algal productivity and the relative values of the foods produced.

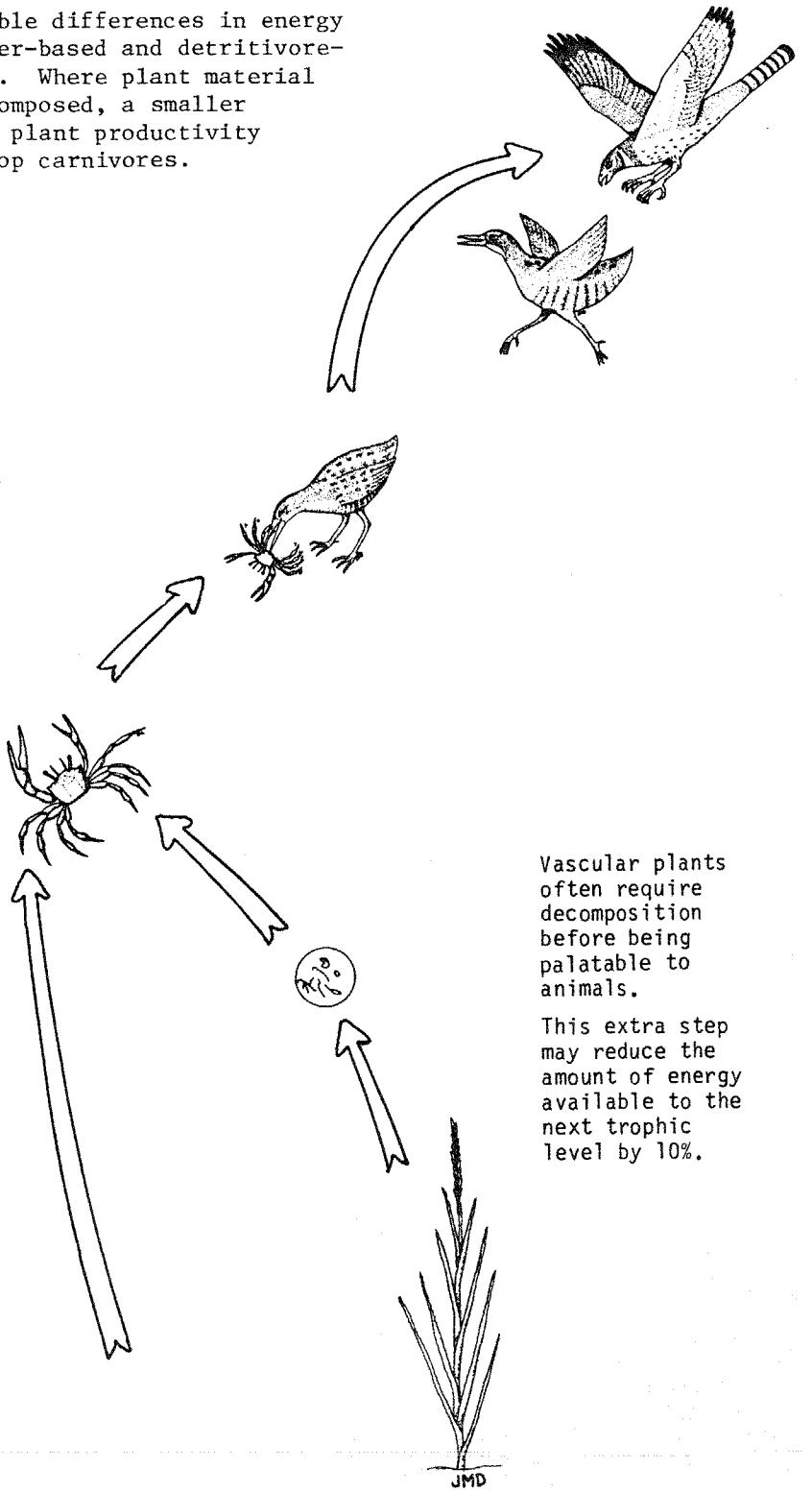
Vascular plants of southern California marshes are probably utilized by detritivores, as in Georgia marshes. But since algae are more productive, both on an absolute and relative scale, the grazer pathway may be more important in channeling primary productivity to higher trophic levels. Energy is lost to respiration at every feeding level and, because decomposers attack the vascular plants prior to their consumption by higher trophic levels, a large portion of the energy fixed by this group of producers is used up by fungi and bacteria. This leaves a smaller amount of energy for consumption by detritivores. Hence, a given amount of vascular plant energy would support a smaller biomass of top carnivores than the same amount of energy fixed by algae and used directly by grazers (cf. Figure 36).

4.4 FLUX OF ORGANIC CARBON AND THE FUNCTION OF MARSH PLANTS AS NUTRIENT TRAPS

Tidally flushed wetlands are open systems; they exchange materials, both living and dead, with adjacent upland and ocean ecosystems. In southern California, where there is usually little input of freshwater, tidal waters provide the major route of exchange with the ocean. Measurements of the concentrations of organic matter and nutrients on incoming and outgoing tides allow net fluxes to be determined. When followed over the year, it becomes possible to determine if a system functions as a net exporter or importer of various substances.

For many years coastal marshes were viewed as accumulators of nutrients and exporters of organic matter, with the highly productive cordgrass being moved into bays and providing food for fish and shellfish (e.g. Odum 1971). However, this model of estuarine functioning has recently been challenged by Haines (1979), and Nixon (1980) has critically reviewed evidence which concerns these functions of coastal wetlands. An alternative model of wetland-coastal interactions has emerged, which itself must stand the test of future investigations before being accepted as fact. As summarized by Haines (1979), East Coast wetlands have four major features: (1) Marsh soils and estuarine sediments function as dominant sites for accumulation, consumption and remineralization of particulate organic carbon (POC). Dissolved organic carbon (DOC) and nutrients move into the estuarine waters. (2) Salt marsh productivity is utilized by fish, shrimp, crabs, and other consumers which move into the marsh to feed. The marsh thus serves both as a food source and feeding habitat. (3) Phytoplankton are important producers in estuarine waters; their productivity is responsible for much of the bay's fish and

Figure 36. Possible differences in energy flow through grazer-based and detritivore-based food chains. Where plant material must first be decomposed, a smaller proportion of the plant productivity is channeled to top carnivores.



shellfish productivity. (4) Estuarine food webs are highly complex; many species are generalistic feeders which can function as herbivores, carnivores, and detritivores.

At the same time that Haines was challenging the Georgia model of wetland functioning, the California Sea Grant Program provided funds to investigate Tijuana Estuary and Mugu Lagoon. Both studies sought to determine if southern California wetlands conform to the export model originally ascribed to Georgia marshes. Data obtained by Winfield (1980) for Tijuana Estuary included frequent measurements of POC, DOC, and inorganic forms of nitrogen (IN). Onuf's work at Mugu Lagoon (Onuf et al. 1978) included measurements of POC over selected tide cycles in a two-year period.

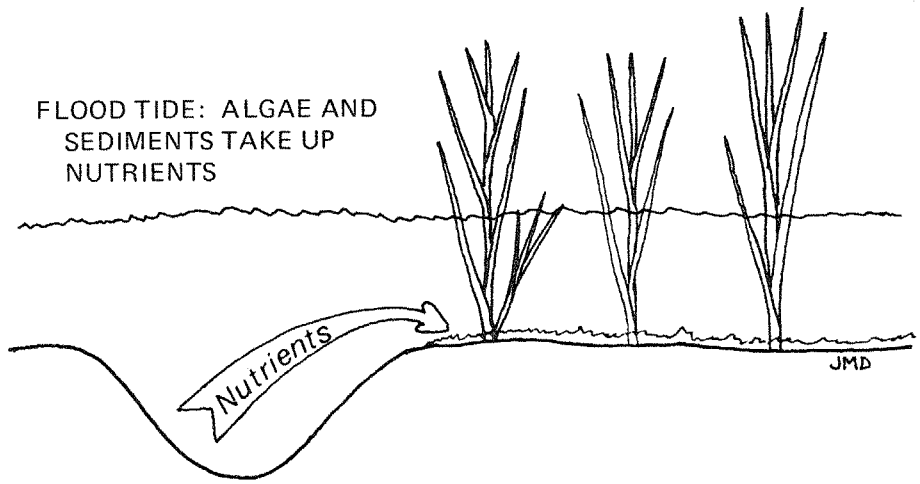
At Tijuana Estuary the results contrast with the outwelling model of Teal (1962) and Odum (1971). Inorganic nitrogen was imported from small tidal creeks onto the salt marsh, with most of the flux occurring as imported ammonia. Organic carbon was exported, but in the dissolved form, not as particulates. During periods of flooding witnessed in 1978 there appeared to be a measurable export of both POC and DOC, corresponding to the net outflow of water. Yearly fluxes were compared with estimated organic carbon production and nitrogen uptake to determine the relative magnitude of C and N movements. Winfield (1980) suggests that about 6% of the nitrogen required for vascular plant and algal productivity is met by imported nitrogen. Hence, most of the nitrogen must be generated by processes within the marsh, e.g. nitrogen fixation and remineralization. The amount of organic carbon exported was a small fraction (at most 25%) of that produced on the marsh (Winfield 1980).

The results of Onuf et al. (1978) concur that there is little evidence to support the concept of major POC export in southern California wetlands. In both Winfield's and Onuf et al.'s studies, however, large pieces of floating matter, such as make up the debris deposits at high water mark, were not measured. From observations of the wood and seaweed deposits sometimes seen within coastal marshes, it is clear that some fluxes are missed by studies which are restricted to the water column. Still, these larger materials may be refractory to utilization by mircoorganisms. As Pomeroy et al. (1976) point out, we need much more study of both the quality and quantity of POC and DOC in marsh ecosystems.

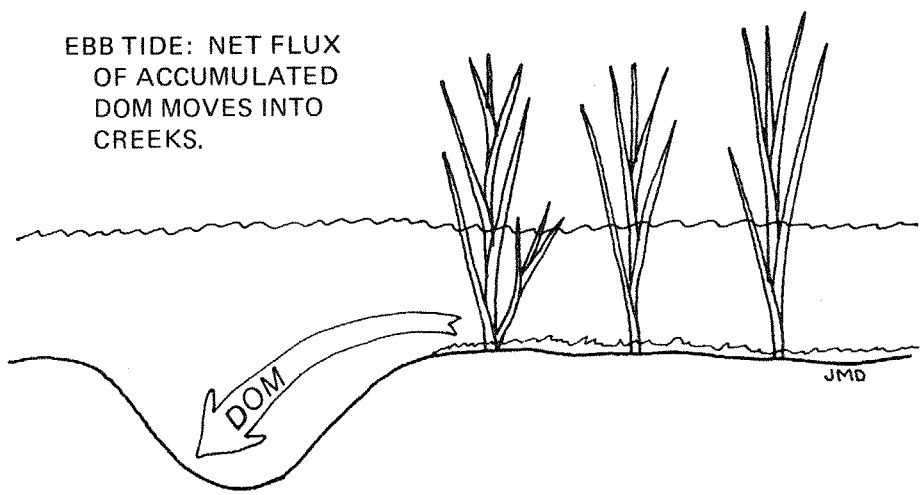
The combined work on nitrogen and organic carbon flux suggests a model of estuary-coastal interaction which bears some similarity to Haines' (1979) alternative hypothesis for the Georgia marshes (Figure 37). However, there is one important difference. Most of the East Coast marshes are next to large bays, and aquatic habitats are more important. Except for San Diego Bay and the artificially enlarged bays of Mission Bay and Los Angeles Harbor, southern California lacks these coastal embayments.

In the model, flood tides provide a source of nutrients for algae, soils and vascular plants; ebb tides leach dissolved organic carbon from the microbial mats, litter and standing vegetation. At all times, microorganisms and invertebrate larvae incorporate dissolved organic carbon into biomass, which is then available to larger consumers. Decomposition returns nutrients to the water, which then floods the marsh again.

In this scheme, microorganisms may well be the principal transformers of inorganic to organic materials. By virtue of the rapid growth rates, high surface area-to-volume ratios, and thin cell walls, the algae, bacteria and fungi are capable of rapid exchange rates. The algal mats may be the most important nutrient absorbers, as well as the most important source of dissolved organic carbon. The rate at which inorganic nitrogen is absorbed and DOC is leached from these algal mats is currently being investigated (Pat Dunn, graduate student, San Diego State University).



DURING HIGH TIDE: ORGANIC MATTER FROM ALGAE AND OTHER MICROBES, AND FROM VASCULAR PLANTS GOES INTO SOLUTION AS DOM.



WITHIN WATER COLUMN: MICROBES, INVERTEBRATE LARVAE AND ADULTS TAKE UP DOM AND INCORPORATE IT INTO BIOMASS. ACTIVELY METABOLIZING MICROBES BREAK DOWN ORGANIC MATTER INTO NUTRIENTS.

Figure 37. Conceptual model of southern California marsh and tidal creek interactions. Net fluxes are probably greatest at high spring tides when the largest area of marsh is covered by water. Developed from information in Winfield (1980).

During neap tides and between the higher tides, water levels are generally below the marsh. Dissolved organic matter is probably absorbed and incorporated into microbial and animal biomass. Both larvae and adults of several marine invertebrates are known to take up DOC rapidly (Manahan 1980), and even photosynthetic diatoms can function as heterotrophs by taking up DOC (Darley et al. 1979).

4.5 SUMMARY OF CHAPTER 4

The quality of food produced by vascular plants and algae differs. Salt marsh consumers, such as snails and crabs, can feed directly on algae and probably assimilate a large proportion of the algal organic matter which they ingest. However, vascular plants are relatively indigestible until they have been partially decomposed by microbes. Then the fungi and bacteria provide nutritious food sources for snails, crabs, isopods, and amphipods. Adding the decomposer step to the food chain reduces the proportion of plant productivity which can be funneled to higher trophic levels. Hence, in this conceptual model of southern California salt marshes, algal mats take on a food producer role which is greater than that measurable by productivity or biomass alone.

CHAPTER 5

SALT MARSH ANIMALS

The salt marsh contains an interesting mixture of animals and plants that come from two extremely different environments: the land and the sea. The vascular plants, insects, amphibians, reptiles, birds and mammals are familiar terrestrial forms. In contrast, algae, molluscs, crustaceans, and fish are all expected to occur in aquatic habitats. Intertidal marshes, which are alternatingly wet and dry, harbor all of these forms. We might expect the "terrestrial" organisms to be stressed during high tides when the aquatic biota are not, and vice versa at low tide. It is intriguing to consider whether the species which manage to live here do so out of preference or default. As considered earlier, the vascular plants generally find southern California wetlands stressful; they appear to owe their success to tolerance of rather than preference for the marsh environment. Insects and mammals somehow cope with occasional inundation and salty foods, but we are ignorant of how stressful these conditions are. The highly mobile birds can easily avoid inundation, but they must expend considerable energy to excrete excess salts. For the marine organisms, desiccation and variable temperatures surely pose a threat to survival. Although algal productivity seems to increase as tide waters subside, (R. Holmes, University of California, Santa Barbara) molluscs close up when they're exposed; crustaceans seek shelter; and fish move back to channels. These animal behavior patterns all suggest tolerance, rather than preference for marsh environments. Yet there must be some advantage to life in the salt marsh; otherwise we would find salt marsh animals more numerous elsewhere instead of dependent on this unique community.

This chapter summarizes what is known about southern California salt marsh animals. How the various groups tolerate their fluctuating environments is not well understood, and there is much to learn about their interactions with one another. These topics and questions concerning ecosystem energy flow should provide future wetland ecologists with substantial material for study.

5.1 INVERTEBRATES

Investigations of the invertebrates of bay, lagoon and intertidal flat habitats have been conducted in recent years (Peterson 1975, 1977, Seapy 1981, Quammen 1980), but information on the salt marsh invertebrates is quite restricted. Macdonald (1967) and McCloy (1979) have studied molluscs in selected Pacific Coast marshes; Phleger (1977) and others have investigated the Foraminifera; Willason (1980) has studied crabs; and Nagano (1981) is investigating insects in a variety of coastal habitats. Our knowledge of marsh nematodes, harpacticoid copepods, annelids, amphipods, isopods, and arachnids is extremely limited. Since these small animals are likely to be major consumers in the salt marsh food chain, as well as important food sources for birds and fish, further research is needed to quantify their habitat requirements and roles in the marsh ecosystem.

Foraminifera

Marsh Foraminifera are useful in unraveling the history of sediments. These small protozoa live in the upper 1 cm of marsh soils; their shells are readily identifiable and well preserved. However, because of their calcareous composition, they do not persist in acidic substrates. Some forms (called arenaceous) build their shells by cementing sand grains.

Phleger (1977), Phleger and Bradshaw (1966), and Scott (1976) discussed the Foraminifera of salt marsh soils and

indicated that species composition shows geographical, salinity and local intra-marsh patterns. The southern and Baja California assemblage identified by Phleger (1967, in Macdonald 1977b) had several dominants (Trochammina inflata, Miliammina fusca, Jadammina polystoma) in common with more northern Foraminiferan communities, but included more species (Ammonia beccarii, Arenoparrella mexicana, Cellanthus discoidale, Discorinopsis aguayoi, Glabratella sp., and Protoschista findens). As with the marsh flora, dominant Foraminiferan species extend over a broad latitude, but southern California has additional species of more tropical distribution.

Phleger (1970, 1977) provided lists of species which have been classified according to their general ecological distribution. Scott's (1976) data on live specimens from Mission Bay and Tijuana Estuary include two of the four species listed as common in marshes, three of the five hypersaline species, but no brackish forms (Table 9).

Comparisons of low and high marsh at Mission Bay and Tijuana Estuary (Scott 1976) showed distinctive communities, with higher densities above MHHW in the upper marsh. Species characteristic of the upper marsh were T. inflata, J. polystoma, D. aguayoi, and Quinqueloculina seminulum at both locations. However, low marsh habitats were characterized by high percentages of Cribroelphidium spinatum translucens and Cellanthus tumidum at Mission Bay and Protoschista findens at Tijuana Estuary, where calcareous species were generally less common.

Using the relatively high consistency of composition and marsh type, Scott (1976) interpreted the history of Mission Bay and Tijuana Estuary from auger cores taken within each marsh. The Mission Bay core was dated with carbon-14 to be 2380 ± 60 years at 3.1 m. At that time, the Foraminifera indicate that the present high marsh was an intertidal mudflat, which subsequently changed to low and then high marsh as sediments and organic material accumulated. At Tijuana Estuary, material at 1.1 m was dated at 1180 ± 50 years B. P. with carbon-14, at which time the core location was a mudflat. The sequence from that time on was similar to that at Mission Bay. However, a thick layer of sediments below 1.1 m was depauperate in Foraminifera, and Scott suggested the area may have been a closed, brackish lagoon at the time. This suggestion is difficult to reconcile with modern - day observations of water accumulation patterns in southern California lagoons. Usually, only the lagoons with relatively small watersheds

Table 9. Foraminiferal categories (from Phleger 1977) and occurrences in Mission Bay (MB) and Tijuana Estuary (TE) (from Scott 1976).

Categories	Lower Marsh	Higher Marsh
Abundant and dominant cosmopolitan spp.		
Miliammina fusca	x	x
Trochammina inflata	x	dom.
Jadammina polystoma	x	v.abun.
Spp. confined to hypersaline marshes		
Discorinopsis aguayoi	x	x
Textularia earlandi	x	
Spp. common in marshes		
Protoschista findens	dom. @ TE	
Ammonia beccarii	x	
Additional abundant species found by Scott (1976)		
Quinqueloculina spp.	x	x
Cellanthus tumidum	x	
Cribroelphidium spinatum translucens	dom. @ MB	

dom.= dominant; v. abun. = very abundant

become closed and brackish for very long. If Tijuana Estuary were to close off from tidal inundation for long periods of time, it would probably be marine or hypersaline in response to drought conditions. If runoff were sufficient to create brackish water, the stream flow collected from over 700 ha (1,730 ac) would probably be sufficient to breach the sand bar and return tidal conditions.

Changes in the Foraminifera of Goleta Slough following recent sedimentation have been documented by Lohmar et al. (1980). Stenohaline species, present in earlier sediments, have been replaced by species which can tolerate the fluctuating conditions that accompany the more frequent closure of lagoons with small tidal prisms. Trochammina inflata was the living dominant of salt marsh and tidal creek habitats, while Ammonia becarri was abundant in the deeper lagoon channels. Species with less tolerance for varying salinities (e.g. Elphidium clavatum variants) were restricted to seaward portions of the Slough.

Foraminifera are helpful in understanding the history of wetlands, and additional detailed studies are needed to determine how regional wetland resources (i.e. areas of channels and low and high marsh habitat) have changed in recent times.

Molluscs

The molluscan faunas of Pacific Coast marshes and tidal creeks have been thoroughly sampled and analyzed by Macdonald (1967, 1969). As with other marine animals, there was a distinctive species assemblage south of Point Conception. Examination of large-scale distributional data indicated that biomass increased southward and that most species were more abundant toward the centers of their distributional ranges (Macdonald 1967). Otherwise, few patterns of occurrence were identified, nor were their causes explained. However, since molluscs are only a part of the

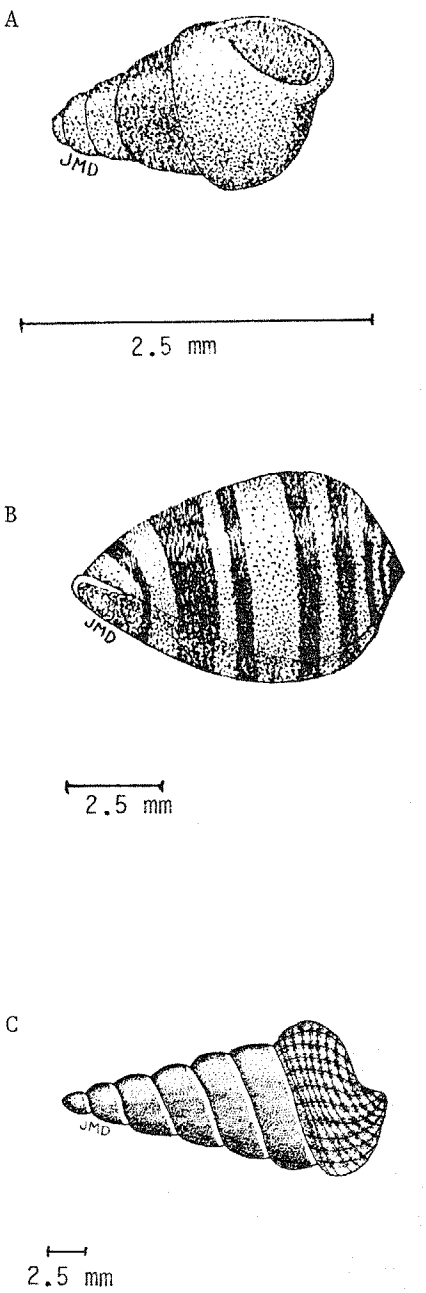


Figure 38. Three common molluscs in southern California salt marshes. Illustrations by J. DeWald.
A = Assiminea californica
B = Melampus olivaceus
C = Cerithidea californica

marsh animal community, it may be unrealistic to expect to explain their occurrences without considering the other invertebrates, and especially their vertebrate predators.

Southern California marsh molluscan communities are consistently dominated by Assiminea californica, Cerithidea californica, and Melampus olivaceus (Figure 38), all of which are epifaunal surface feeders (Tables 10 and 11). These snails are important grazers on the marsh algal mats. Simple field experiments which excluded hornsnails (Cerithidea californica) from small mudflat areas at Mission Bay resulted in local algal mat blooms, while control cages had little algal accumulation (SDSU Aquatic Ecology class, unpub. data). Removal of such grazers by shorebirds should create the same effect, and part of the patchiness of intertidal algal mats and invertebrates may be due to patchiness in the feeding effects of birds and other carnivores.

Marsh tidal creeks usually appear to be dominated by the hornsnail, Cerithidea californica. However, Macdonald (1967) also found abundant Acteocina sp. and several bivalve molluscs (Table 10), all of which are burrowing forms that are rarely visible. McCloy (1979) studied hornsnails in detail at Sweetwater Marsh (San Diego Bay), and documented several factors which influence their population size. Marshes often support densities over 1,000/m^2; individuals under 0.5 cm length are more common in the tidal creeks, and large individuals are more abundant on the marsh soil. McCloy attributed this size zonation to differential desiccation tolerance, since individuals under 0.5 cm in length rarely survived more than 12 hours in a desiccator, while individuals over 1.5 cm all survived for 48 hours (McCloy 1979). Also characteristic of the species is a non-random dispersion pattern. Individuals usually appear to be evenly spaced, suggesting some behavioral mechanism which avoids crowding. McCloy experimentally crowded the snails, first in the open without restricting snail movements, and later within cages. The response was then examined over several months. In the open, enhanced and depleted densities returned to normal within a month, as snails moved away from high density areas and into low density areas. Behavior, then, is density dependent and can regulate small-scale dispersion patterns. Within cages, McCloy tested to see if mortality and recruitment also changed with crowding or depletion. Again, the results showed density dependence of the population behavior. Growth rates declined under crowded conditions, suggesting food limitation. Some snails in the high-density cages moved up the cage sides, while others attached to the incoming tide water surface, probably in an attempt to disperse by flotation. Cages with fewer hornsnails had higher larval settling rates, so that densities converged to normal.

There were also effects on other marsh creek species. Mortality of adult hornsnails was higher under crowded conditions, and the large number of empty shells enhanced settling of the anemone Haliplanella luciae. Anemone densities became nearly four times higher than normal. Some invertebrates are rare in marshes because hard substrates are unavailable for larval settling. This result shows how events within one population can have unexpected effects on other species. The deposit feeder Acteocina culticella was also influenced by altered hornsnail densities. It was eliminated in crowded cages and enhanced by decreased densities of hornsnails, suggesting that competitive interactions occur between the two deposit feeders, and perhaps food is a limiting factor (McCloy 1979).

Other factors which McCloy determined to affect hornsnail densities were smothering by deposits of dense floating algae (e.g. Ulva), shorebird predation and crab predation. Shorebirds appear to be less damaging to tidal creek populations of hornsnails than to snails on mudflats. This suggests that creeks are important

Table 10. Molluscs at Mugu Lagoon and Mission Bay found live in either marsh or tidal creek habitats by Macdonald (1969, cf. Table 4, p. 62). Rare species are excluded. Data are mean no./m^2.

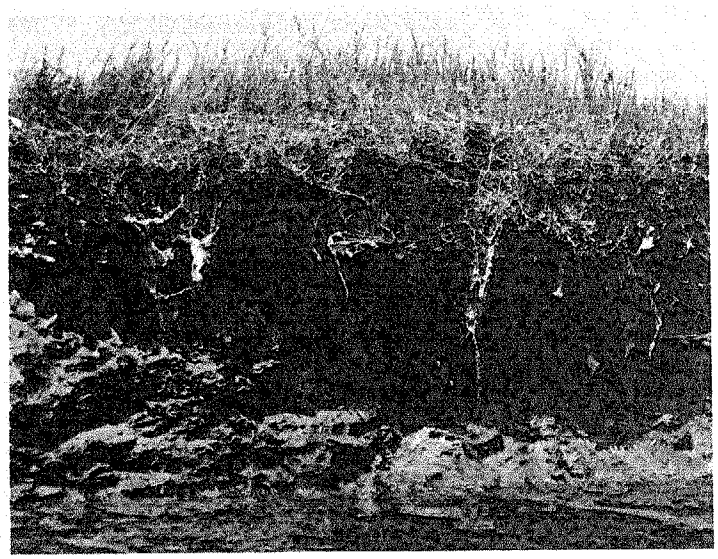
	Mugu Lagoon		Mission Bay	
	Marsh	Creek	Marsh	Creek
Gastropoda				
Subclass Prosobranchia				
Assiminea californica (Tryon)	1772	0	874	0.5
Cerithidea californica (Haldeman)	113	648	250	315
Nassarius tegula (Reeve)	0	0	0	15
Subclass Opisthobranchiata				
Acteocina sp. cf. *A. culcitella* (Gould)	0	88	22	771
Subclass Pulmonata				
Melampus olivaceus Carpenter	16	0	7	0
Pelecypoda				
Subclass Pteriomorphia				
Modiolus (*Brachiodontes*) *senhousei* (Benson)	0	0	0	7
Subclass Teleodesmata				
Chione fluctifraga (Sowerby)	0	0	0.5	7
Macoma nasuta (Conrad)	0	5	0	0
Protothaca staminea (Conrad)	0	21	0	2
Tagelus californianus (Conrad)	0	0	0	3

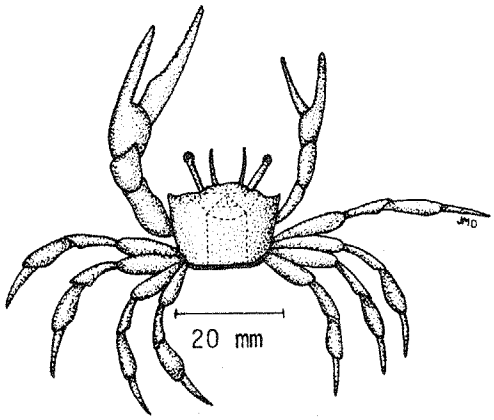
refuges for invertebrates, and raises the question of why birds spend less time there than on intertidal flats. Crabs are also snail predators, but their effect appeared to be limited by the availability of refuges for the crab. At Goleta Slough, McCloy (1979) demonstrated higher hornsnail mortality near an area of artificial rock substrate, where shore crabs (*Pachygrapsus crassipes*) found shelter. Again, a seemingly minor alteration of the marsh channel had an unexpected impact on a variety of populations within the ecosystem.

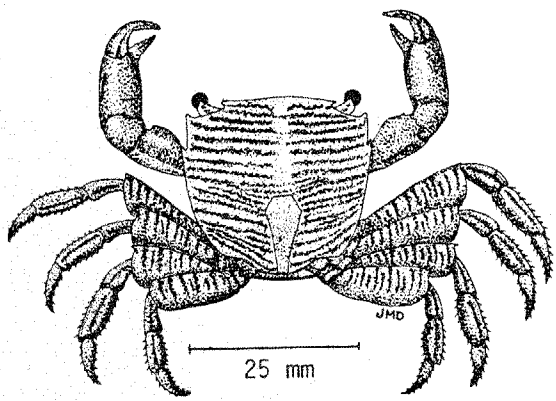
Hornsnails (*Cerithidea californica*) are of importance to marsh ecosystems in other ways as well, because they host a large number of flukes whose cercariae larvae parasitize shorebirds, fiddler crabs (*Uca crenulata*), killifish (*Fundulus parvipinnis*), and mudsuckers (*Gillichthys mirabilis*). Cercariae sometimes burrow into human skin and cause an annoying itch. They are especially easy to contract in late summer while wading for long periods of time through water or tidal creeks in the marsh.

Crustacea

Crabs are the most conspicuous crustaceans of the marsh, but they tend to evade study by burrowing. More elusive still are the salt marsh amphipods (*Orchestia traskiana* and *O. californica*) and isopods which enter the high marsh from more terrestrial habitats (Macdonald 1977b). These crustaceans are most abundant under rafted debris. Ghost shrimps (*Callianassa californiensis*) are well known because of their utility as bait. However, they are more common in channel sediments than in the marsh. All of these crustaceans are important to marsh food chains since they seem to be omnivores and are all utilized by birds and (at least in their larval forms) by fish. However, only the crabs (Figure 39) have been studied in detail in southern California (Kutilek 1968, Betz 1978, Willason 1980).







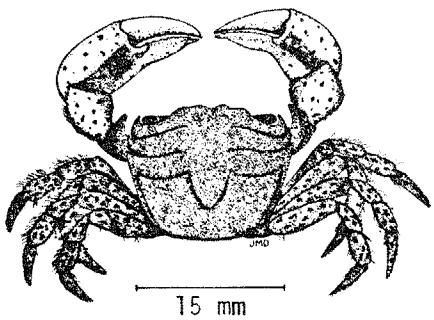


Figure 39. Creekbank habitat and three southern California crabs: the fiddler crab (Uca crenulata), the lined shore crab (Pachygrapsus crassipes), and the yellow shore crab (Hemigrapsus oregonensis). Photo by C. Nordby; illustrations by J. DeWald.

Table 11. Depth of occurrence and feeding characteristics of molluscs found in Mugu Lagoon and Mission Bay marshes and tidal creeks (from Macdonald 1969, Table 5). [e=epifauna, i=infauna, followed by depth of burial]

Mollusc species	Depth of occurrence	Rasp Algae & detritus from substrate	Ciliary suspension feeder (plankton)	Deposit feeder (organic detritus)	Predator	Scavenger
Assiminea californica	e	x				
Cerithidea californica	e	x				
Nassarius tegula	i<5cm				x	x
Acteocina sp.	i<5cm				x	x
Melampus olivaceus	e	x				
Modiolus senhousei	i<5cm		x			
Chione fluctifraga	i<5cm		x			
Macoma nasuta	i<5-20cm			x		
Protothaca staminea	i<5cm		x			
Tagelus californianus	i>20cm		x			

The smallest of the marsh crabs are the fiddler crabs (Uca crenulata). They are best known for their elaborate mating behavior in which the male waves his one large cheliped or "fiddle." The genus Uca is restricted to warm seas, and U. crenulata is not found north of Bolsa Chica. Fiddler crabs usually coexist with two grapsid crabs, Hemigrapsus oregonensis and Pachygrapsus crassipes, in southern California marshes.

Willason (1980) compared ecological preferences and examined interactions between the shore crabs, Hemigrapsus oregonensis and Pachygrapsus crassipes, at Goleta Slough in order to understand their distributions in the tidal creeks. Both species are nocturnal, but he made nighttime observation and excavated burrows to collect crabs for field and laboratory experiments. Densities of Hemigrapsus averaged about $75/m^2$, while Pachygrapsus averaged about $20/m^2$. On the average, Hemigrapsus individuals were smaller (mean carapace width 15 mm) than Pachygrapsus (mean = 26 mm), which may relate to their different densities. Both species were reproductively active during spring and summer. Hemigrapsus had high recruitment of young along the mudbanks, while young of Pachygrapsus were most numerous near the mouths of both Goleta Slough and Carpinteria Marsh (Willason 1980). More solid substrates may be necessary to estimate larval settling of Pachygrapsus, or larval mortality may be high in the muddier creeks. Within different tidal creeks, there appeared to be a negative correlation of the two species, with an indication that Pachygrapsus inhibited Hemigrapsus from occupying its preferred lower bank habitat. Experiments were designed to

determine how the two crabs interact. When each species was caged alone, Willason found that Pachygrapsus crassipes did not burrow; hence its common use of burrows is dependent on excavations of other species. Hemigrapsus oregonensis was found to dig burrows readily. Further study showed that Pachygrapsus could expand Hemigrapsus burrows to accommodate its larger carapace. Pachygrapsus ate Hemigrapsus in the field, and laboratory experiments confirmed that equal or larger-sized Pachygrapsus killed Hemigrapsus, but smaller Pachygrapsus did not. Cannibalism occurred among Pachygrapsus, but only after recent molting of the victim. Field experiments demonstrated substantial mortality of Hemigrapsus when both species were placed together in cages, but better survival of Hemigrapsus when it was given time to burrow before individuals of Pachygrapsus were added to the cage. Thus, burrows provide a partial refuge from predation, but even burrowing Hemigrapsus can be displaced by the aggressive Pachygrapsus. How, then, do Hemigrapsus populations persist?

The greater recruitment of Hemigrapsus in muddy habitats is one possibility; however, differential sensitivity to salinity may also play a role. Experiments on salinity tolerance suggest that Pachygrapsus crassipes (especially small individuals) is less tolerant of the low salinities which occasionally occur following winter and spring rainfall (Willason 1980).

Insects[1]

By virtue of their high species and trophic diversity, insects have many roles in coastal salt marshes. They feed on both vascular plants and algae; they feed on decaying plant and animal material; some are carnivores; and many serve as a food source for birds and other marsh vertebrates. Marsh insects are also important to the pollination of marsh halophytes. While most of the marsh plants lack the showy flowers that attract insects, at least one may owe its existence to insect pollinators. The salt marsh bird's beak (Cordylanthus maritimus ssp. maritimus, previously mentioned as an endangered species, is pollinated by bees. Certainly its long closed tubular flowers prevent wind pollination. Since this species is an annual, it relies on seeds to reproduce, and hence pollinators are important both for fertilization and the maintenance of genetic diversity through cross-pollination.

Some insect species are very sensitive to human impacts and can assist in indicating the general quality of coastal habitats. Unfortunately, they generally receive little attention because of their small size, the great difficulty in identifying most species, and the incorrect assumption that they are ecologically insignificant. Where they have been investigated (e.g. Cameron 1972, Davis and Gray 1966, Nagano et al. 1981), salt marsh insect communities were highly diverse both in composition and function.

Foster and Treherne (1976) reviewed the literature on salt marsh insects and suggested a long list of potential environmental problems which must be overcome for insects to survive in intertidal marsh habitats. First to be discussed was the question of how oxygen is obtained for respiration--both for aquatic insects in anaerobic mud and water where many eggs, larvae and pupae develop, and for aerial larvae and adults inundated by tides. The latter may tap oxygen from air tissues in plants, but no evidence supports this suggestion. Escape to the upper plant canopy might allow such insects to avoid inundation, but Cameron (1976) found that San Francisco Bay insects remain within the vegetation during high tides. However, he also indicated the possibility that insect

[1]This section draws heavily on unpublished data, correspondence and references provided by Chris Nagano, Research Associate, Entomology Section, Natural History Museum of Los Angeles County.

behavior may differ depending on activity levels: when inactive, they may cling to vegetation when the tide rises to avoid being swept away, but when active, they may move to higher levels in the canopy to reduce oxygen stress. His study does not solve the mystery of the respiration problem, but it points to another difficulty of the tidal environment, namely removal by water circulation. Foster and Treherne (1976) suggested that water flow sometimes may be advantageous, by providing an effective means of small-scale dispersal for insects which, if they were to rely on flight, might be blown to unfavorable habitats outside the marsh.

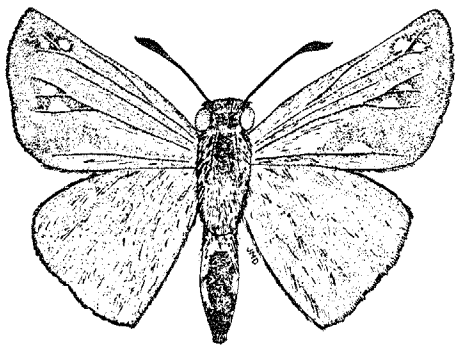
Like the plants which inhabit marshes, insects must deal with the osmotic and ionic problems of variable salinity. In addition to having external contact with salty soil and water, herbivorous insects take in large amounts of salt in their halophyte foods. Waterproof integuments can protect their bodies from the external sources (except perhaps for brief periods after molting). Efficient osmoregulatory systems are necessary for processing the saline plant materials, however, and these are energetically costly. Foster and Treherne (1976) indicated that some salt marsh insects are selective in their herbivory and take algae of lower salt content, while others regulate the movement of foods through their alimentary canal to reduce the salt load in the midgut. Some even capitalize on the rinsing effect of rainfall by feeding on plants which have been washed and by reducing intake between rains. In southern California, however, such a strategy would be impractical, unless life cycles were timed to coincide with the rainy season.

Only one southern California coastal wetland has been comprehensively surveyed for insects (Nagano et al. 1981). The 110 ha (270 ac) Ballona Wetland, already disturbed by urban encroachment and reduced tidal circulation, was estimated to support 1,200 species of insects, based on the identification of about 500 species within 146 families. Surveys of the entire insect fauna of a locality are always restricted by the difficulty in capturing all species present. Many require the use of special collecting techniques, such as ultraviolet light traps, yellow pan traps, pitfall traps, and berlese funnels. Studies which use nets in vegetation canopies will collect only a fraction of the fauna. At Ballona Creek, many rare species were obtained only in special devices. A new genus of wasp appeared in a yellow pan trap, and a springtail (Onychiuris debilis; Collembola: Onychiuridae), known only from France and Alaska, was collected with a berlese funnel (Nagano, pers. comm.).

The majority of coastal insect papers comment only on selected species and contain little ecological information. Because so few of the insects are well known, and because habitat continues to be developed, Nagano (1981, in press) and Moore and Legner (1972, 1974) express great concern that many insects will become extinct before they are discovered. At least one, the Antioch shield-back cricket (Neduba extincta; Orthoptera: Tettigoniidae) already has: the only specimen known was found preserved in a museum after most of its habitat had been destroyed.

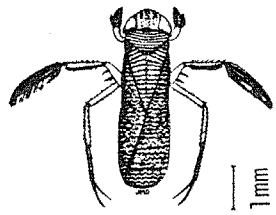
Several insects known to be linked to coastal habitats are described below. The following examples of marsh-dependent species were provided by Nagano.

The salt marsh water boatman (Trichocorixia reticulata, Figure 40) is one of a few species in the family Corixidae (Hemiptera) which can survive the saline habitat. It eats algae and protozoa from pools and comes to the water surface to renew the oxygen content of its air bubble or plastron. Cox (1969) found adult T. reticulata in coastal ponds ranging from slightly brackish to 160 ppt salinity in southern California. Occurrences in freshwater were rare, and the species probably breeds only in saline water. Reproduction occurred year-round during Cox's study, but laboratory



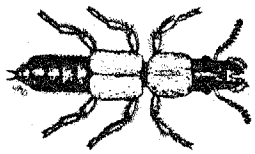
10 mm

The wandering skipper (Panoquina errans) is closely associated with salt grass (Distichlis spicata) which provides food for its larvae.



1mm

The salt marsh water boatman (Trichocorixia reticulata) develops high densities in saline pools.



0.25mm

Staphylinid beetles (e.g. this Bledius sp.) are probably responsible for the "fluffy" appearance of some salt flats. Their burrowing activities loosen and aerate the soils and may play a major role in rehabilitating soils compacted by off-road vehicle use.

Figure 40. The role of insects in the salt-marsh community is largely unstudied. These are but a few of the hundreds of species whose ecology needs to be investigated. Illustrations by J. DeWald. Photo by J. Zedler.

experiments suggested that both salinity and adult densities influenced egg-laying and maturation of young. Salinities of 35-58 ppt produced the largest numbers of nymphs and adults, while 150 ppt produced none. Crowding adults led to increased numbers of eggs per female.

A large number of true flies (Diptera) inhabit coastal salt marshes. Sanders (1964) listed 23 species from Mugu Lagoon in Ventura County. However, Nagano and Hogue (in press) note that he did not use specialized collecting techniques and hence missed a number of species. Assis de Moraes (1976) found 97 species at Anaheim Bay, and Nagano et al. (1981) collected 55 species at Ballona Creek.

Various species of flies (Diptera) serve as herbivores, carnivores, or decomposers in the salt marsh ecosystem. Adults as well as the aquatic larvae of the brine fly (Ephydridae) are an important food source for other insects and for fish and shorebirds.

The larvae of long-legged flies (Dolichopodidae) are common subterranean inhabitants of coastal mudflats. The adults are often seen on the surface of pools in the salt marsh where they hunt prey such as brine flies and other soft-bodied insects.

The salt-marsh mosquitos such as Aedes taeniorhynchus and A. squamiger (Culicidae), are common in southern California coastal wetlands where they breed in saline and brackish pools. The aquatic larvae can tolerate highly variable salinities because of their effective osmoregulatory systems. Because of their blood-feeding habit, they are targets for various abatement programs.

There are a number of species of moths and butterflies (Lepidoptera) that utilize plants in coastal ecosystems as a larval food source. The adult of the salt marsh measuring worm (Perizoma custodiata; Geometridae) is a conspicuous moth often observed flying about on sand dunes and salt marshes in the spring, summer and fall. Other moths restricted to the southern California coastline are the salt marsh plume moth (Agdistis americana; Pterophoridae) and the salt marsh cutworms (Lacinopolia stricta; Euxoa riversi Noctuidae).

The adult pygmy blue butterfly (Brephidium exilis; Lycaenidae) is often seen fluttering around Atriplex and Chenopodium plants. Nagano et al. (1981) found the pygmy blue to be an indicator of saline soils.

The wandering skipper (Panoquina errans; Hesperidae, Figure 40) is found along the sea coast of southern and Baja California in close association with salt grass (Distichlis spicata), which is the food of its larvae. Populations of the wandering skipper are so reduced in number that it was proposed for threatened status in 1976. Nagano is currently investigating the distribution of this species; he estimates that the largest population in the United States exists at Tijuana Estuary. Habitat destruction is the primary cause of its declining abundance.

Beetles (Coleoptera) are common inhabitants of coastal salt marshes. Leaf beetles (Chrysomelidae), darkling beetles (Tenebrionidae), and soft-winged flower beetles (Melyridae) are a few of the families common in coastal ecosystems. Minnesang (1980) found 114 species at Anaheim Bay, while Nagano et al. (1981) collected 86 species at Ballona Wetland.

A number of rove beetles (Staphylinidae) inhabit salt marshes and have been investigated by Moore (1956, 1964). Many of the species burrow in the mud and salt flats (Figure 40), and their subterranean activities must be important in aerating soils and in reversing the compaction of soils which follows off-road vehicle use of these habitats.

Ground beetles (Carabidae), especially members of the genus Bembidion, are often seen running about hunting prey on the marsh mud. The taxonomy of this

worldwide genus is still unsettled, and geographic distributions are hence uncertain. Other genera that have been collected in salt marshes include Agonum, Calathus and Bradycellus.

Tiger beetles of the genus Cicindela (Cicindelidae) are common insects on coastal mud and salt flats. The eggs, larvae and pupae are subterranean, while the adults are highly active terrestrial predators. Among their prey are the abundant kelp and brine flies, which are often nuisances to beach-goers. Some species are useful indicators of environmental quality (Nagano 1981 and in press, Nagano et al. 1981). C. hirticollis gravida, C. gabbi and C. latesignata are able to survive only in localities that have not been impacted by excessive recreation, urban expansion or other human disturbances.

This section discusses only a minute fraction of the coastal salt-marsh insect fauna. Their large numbers of species, importance in food chains and potential value as indicators of undisturbed marsh habitats suggest a great need for further study. Clearly, any attempt to describe salt marsh ecosystems thoroughly must include the insect components.

5.2 FISH[1]

Southern California wetlands are often reported to be essential nurseries for commercially important fish, which in turn depend on productivity of marsh vegetation. Such statements derive from work on the East and Gulf coasts of the United States, and conclusions are often transferred (without critical evaluation) to wetlands of the Pacific Coast. By now it should be obvious that many of the physical and vegetational features of southern California marshes differ substantially from eastern marshes, and the reader should begin to be skeptical about extrapolating conclusions about the role of wetlands in supporting fishes. As it turns out, the southern California marshes and tidal creeks are utilized by a large number of fish and invertebrate larvae, and the composition bears some resemblance to east coast wetlands. But only a single study has directly investigated the role of marshes in comparison with offshore habitats (Nordby, in prep.).

Much of the research conducted on coastal wetland fishes has emphasized adult and juvenile forms collected from bays and deep channels. Studies of fish larvae and eggs from these deeper water habitats are somewhat less numerous. Fish utilization of tidal creeks and the associated salt marsh habitat is least well known. Allen (1980), Dickert et al. (1981) and Swift and Frantz (1981) provide data on juveniles and adults in shallow channels, but only Nordby (thesis in progress) and Swift and Frantz (1981) investigated larval and egg densities within marsh tidal creeks in southern California.

Tidal Creeks and Marsh Utilization

The smaller tidal creeks found within salt marsh vegetation provide habitat for a number of smaller fish species, as well as eggs and larvae of larger fish. Fish collected within tidal creeks probably move within the marsh vegetation during high tides, and at least one species, the California killifish (Fundulus parvipinnis, Figure 41), appears to utilize the marsh in preference to creeks and channels.

Nordby (in prep.) sampled eggs and larvae of tidal creeks (2-3 m wide, <1 m deep) at Tijuana Estuary (Table 12). The larval dominants were silversides (Atherinidae), the longjaw mudsucker (Gillichthys mirabilis) and the northern anchovy (Engraulis mordax). A goby

[1]This section was researched by Chris Nordby, M. S. student, San Diego State University.

Table 12. Relative abundance of the more common taxa of fish larvae and eggs in tidal creeks, channels, and nearshore habitats of Tijuana Estuary. Data from channels and nearshore habitats spanned one year; tidal creek results are explained below. Data from Nordby, in prep.

	Larvae			Eggs		
	Tidal Creek	channel	Near-shore	Tidal Creek	Channel	Near-shore
Depth of sampling areas	1m	2m	3-11m	1m	2m	3-11m
Total number caught	96*	13,138	8,232	86*	8,844	41,127
Silversides (Atherinidae)	69.8%	5.3%	4.5%			
Topsmelt (*Atherinops affinis* Ayres)				22.1%	1.3%	
Goby complex (Gobiidae)	8.3	61.3	39.6			
Longjaw mudsucker (*Gillichthys mirabilis* Cooper)	3.2	29.5	1.1			
Northern anchovy (*Engraulis mordax* Girard)	8.3	0.9	15.1	16.3	5.3	6.0%
Queenfish (*Seriphus politus* Ayres)	6.2	1.9	19.9			
California killifish (*Fundulus parvipinnus* Girard)	2.0					
White croaker (*Genyonemus lineatus* Ayres)	1.0	0.4	16.3			
Pacific sardine (*Sardinops sagax caeruleus* Svetovidov)	1.0	0.1		3.5	12.4	11.0
Croakers (Sciaenidae)				36.0	69.2	69.9
Sanddabs (*Citharichthys* spp.)				14.0	7.5	7.9
California tonguefish (*Symphurus atricauda* Jordan & Gilbert)				6.9	1.0	
Diamond turbot (*Hypsopsetta guttulata* Girard)				1.2		
Community similarities**	20%		50%	55%		90%

*These data, from two tidal creeks sampled between April 7 and June 26, 1981, were obtained using plankton nets similar to those used in channel and nearshore habitats. The sample size is small. One of the creeks was also sampled from Dec. to Mar. with a channel net (cf. Shenker and Dean 1979), yielding an additional 864 larvae and 455 eggs. **Combining the two data sets and recalculating similarities between tidal creeks and channels gave larval similarities of 35% and eggs similarities of 45%.

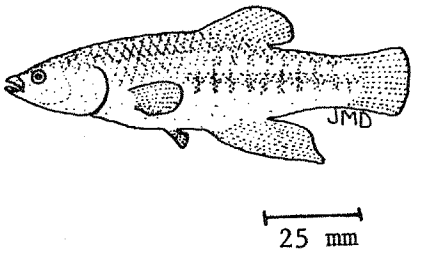


Figure 41. The California killifish (Fundulus parvipinnis) spawns and develops in salt-marsh pools. Illustration by J. DeWald.

"complex," composed of arrow gobies (Clevelandia ios), shadow gobies (Quietula y-cauda) and cheekspot gobies (Ilypnus gilberti) and staghorn sculpin (Leptocottus armatus) were less numerous. The most abundant eggs were those of the croaker family (Sciaenidae), topsmelt (Atherinops affinis), and northern anchovy (Engraulis mordax), respectively. Other egg types included the sanddabs (Citharichthys spp.), slough anchovy (Anchoa delicatissima) and Pacific sardine (Sardinops sagax caeruleus). In the process of capturing eggs and larvae, many adult and juvenile fish were collected. The most abundant were topsmelt, followed by California killifish, staghorn sculpin and longjaw mudsucker.

Larger channels at Tijuana Estuary, also sampled by Nordby, supported larval fish communities of similar species but in different abundances than in the tidal creeks. Topsmelt appeared to be the dominant pelagic fish, while the benthic species, mostly gobies, were numerous and widely distributed. Densities of larvae and eggs peaked in late winter to early spring 1981. Densities of larvae (90% gobies) were generally under $5/m^3$, but rose to a maximum of $65/m^3$ during one reproductive pulse. The absence of California killifish in the egg and larval catches is explained by its use of marsh pools for spawning (Fritz 1975). Eggs are clumped together to resist tidal removal. Larvae hatch and develop quickly in the warm pools. Their ability to withstand a wide range of salinities and temperatures (Carpelan 1961) makes it possible for killifish to inhabit the variable environment of the salt marsh. The species appears to depend on intertidal marsh pools for reproduction.

In comparing Nordby's data on tidal creeks and channels with his nearshore samples (Table 12), it becomes clear that tidal creeks provide different habitats for fish utilization. Tidal creeks were less than 20% similar to channels in their larval communities because Atherinids (most likely topsmelt), the tidal creek dominant, attaches its eggs to floating mats of Enteromorpha and other algae. After hatching, many of the larvae remain among the thick algal mats. This close association was documented by sampling creek areas with and without such mats (Nordby, in prep.). In contrast, gobies dominated the channels, and their distribution may depend on adult preferences for burrowing habitats, e.g. the substrate type, current speed and water temperature found in larger channels.

Egg composition was more similar between tidal creeks and channels, and especially between channels and nearshore habitats. While the presence of eggs in an estuary indicates some spawning function, similar egg catches nearshore make it unclear where the spawning has occurred. Nordby argues that the estuary is used by transient species (e.g. croakers, sanddabs, sardines) which come in to spawn. While such species don't depend on this habitat for reproduction, they do exploit it. In addition, larvae may encounter less predation in enclosed waters. Nordby found that copepods and chaetognaths were more abundant outside the estuary, where they were often caught in the process of eating fish larvae. Hence, enclosed waters may provide a refuge and contribute significantly to coastal water fish production.

Other Tidal Creek Studies

Swift and Frantz (1981) sampled 13 tidal creeks for adult and juvenile fishes at the highly modified Ballona Wetland. One larger channel (5 to 6 m wide x 1 to 1.5 m deep) was sampled for fish eggs and larvae. The authors found that five species comprised 85% of the total adults and juveniles collected. These were arrow goby, mosquito fish (*Gambusia affinis*), topsmelt, killifish, and longjaw mudsucker in order of relative abundance. Only 1 California halibut (a juvenile) and 12 diamond turbot (juveniles) were collected, which indicated that this wetland plays a limited role as a nursery ground, in comparison with more natural southern California wetlands (Table 13).

Plankton tows at the Ballona Wetland yielded only 278 larvae and 439 eggs (Swift and Frantz 1981). Topsmelt dominated the larval fraction, with 226 collected. Only 29 individuals, representing 5 taxa of the family Gobiidae were collected. No Sciaenid or topsmelt eggs were identified, and only two northern anchovy eggs were collected. The absence of gobiid species indicates reduced functioning of the area for these resident estuarine species.

Elkhorn Slough is north of Point Conception; however, its tidal creek fish communities share many similarities with Tijuana Estuary. Data on adult and juvenile fishes (Dickert et al. 1981) indicate that staghorn sculpin, topsmelt, northern anchovy, and arrow goby were dominant. Tidal creeks were thought to be nurseries for sculpin (Cottidae), flounders (Pleuronectidae), halibut (Bothidae), and anchovies (Engraulididae), and breeding areas for herring (Clupeidae), topsmelt, and jacksmelt (*Atherinopsis californiensis*). Unfortunately, these functions were not documented by larval or egg sampling.

Larger Embayments

Adult and juvenile fishes have been collected from embayments and larger channels from several southern California wetlands (Table 14). These data sets have three similarities: (1) Topsmelt, California killifish, staghorn sculpin, arrow goby, and anchovy species are common dominant species. (2) All of these except the anchovies are considered the main residents. (3) The commercial species most often cited as using wetland channels for nursery grounds are the California halibut (*Paralichthys californicus*) and diamond turbot (*Hypsopsetta guttulata*). White et al. (unpub.) estimated that 30,000 juvenile halibut and 17,000 juvenile turbot occurred in the Tijuana Estuary channels. However, this is an extrapolation from five sampling stations. Eggs and larvae of both species were only occasionally found in Tijuana Estuary by Nordby (in prep.), so apparently they breed offshore (cf. Haaker 1975) and enter the estuary as juveniles. Onuf et al. (1978) reviewed the literature for central and southern California fish-wetland dependency and suggested that more northerly estuaries or those of larger area have greater abundances of commercially important species. They cite only information on adult and juvenile fishes, however. The data available for larvae and eggs provide better information on the importance of southern California bays and channels for fish breeding (Table 13).

Four of the embayments examined are small, enclosed wetlands, while San Pedro Bay is a relatively open system encompassing the Los Angeles-Long Beach Harbors. Larvae in all four enclosed wetlands were dominated by a complex of goby species. San Pedro Bay had many more larval species and different dominants, probably due to its greater communication with the open ocean. The contrast between these two wetland types suggests that the smaller, more enclosed wetlands provide different habitat for fish. More recent comparisons of Cabrillo Beach (within Los Angeles Harbor) and nearby Upper Newport

Table 13. Number of taxa and dominant taxa of larval fishes and eggs collected from six southern California wetlands. Taxa are listed in decreasing order of abundance (na = data not available).

Location	Source	No. of Taxa Larvae	No. of Taxa Eggs		Dominant Taxa
Tijuana Estuary	Nordby in prep.	29	17	Larvae:	goby complex longjaw mudsucker silversides queenfish
				Eggs:	croaker Pacific sardine sanddab northern anchovy
San Diego Bay	McGowen 1977	18	4	Larvae:	goby complex
				Eggs:	deepbody anchovy diamond turbot
Newport Bay	White 1977	33	10	Larvae:	goby complex deepbody anchovy slough anchovy
				Eggs:	deepbody anchovy slough anchovy
Anaheim Bay	Leithiser 1977	22	na	Larvae:	goby complex longjaw mudsucker
				Eggs:	not identified
Ballona Wetland	Swift & Frantz 1981	16	14+	Larvae:	topsmelt
				Eggs:	not given
San Pedro Bay (west of Alamitos Bay)	Brewer 1975, 1979	45	na	Larvae: in 1975	northern anchovy blennies croakers rockfishes gobies
				Eggs:	most not identified

Table 14. Dominant species, resident species, and commercial species that use coastal wetlands for spawning or nursery grounds in southern California.

Location, source and sampling program	Dominant species	Resident species	Commercial spp. using wetland for spawning or nursery grounds
Tijuana Estuary Ford et al. (1971): 11 stations in Dec. 1970 + spring 1970 data of McIllwee (1970)	arrow goby cheekspot goby Ca. killifish topsmelt striped mullet	arrow goby Cheekspot goby Ca. killifish topsmelt striped mullet	California halibut diamond turbot kelp bass spotted sand bass barred sand bass
Upper Newport Bay Allen (1980): 3 stations, monthly from Jan. 1978–Jan. 1979	topsmelt Ca. killifish Ca. mosquitofish arrow goby deep body anchovy	topsmelt Ca. killifish Ca. mosquitofish arrow goby longjaw mudsucker	not assessed; possibly *Anchoa* sp. and diamond turbot
Anaheim Bay Lane & Hill (1975): various dates, 1971–1974	topsmelt gobies Ca. killifish deep body anchovy shiner surfperch	topsmelt Ca. killifish shiner surfperch staghorn sculpin goby species	deep body anchovy shiner surfperch California halibut diamond turbot
Ballona Wetland Swift & Frantz (1981): 13 stations, monthly from June 1980–June 1981	arrow goby Ca. mosquitofish topsmelt Ca. killifish longjaw mudsucker	arrow goby Ca. mosquitofish Ca. killifish longjaw mudsucker	diamond turbot?
Colorado Lagoon Allen & Horn (1975): 3 stations, monthly in 1973	northern anchovy topsmelt slough anchovy shiner surfperch	topsmelt shiner surfperch Ca. killifish staghorn sculpin slough anchovy	not assessed; possibly slough anchovy
Mugu Lagoon Onuf et al. (1978): 4 stations, 20 monthly samples, 1977–1978	shiner surfperch topsmelt staghorn sculpin Ca. killifish Ca. halibut diamond turbot white croaker bay pipefish longjaw mudsucker	topsmelt Ca. killifish Ca. halibut diamond turbot longjaw mudsucker grey smoothound bay blenny shadow goby	shiner surfperch Ca. halibut diamond turbot
Elkhorn Slough Nybakken et al. (1977): 4 stations, 23 months	surfperches flatfishes staghorn sculpin	not assessed	black surfperch white surfperch starry flounder & other flatfishes

Bay indicate that modified harbors do not retain the natural habitat values of less altered wetlands (Horn and Allen 1981).

The egg and larval studies (Table 13) document that southern California bays and estuaries are breeding grounds for the resident gobies and silversides, as well as for the transient croaker and anchovy families, diamond turbot, and Pacific sardines. The high density of Pacific sardine eggs in Tijuana Estuary (Table 12) was unexpected. This is the first report of the species in an enclosed estuary (about 60 ha [150 ac] of channels).

Most of the fish common to southern California bays and estuaries are low in the trophic level, consuming either plants, detritus, or small invertebrates. They are in turn fed upon by larger fish, many of which are commercially important. In fact, mudsuckers and topsmelt are commonly collected for use as fish bait.

Ecological Roles

Perhaps the best example of an estuarine resident fish is the arrow goby (Figure 42). This small fish (average adult length 5 cm; Miller and Lea 1972) resides in the shallow water of mudflats. It lives freely or in burrows with commensal hosts of one or all of the following invertebrates: ghost shrimp (*Callianassa* spp.), the echiuroid worm (*Urechis caupo*), and the blue mud crab (*Upogebia pugettensis*). Arrow gobies reached densities of up to 20/m^2 in Anaheim Bay (MacDonald 1975). This species attaches its eggs to the walls of the burrow, thus explaining its absence from egg collections when larvae are so abundant. According to MacDonald (1975), they recede into burrows at low tide and, if a film of water is present, will journey from one burrow to another. MacGinitie and MacGinitie (1949) found 28 individuals in one burrow.

Arrow gobies have a wide dietary range but preferred polychaetes and copepods in Allen's (1980) study of Newport Bay, while MacDonald (1975) describe them also as benthic carnivores and included oligochaetes and nematodes in their diet. The arrow goby is an important source of food for the California halibut and staghorn sculpin (MacGinitie and MacGinitie 1949, Brothers 1975, MacDonald 1975). Other Fish predators include white croaker (*Genyonemus lineatus*), diamond turbot, deepbody anchovy (*Anchoa compressa*), and California killifish. MacGinitie and MacGinitie (1949) suggested that arrow gobies may be an important food source for willets, godwits and curlews, which are capable of probing the burrows at low tide. Topsmelt, shadow gobies and California killifish are considered competitors as well as predators (MacDonald 1975).

The long-jaw mudsucker (Figure 43) has been collected from the burrows of the yellow shore crab (*Hemigrapsis oregonensis*). Presumably these larger-bodied gobies (up to 20 cm; Miller and Lea 1972) cannot enter the burrows of the commensal hosts of the arrow goby. Ghost shrimp and yellow shore crabs appear to be important food items (MacDonald 1975).

Staghorn sculpin (Figure 44) appear to have a preference for decapod crustaceans (Tasto 1975). The most common prey items were yellow shore crab, ghost shrimp and pea crabs (*Pinnixia* sp.) in his Anaheim Bay study. Arrow goby remains were found in 10% of the guts analyzed. The staghorn sculpin is preyed upon by the caspian tern, great blue heron, and a variety of gulls, cormorants and waterfowl (Tasto 1975).

Topsmelt (Figure 45) are opportunistic feeders. Allen (1980) found that diet was related to size and season. Individuals smaller than 5 cm preferred copepods in spring but converted to floating algae (*Enteromorpha* sp., *Chaetomorpha* sp. and *Ulva lobata*) during the summer. When algae declined in fall, the small topsmelt reverted to a copepod diet. Larger individuals (5 to 10 cm) fed

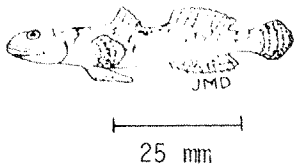


Figure 42. The arrow goby (Clevelandia ios) lives in mudflat burrows, preferaby with commensal hosts, such as ghost shrimp. Illustration by J. DeWald.

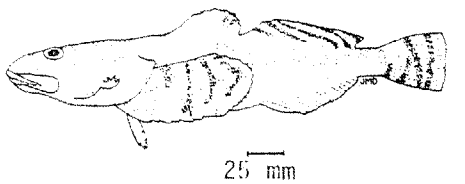


Figure 44. The staghorn sculpin (Leptocottus armatus) is a free-living benthic carnivore. Illustration by J. DeWald.

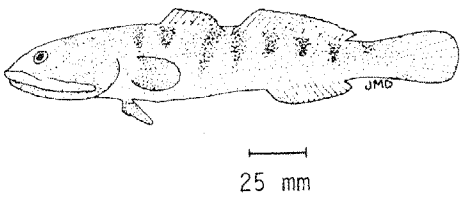


Figure 43. The long-jaw mudsucker (Gillichthys mirabilis) uses crab burrows. Illustration by J. DeWald.

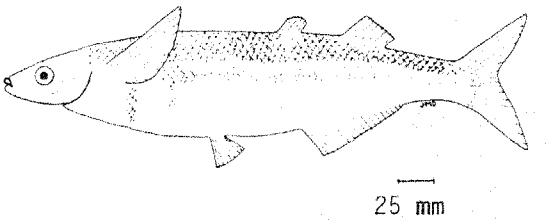


Figure 45. Topsmelt (Atherinops affinis) is closely associated with green algae, using it both as a food source and attachment site for eggs. Illustration by J. DeWald.

on algae throughout the year, and individuals over 10 cm ate plant material almost exclusively with the composition changing seasonally but including green detritus, pennate diatoms and algae. Topsmelt are rapid swimmers and utilize the entire water column as opposed to gobies and sculpins which are benthic species.

5.3 HERPETOFAUNA

Several factors limit the occurrence of reptiles and amphibians in salt marshes. Reptiles require a subterranean refuge and egg deposition sites which are above the high tide line; they cannot burrow in the compacted soils of the upper marsh and hence rely on burrowing mammals for these refuges (Hayes and Guyer 1981). Amphibians require fresh water in order for their eggs to develop, and the temporary nature of southern California streams and pools restricts the time available for aquatic stages.

The herpetofaunal study of Ballona Wetland (Hayes and Guyer 1981) identified four species which were associated with salt-marsh habitats. The Pacific treefrog (Hyla regilla) occurred within pickleweed (Salicornia virginica), but was most common in the bulrushes (Scirpus sp.), where fresh water is more likely to provide suitable breeding habitat. Two lizards were found in both the pickleweed and salt grass habitats. The southern alligator lizard (Gerrhonotus multicarinatus) and the western fence lizard (Sceloporus occidentilis) are both widespread species which eat a variety of insects and spiders. The larger and fast moving alligator lizard has also been known to take other small vertebrates as prey. In turn, these lizards are food for snakes, predatory birds, feral cats and dogs. Gopher snakes (Pituophis melanoleucus) were frequently caught in the areas above tidal inundation and were commonly associated with salt grass (Distichlis spicata). This large (up to 1.6 m) and highly mobile snake reportedly feeds on mammals, birds, eggs and other reptiles (Hayes and Guyer 1981). The species hibernates and is most active from April to June at Ballona.

While reptiles and amphibians do not appear to depend on salt-marsh habitats for their existence, the marsh vegetation provides cover and the fauna provides food. Hayes and Guyer (1981) found native vegetation to support more individuals than exotic species, perhaps because fewer insects are associated with introduced plants.

The least disturbed area of Ballona Wetland supported the largest number of herpetofaunal species and the highest relative densities of three species. This indicates that human activities and urban encroachment may impact reptiles and amphibians.

5.4 BIRDS

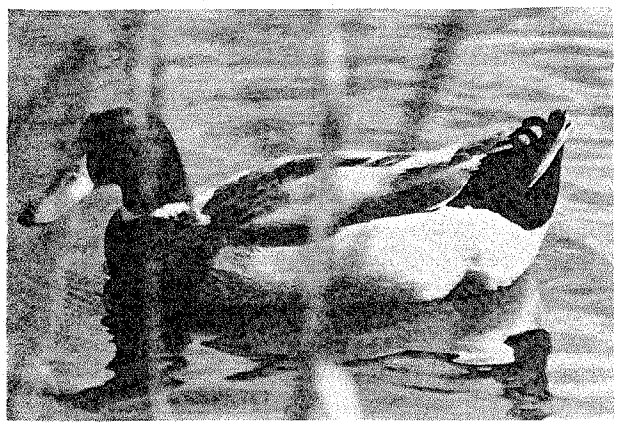
Southern California's coastal wetlands support hundreds of thousands of birds and dozens of species which migrate along the Pacific Flyway. Hence, these areas take on international importance as feeding and resting grounds for species also found from Alaska to Antarctica. Herons, egrets, gulls, terns, shorebirds, ducks, geese, coots, gallinules, and rails can be seen in southern California coastal wetlands throughout most of the year. Even small wetlands (e.g. the 8.1 ha Famosa Slough near Mission Bay) support about 40 species of water-related birds, while lists for large areas such as San Diego Bay include nearly 100 species. Habitats where disturbance is less severe support more species than areas which have been highly modified. For example, Dock and Schreiber (1981) found 70 species in the least disturbed portion of Ballona Wetland, while only 32 waterbird species used the adjacent, highly modified area (weedy pickleweed and field habitat). Similarly, Sully (1977) recorded 60 species in the less disturbed Outer Bolsa Chica Bay and only 35 species in Huntington Harbour. Some of the migrants winter in southern California (e.g.

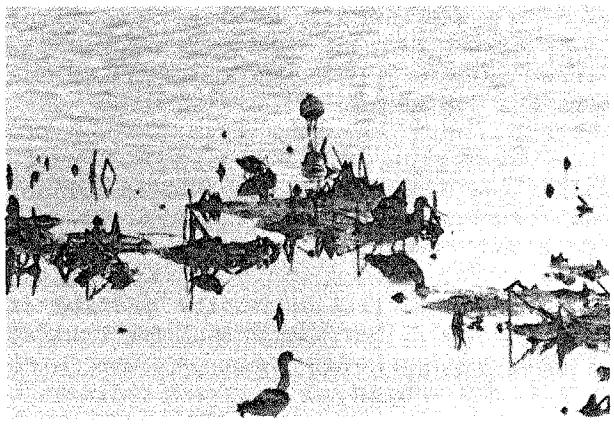
dowitchers); others go on to Central and South America. May and June are the months of least abundance of birds in southern California wetlands (Collier 1975; Figure 46); at this time most of the migrants have moved north toward their breeding grounds.

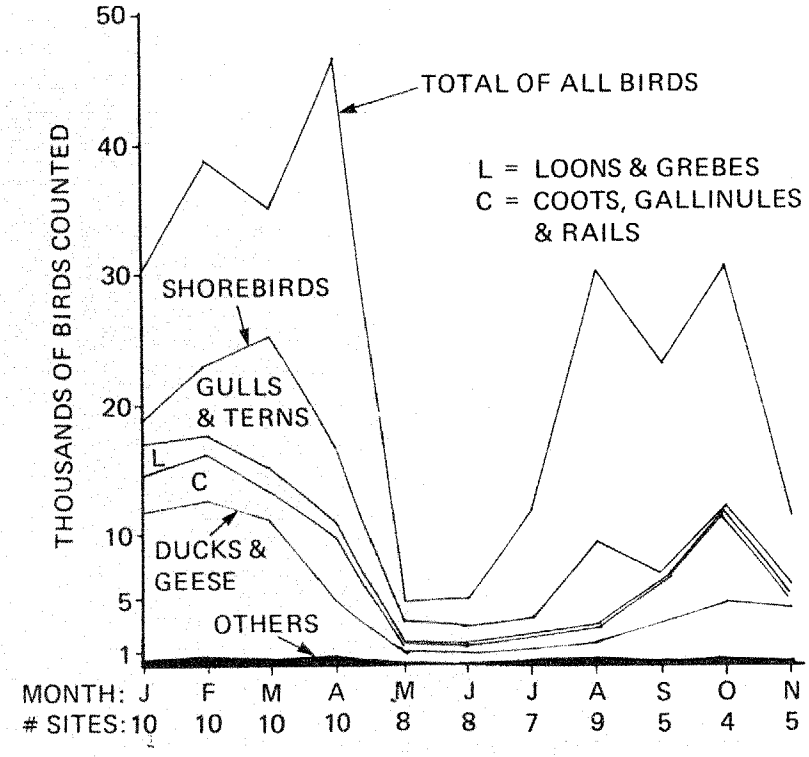
The role of the salt marsh in supporting these bird communities is not well understood. Most of the birds seem to prefer intertidal flats to marsh canopies for feeding and other activities. The intertidal flat community profile of Nybakken and Oliver (in prep.) for central California includes many of the bird species which also use southern California wetlands. In addition, Boland (1981) describes habitat utilization of Tijuana Estuary by shorebirds, Dawes (1975) discusses bird use of Los Penasquitos Lagoon, and Quammen (1980) examines the shorebird-invertebrate interactions at Upper Newport Bay and Mugu Lagoon. While the details of marsh and bird relationships are unclear, we can at least identify four ways in which marshes contribute to the support of wetland birds and suggest some ways in which birds in turn influence salt marsh communities. Marshes provide (1) bird food--either directly as animals, plants, and plant seeds which grow in the marsh or indirectly by releasing organic matter to tidal creeks which support food chains leading to carnivorous birds, (2) cover for protection against predators, (3) habitat for nesting, and (4) habitat for roosting. From the opposite perspective, birds affect marsh communities by (1) reducing densities of prey species and (2) returning nutrients to tidal waters or directly to the marsh in the form of guano. Birds provide one of the few links in the nutrient cycle which reverses the net flow of materials to the sea. Their feeding on marine fishes and defecation on land provides the potential for continuous recycling of elements which are essential for marsh plant growth. Katsuo Nishikawa of the Centro de Investigacion Cientifica y Educacion Superior de Ensenada, Baja California, is currently determining the magnitude of nutrient return via pelicans, cormorants, and other fish-eating birds. His data should suggest some interesting differences in nutrient availability for marshes adjacent to large bird-feeding areas compared to isolated marshes with little nutrient input. Perhaps we will someday understand how the artificial cormorant perches (power lines) across the San Diego River channel contribute to the high algal productivity of the upstream mudflat and marsh communities. Since cormorants release their wastes at their roosts instead of in flight, substantial nutrient additions may derive from the hundreds of birds that rest over the river channel each night.

Because birds are of great interest to the general public, they have been a major consideration in the preservation and conservation of coastal wetland habitat. Using the southern California wetlands are four Federally listed endangered birds: the California least tern (Sterna albifrons browni), the brown pelican (Pelecanus occidentalis californicus), the peregrine falcon (Falco peregrinus anatum), the light-footed clapper rail (Rallus longirostris levipes), and the State listed (endangered) Belding's savannah sparrow (Passerculus sandwichensis beldingi). The latter two species are residents of the salt marsh, and hence will be discussed in detail. Other species which are commonly seen feeding within the marsh are long billed curlews (Numenius americanus) and willets (Catoptrophorus semipalmatus). Their habitat requirements are fairly broad, whereas the rail and sparrow are closely associated with only a portion of the marsh and absolutely depend on it for survival.

The light-footed clapper rail (Figure 47) is restricted to coastal salt marshes of southern California and northern Baja California. Its Federal endangered status is linked to the widespread habitat destruction and modification which has occurred in the region. Two other subspecies of clapper rail are found in the western United States, Rallus longirostrus obsoletus in the San Francisco Bay area and R. l. yumanensis







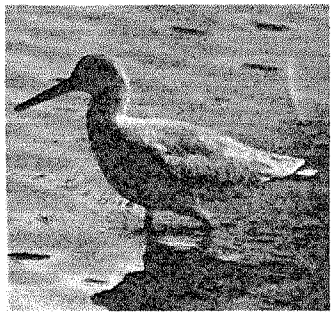


Figure 46. Counts of 92 water-bird species censused in 4 to 10 San Diego County coastal wetlands in 1970 (modified from Collier 1975). Photos by J. DeWald.

Figure 47. The endangered light-footed clapper rail (Rallus longirostris levipes) amongst tidal debris. Photo by D. Echols.

along the lower Colorado River and the Salton Sea (Jorgensen 1975).

Ongoing monitoring of the light-footed clapper rail populations in southern California (Zembal and Massey 1981) suggests that populations within a marsh can undergo dramatic changes from year to year, with some wetlands increasing in numbers of birds (e.g. Upper Newport Bay), while other populations have been eliminated (e.g. Los Penasquitos Lagoon) (Table 15). Overall, 1981 censuses revealed fewer birds than 1980, and the authors attribute some of these changes to the heavy storms which occurred prior to the 1980 nesting season.

Table 15. Census of the light-footed clapper rail in southern California (blank space = no census). From Zembal and Massey 1981.

Location	No. of pairs 1980	1981
Tijuana Estuary	26	31
South San Diego Bay Marine Reserve	3	3
Otay River Mouth	3	4
J Street Marsh		1
F Street Marsh	0	1
E Street Marsh	3	1
Sweetwater Marsh	4	5
Paradise Creek Marsh	1	2
San Diego River Marsh		3
Mission Bay Marsh	18	16
Los Penasquitos Lagoon		0
San Elijo Lagoon		5
Batiquitos Lagoon	0	0
Agua Hedionda Lagoon	1	2
Buena Vista Lagoon	0	0
Santa Margarita	0	0
Upper Newport Bay	98	66
Huntington Beach Strand		0
Bolsa Chica	0	0
Anaheim Bay	30	19
Mugu Lagoon		0
Carpinteria Marsh	16	14
Goleta Slough	0	0

It is easy to visualize the value of a cordgrass marsh for bird feeding and cover because the invertebrate fauna is abundant and the vegetation is tall and dense. However, there is a major limiting factor for nesting--namely, the fact that high tides inundate the habitat year round, and the canopy is both too short and too flexible to allow nest construction off the ground. The solution to this dilemma is a platform nest, complete with ramp, built of dead Spartina stems, which can float in situ with the rising tide. Clapper rail nest rims were 15 to 20 cm above the ground at Tijuana Estuary (Jorgensen 1975), 15 to 50 cm high at Upper Newport Bay, and 18 to 55 cm high at Anaheim Bay (Massey and Zembal 1979). Tall Spartina stands are the preferred nesting habitat and the surrounding grass stems are bent over the nest to form a canopy, perhaps to provide protection from flying predators. Incubation nests in middle and upper marsh habitats were found to be constructed closer to the ground, and sometimes without the gazebo-like canopy (Jorgensen 1975).

A second type of nest is often built shortly after hatching occurs in the nearby incubation nest. These brood nests are much less complicated in structure, sometimes consisting of floatable debris from natural and urban origins. Presumably, these are used for nocturnal roosting to avoid tidal inundation.

Nesting can occur from April to late July; clutch sizes range from one to eight (based on numbers of eggs found in nests by Jorgensen 1975 and Massey and Zembal 1979). The average size of full clutches was just over five eggs in all three study areas. Renesting following nest failure was recorded in both studies. Incubation time appears to be at least three weeks (Massey and Zembal 1979). The elaborate nesting habits of light-footed clapper rails appear to be essential for hatching success, for even with the presumed protection from inundation and predation, some nests fail to produce any young. Actual recruitment rates and causes of mortality after hatching both require further study.

The feeding habits of light-footed clapper rails have been examined by direct observation and by dissection of regurgitated pellets. Because crab parts were often found in the pellets of Tijuana Estuary rails, Jorgensen (1975) felt they were an important part of their diet. Observations of Massey and Zembal (1979) suggested a broad diet, including larval and adult insects (beetles, craneflies, and even grasshoppers), spiders, isopods, decapods (ghost shrimp), snails (Cerithidea californica and Melampus olivaceus), crabs (Pachygrapsus crassipes, Hemigrapsus oregonensis and Uca crenulata), crayfish, killifish (Fundulus parvipinnus), tadpoles (Hyla sp.), and even meadow mice (Microtus californicus), although the rail's ability to catch mice may be restricted to high tides when mice are stranded or drowned. On occasion rails have been seen to take pickleweed branch tips and to eat pith of broken cordgrass stems.

The critical factor which limits light-footed clapper rail populations is nesting habitat (Zembal and Massey 1981). Changes in rail density are roughly correlated with the quality and quantity of marsh vegetation. At Upper Newport Bay, rail populations expanded substantially following the 1969 winter storm which broke a dike, restored tidal circulation to the upper bay, and led to the doubling of salt marsh acreage in the wetland. Counts of rails have gone from 30 to 35 in 1974 to 196 birds in 1980, many of which were nesting in the newer marsh area. Upper Newport Bay supports the most robust, pure cordgrass marsh in southern California. In contrast, rail populations at Anaheim Bay have declined from a hundred or more (not an actual count) in 1974 to 60 in 1980 and 38 in 1981 (Massey and Zembal 1979, Zembal and Massey 1981). This bay has been subsiding in recent decades, perhaps due to oil pumping, and elevations where nests were found averaged 30 cm lower at Anaheim than Upper Newport Bay and Tijuana Estuary. At Los Penasquitos Lagoon, 30 birds were were noted in 1974 and none in 1981. The degree to which these decreases are due to migration rather than mortality is unknown. Movements of birds from one wetland to another have not been observed. The bird is a poor flyer, but its sudden appearance at the San Diego River marsh in 1981 suggests that it has some local mobility. Attempts to monitor rail movements by banding and telemetry are underway (Zembal and Massey 1981).

While tall, dense cordgrass is recognized as the preferred rail habitat, other marsh communities have become important in supporting the species, especially following the 1980 flooding. Zembal and Massey (1981) noted a shift to nesting locations in upper marsh habitats at both Anaheim and Upper Newport Bays. In addition, rails have been found to utilize areas of freshwater marsh, when they occur near salt marshes, for feeding, loafing, and escape from high tides. The large marsh at Upper Newport Bay supports the largest number of rails in southern California, but even small marshes can harbor nesting pairs. The small urban marshes near E, F and J Streets in Chula Vista each had a pair of rails in 1981.

Management plans for this endangered species call for improved and expanded salt marsh habitat. Toward this end, the U. S. Navy has supported marsh enhancement projects at the Tijuana Estuary sewage lagoons (Nordby et al. 1980), and the California Sea Grant College Program has sponsored research for establishing and enhancing marsh vegetation, especially cordgrass (Zedler 1981a).

Belding's savannah sparrow (Figure 48) has been recognized by the State of California as an endangered species species since 1974. Like the rail, it is dependent on salt-marsh habitat, and populations decline when marsh habitats are destroyed. Unlike the rail, it prefers the higher salt marsh habitats, and is particularly abundant in areas dominated by pickleweed (Salicornia virginica). Pickleweed is used for nesting, perching, feeding cover, and as a food source (Massey 1979).

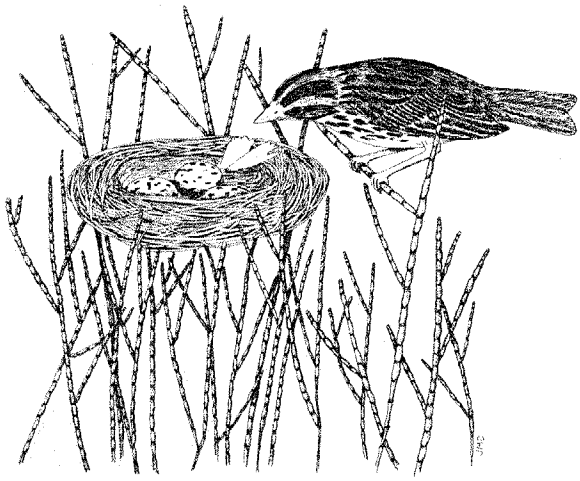


Figure 48. Belding's savannah sparrow (Passerculus sandwichensis beldingi). Illustration by J. DeWald.

Barbara Massey's long-term study of this species' breeding habits and her surveys of its distribution provide a thorough description of its natural history. Other investigators (e.g. Poulson and Bartholomew 1962) have been intrigued by the bird's physiological mechanisms which allow it to live in saline habitats. Its highly efficient urinary system concentrates chlorides up to five times levels in the serum; thus the bird can drink and process sea water, even though it lacks nasal glands which are the usual mechanism of salt excretion in marine birds.

Males of the species are easiest to see because they set up breeding territories in December or January and maintain them until mid-August. Territories are not necessarily large, perhaps because they are not relied upon for feeding, but mainly for attracting a mate and protecting the nest. Feeding often takes place away from the pickleweed habitat, which may explain the birds' ability to use non-tidal areas for breeding. Boland (pers. comm.; graduate student, UCLA) has commonly observed the sparrows taking insects along the sand dunes and intertidal flats at Tijuana Estuary, and Massey (1979) has documented feeding on insects in several habitats, and Salicornia tips and Atriplex seeds within the marsh. Massey's densest breeding area, at Anaheim Bay (Table 16), had 14 territories within an area of about 1 acre, and the smallest territory measured about 250 m^2.

Females build their first nests in March, using Salicornia twigs for the shell and usually anchoring the nest above the ground in dense vegetation. Two to four eggs are laid, one per day. However, if disturbed before the final egg is laid, the female commonly deserts the nest. Incubation seems to require about two weeks. Chicks are fed by the adults for another week or two, after which time the pair may establish a second and possibly a third brood. The latest date when parents were seen feeding young was 12 August (Massey 1979). This very long active breeding season, coupled with the species' sensitivity to disturbance, means that human activities in the upper marsh must be restricted for most of the year in order to avoid further declines in Belding's savannah sparrow populations.

5.5 MAMMALS

The study of salt marsh mammals in southern California has not progressed much beyond development of species lists. Yet there are a number of very interesting questions raised by the presence of mice, rabbits, and other small mammals in an intertidal habitat. For example, how many rodents can tolerate the salt marsh environment? How do they avoid drowning? Can they use salt marsh plants as food? Where do they obtain their drinking water?

Some of these questions are answered in Coulombe's (1965) study of Mugu Lagoon and Ballona Creek marshes. During an extensive trapping period in the early 1960's he found several residents of the intertidal marsh (Table 17). Of these, he studied the western harvest mouse (Reithrodontomys megalotis limicola),

Table 16. Breeding pairs of Belding's savannah sparrows in southern Calif. From Massey 1979.

Location	No. of Pairs 1973	1977
Tijuana Estuary	100	95
South Bay Marine Reserve		25
South Bay salt ponds		100
E Street Marsh		18
Sweetwater Marsh		40
Paradise Creek Marsh		16
Beacon Island (in Mission Bay)		4
San Diego River Marsh		70
Mission Bay Marsh		45
Los Penasquitos Lagoon	160	52
San Dieguito Lagoon	0	9
San Elijo Lagoon	17	30
Batiquitos Lagoon	0	20
Agua Hedionda Lagoon	37	16
Buena Vista Lagoon	0	5
Santa Margarita River	125	106
Upper Newport Bay	130	83
Huntington Beach		34
Bolsa Chica	40	186
Huntington Harbor & Sunset Aquatic Park		6
Anaheim Bay	125	106
Los Cerritos Wetland Channel		5
Playa del Rey	25	37
Mugu Lagoon	175	250
Ormond Beach		17
McGrath Beach State Park		12
Carpinteria Marsh	100	34
Goleta Slough	50	28

meadow mouse (Microtus californicus stephensi) and feral house mouse (Mus musculus) populations in detail. All three were frequently trapped at Ballona Creek, while feral house mice were only found in areas adjacent the marsh study site at Mugu Lagoon. Absence of Mus musculus was suggested as being important to the occurrence of the deer mouse (Peromyscus maniculatus) at Mugu Lagoon, since others have shown feral house mice to be aggressive competitors Coulombe (1965) found that the feral mice at Ballona Creek underwent radical changes in population size, from a peak in December 1962 to a crash by April 1963; a much smaller peak population occurred in October 1963 with another decline by February 1964. These data may bear on the question about drowning--perhaps the exotic species cannot avoid the problems posed by high spring tides. The native meadow mice also increased in December 1963 and crashed by July 1964. However, the western harvest mouse apparently copes very well with its intertidal environment; its populations were remarkably stable at both sites. This in turn raises the question of how they maintain their densities while other species fluctuate widely. Coulombe (1965) suggests only that social interactions may be important, since he could not establish causes of mortality for either young or adults. The diets of the two native species differ somewhat. Meadow mice are primarily herbivorous, while harvest mice are granivorous. Coulombe's feeding experiments indicated that neither species can feed on pickleweed. Mortality may have been due to the high chlorine (1.8 x sea water) or other ion concentrations, or to toxic substances such as oxalates Coulombe (1965). This also means that mice cannot use pickleweed as a source of moisture, although MacMillen (1964) found that the western harvest mouse could drink sea water and release highly concentrated urine. Coulombe (1965) suggested that dew provides a water source, but that long-term survival may be due to the mice's ability to tolerate periods of moisture stress; the meadow mouse by tolerating dehydration and the western harvest mouse by going into torpor (a temporary period of low metabolic rate).

5.6 SUMMARY OF CHAPTER 5

This chapter describes a number of animals which are uniquely adapted to life in a fluctuating environment. Although we do not understand fully how they cope with the salt marsh habitat, we realize that a number of species are dependent on the marsh and several have neared extinction as marsh habitats have been eliminated.

Table 17. Mammals noted at two southern California marshes by Coulombe (1965).

	Ballona Wetland	Mugu Lagoon
*Western harvest mouse (Reithrodontomys megalotis limicola)	resident	resident
*Ca. meadow mouse = Ca. vole (Microtus californicus stephensi)	resident	resident
*Ornate shrew (Sorex ornatus salicornicus)	resident	resident
Deer mouse (Peromyscus maniculatus)	uncertain	nearby
House mouse (Mus musculus)	resident	nearby
California ground squirrel (Citellus beecheyii beecheyii)	nearby	nearby
Botta pocket gopher (Thomomys bottae bottae)	resident	uncertain
Black-tailed jack rabbit (Lepus californicus)	resident	resident
Desert cottontail (Sylvilagus audubonii sactidiegi)	resident	nearby
Longtail weasel (Mustela frenata latirostra)	uncertain	nearby
Striped skunk (Mephitis mephitis holzneri)	nearby	nearby
Gray fox (Urocyon cinereoargenteus californicus)	nearby	nearby
Domestic cat (Felis domesticus)	nearby	nearby

What aspects of the salt marsh provide survival advantages for marsh-dependent species? Once a species can tolerate its alternating inundation and submergence pattern and can deal with a saline diet, does the salt marsh provide a refuge from competition or predation? Does the small number of species which live there result in fewer negative interactions? Does the vegetation canopy provide protection from carnivores? Or, alternatively, is the salt marsh habitat optimal from a physiological standpoint? Would this fauna do poorly outside the intertidal zone if competitors and predators were not a problem?

Some insights into these questions are provided by some of the examples in this chapter. McCloy (1979) found that hornsnails were more heavily preyed upon on mudflats than in tidal creeks. Boland (1981) found that most shorebirds utilized sand and mudflats, rather than marsh and creek habitats. Willason (1980) suggested that shelter was an important variable in determining the survival of Hemigrapsus oregonensis. The pressure of predation, then, may be lessened underneath the vegetation cover, or within steeply banked creeks where birds are less inclined to feed.

But reduced feeding by carnivores should lead to higher herbivore densities and greater survival stress for vascular plants and algae. How then does this trophic level maintain such high productivity? How do the algal mats keep up with the grazers? Again, the animals

no doubt play an important role. Their consumption of foods in the marsh and on the intertidal flats results in a rapid recycling of nutrients. The excretions of birds, fish and invertebrates can move back to the marsh with the rising tides, resulting in a net influx of nutrients, seen as imported ammonia by Winfield (1980). Rapid uptake by algal mats completes the cycle. Overall, the salt marsh is seen as an area of high productivity; its high turnover rates are driven by short food chains both in the marsh and on adjacent intertidal flats. Fertilization occurs frequently as nutrients are brought by the tides from feeding grounds to marsh "growing grounds."

While speculative, this conceptual model may explain the dependence of many animals on their salt marsh habitat. At the very least, it points out many interactions among marsh organisms and indicates the need for considering the system in its entirety when attempting to manage its wildlife. McCloy (1979) provides a good example of the unexpected results that manipulating one species can have on another. When he crowded hornsnails, adult mortality rose, dead shells accumulated, and an anemone (previously limited by substrate availability) increased four-fold in density. Such case studies make us aware of subtle interactions among populations and should cause us to be cautious about managing for individual species. One conclusion follows with certainty: altering one population will have impacts on others.

CHAPTER 6

MANAGEMENT CONSIDERATIONS

Southern California coastal marshes have been so reduced in acreage by disturbance that they are in danger of total elimination. They occur in such prime locations for developments that the threat of total elimination continues. The California Coastal Act of 1976, which followed a 1972 public initiative to preserve the coastline, clearly identifies coastal wetlands as a valuable resource. The act calls for their maintenance and, where feasible, their restoration. However, much of the wetland habitat is in private ownership, and owners are allowed reasonable use of their property. Hence, unless wetlands or easements are purchased for public management, development in and around wetlands will continue.

6.1 VIEWPOINTS OF MANAGERS

Agencies and persons entrusted with managing coastal wetlands have a difficult job. They make decisions about future developments, attempt to mitigate the effects of future alterations, protect endangered species populations, and restore disturbed areas to more desirable conditions. The groups involved in these tasks are many. At the federal level, the U. S. Fish and Wildlife Service, the U.S. Army Corps of Engineers, U.S. Environmental Protection Agency, and National Marine Fisheries became involved, along with the U.S. Navy, which owns large portions of Mugu Lagoon, Anaheim Bay and Tijuana Estuary. With the proposal to designate Tijuana Estuary as a National Estuarine Sanctuary came the involvement of the Office of Coastal Zone Management as well. At the state level, the Coastal Commission originally had the responsibility of approving or denying alterations of lands within the coastal zone; the California Coastal Conservancy is charged with aiding the implementation of wetland preservation and restoration projects; and the Departments of Fish and Game and Parks and Recreation are actively involved in resource management. Finally, local governments are responsible for developing plans and enforcing ordinances which affect coastal wetlands. Ultimately, they will grant permits for alterations within the coastal zone.

Conflicts among organizations which are concerned with the future of wetlands are bound to develop because their individual goals differ. Public health agencies, required to control disease vectors, develop plans to spray and ditch ponds where mosquitos breed. Cities desiring additional tax bases and increased tourism plan for marinas in place of marshes. Landowners hold out for maximum profits. Even within an agency, conflicts may develop if management for one species impinges on another.

6.2 DEALING WITH DISTURBANCES

The comments which follow must be viewed as emerging guidelines rather than dogma, because the data base is incomplete. Overall, I recommend that scientists be consulted before any of these ideas is applied to a specific project. The variety of wetland situations and individual constraints on planning require that each modification be considered separately, keeping in mind its relation to regional goals and concerns.

Disturbances in southern California wetlands range from large-scale, whole-ecosystem elimination to small-scale, habitat-specific alterations. Urban development, reduced tidal circulation (related to sedimentation and filling), and altered watershed hydrology are examples of the former, major disturbances. Dredging, off-road vehicle use, and mosquito control measures are more site-specific. Unraveling how these

disturbances have altered marshes is difficult and requires a combination of comparisons between more- and less-disturbed wetlands, experimental manipulations, and observations before and after disturbance events.

Urban Development

Because of their location near the ocean and natural harbors, salt marshes have been prime sites for urban development. As stated in the California Coastal Plan (Calfiornia Coastal Zone Conservation Commission 1975):

> "In southern California, 75 percent of the coastal estuaries and wetlands have been destroyed or severely altered by man since 1900. Two-thirds of 28 sizeable estuaries existing in southern California at the turn of the century have been dredged or filled."

Great losses have occurred in the vicinity of Los Angeles and San Diego. Comparison of historical maps with current wetland configurations emphasizes this point (Figure 49). In the case of Anaheim Bay, wetland habitat has largely been lost to marina development and Navy uses (Speth et al. 1976). Just north of Anaheim Bay, an 850 ha (2,100 ac) wetland has been reduced to about 209 ha (517 ac) now known as the Ballona Wetland. Of this acreage, about a fifth is a functioning wetland, about half could be easily restored by breaching dikes which prevent tidal circulation, and the remaining acreage could be restored with some difficulty (Clark 1979). In San Diego Bay, about 240 ha (600 ac) out of 800 to 1,200 ha (2,000 to 3000 ac) of intertidal sand and mudflats remain, and 10 to 15% of the original 970 ha (2,400 ac) of salt marsh are left (Browning and Speth 1973).

These major losses of wetland habitat have certainly had impacts beyond the immediate areas destroyed. Southern California's coastal wetlands were well known for their migratory waterfowl, as evidenced by the numbers of gun clubs that became established in the late 1800's and early 1900's (Speth et al. 1976). Just how much bird usage and populations have declined is immeasurable. Alternative stopping places for migratory waterfowl are rare in the region's arid landscape, and reduced coastal wetland acreage means fewer water-dependent birds.

Locally, urbanization near marshes changes water circulation and water quality, increases noise levels, and alters skylines as tall buildings replace low horizons. Marshes which were once contiguous have become dissected and interrupted by barriers to both animal movements and plant dispersal. We are just beginning to discover the importance of species movements from one wetland to another. It seems particularly important for birds to have alternative resting and feeding sites near tidal wetlands; when tides inundate their mud and sandflat habitats, shorebirds move upstream or to ponds or to drier roosting areas (Boland 1981).

If wildlife protection were the only consideration, a program of major wetland expansion and restoration would be implemented. But, recognizing the impediments to such ideological solutions and accepting the likelihood that even further elimination of wetland habitats will occur, it is important to develop recommendations which will insure the least detrimental changes. Onuf (1980) recommended that protection of natural resources be the highest priority in the management of coastal wetlands. The best available methods of protecting wildlife should be applied.

Discussions among wetland scientists and coastal planners, including a workshop specifically designed to produce guidelines for the protection of wetland resources (Onuf 1979), have led to the development of a number of recommendations for dealing with development around the periphery of wetlands. These are summarized in the following suggestions.

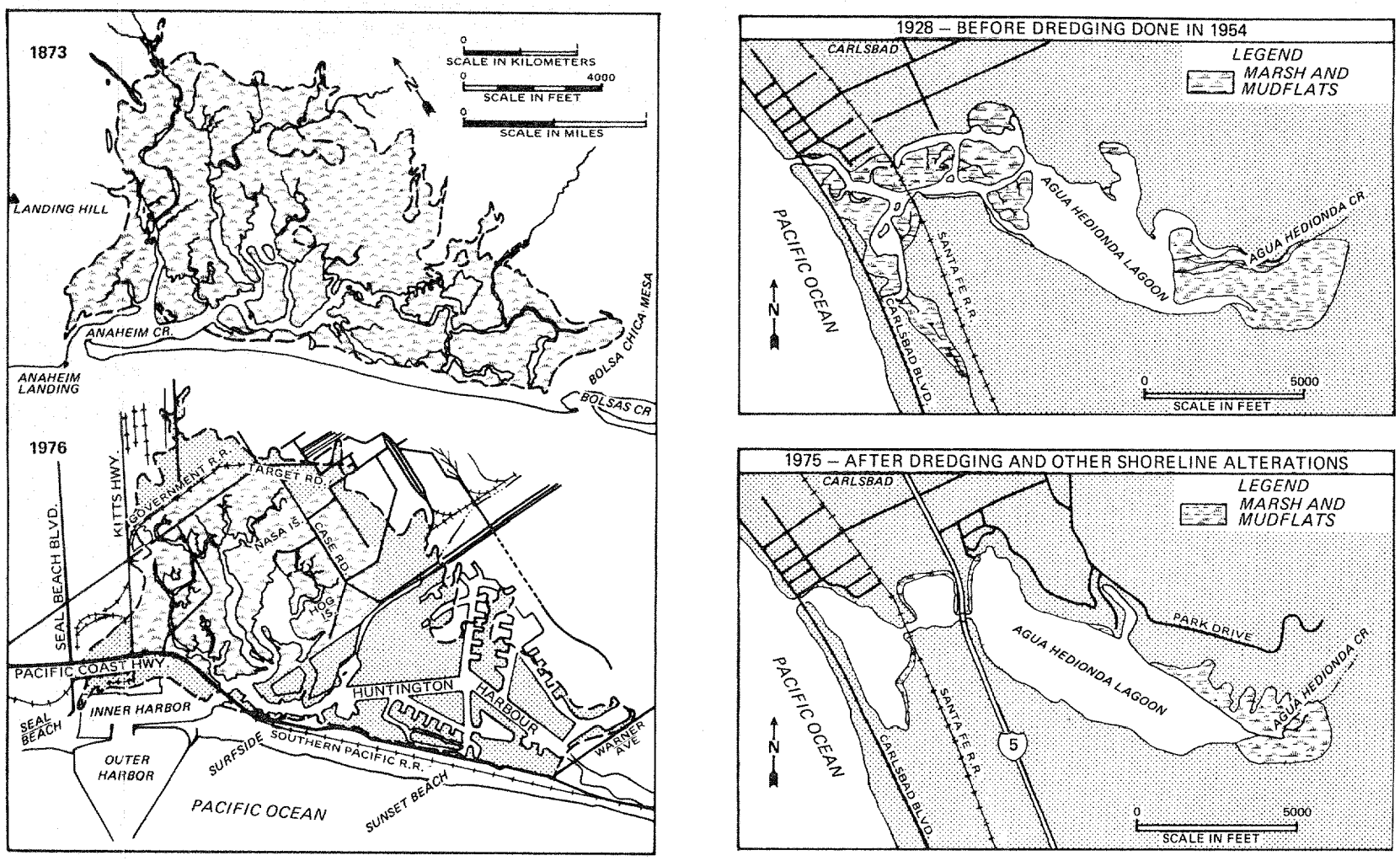


Figure 49. Two examples of wetland habitat loss in southern California. Losses at Anaheim Bay are due to marina development and Navy activities; losses at Agua Hedionda Lagoon are related to dredging to provide cooling water for a power plant. Illustrations from Bradshaw et al. (1976) and Speth et al. (1976).

* Habitats which make up the wetland complex should be contiguous with one another. If development is proposed between segments of the wetland complex, it is advisable to leave a corridor for animal movements between the larger areas.

* The wetland needs to be buffered from adjacent developments by both fencing (to exclude dogs) and vegetation (to reduce noise and visual disturbances). The width of the buffer would depend on the species using the wetland, since sensitivities may differ. More information is needed to determine the buffer requirements necessary for various birds. In general, wetlands surrounded by bluffs could have narrower buffers than wetlands surrounded by flat topography, where wildlife would be more aware of nearby activities.

* Buildings constructed near wetlands could provide a skyline that slopes toward the wetland, so that birds will have wider flight paths.

Developers should be made aware of the positive aspects of wetlands, so their natural features can be used to advantage, rather than ignored. The upper floors of hotels, motels and apartment buildings could focus on the wetland; restaurants could provide windows and other visitor-serving structures to promote their proximity to wildlife habitats and incorporate educational information into their decor. Where attempts to improve public awareness and understanding of wetland resources are made, it may be desirable to provide an opening in the buffer for direct viewing. Disturbances to wildlife may be offset by greater support for wildlife conservation.

Other educational efforts, e.g. viewing telescopes, interpretive signs, etc., could be placed near other parking lots, to minimize the area paved.

Reduced Tidal Circulation

Filling of wetland habitats to build roadbeds or buildings reduces the tidal prism and increases the probability of sand bar formation at the ocean connection, as discussed in Chapter 1. Following closure, channel water becomes stagnant, heating up, losing oxygen, fostering algal blooms, and ultimately causing fish kills and reducing foods for carnivorous birds. Closed lagoons pose management problems because nearby residents complain about bad smells and insects (midges and mosquitos) which breed in quiet water.

If, as discussed in Chapter 2, there are also local species extinctions (such as *Spartina foliosa* and associated clapper rails), closed lagoons may become less useful for the preservation of endangered species. For all of these reasons, managers and biologists have agreed that tidally flushed wetlands are preferable to frequently or persistently closed lagoons (e.g. discussions of Los Penasquitos in Metz 1978).

Furthermore, closed ocean connections prevent movement of accumulated sediments out of lagoons. With development of steep slopes upstream, southern California's highly erodible soils readily move toward the coast. In planning to protect Los Penasquitos Lagoon from further sedimentation while still allowing construction north of San Diego, the San Diego Association of Governments has called for the opening of its inlet, and further studies to determine if continuous or only periodical opening is desirable (Huff 1981).

A variety of techniques are available for dredging sediments and cutting through sand bars, from hand shovelling to use of bulldozers. A sand fluidizing system has been developed recently by Inman and Nordstrom (1977). Although only moderately successful in the Penasquitos Lagoon mouth, where cobbles slowed the movement of materials to 30 m^3/hr, the system should transport up to 100 m^3/hr of pure sand.

The following are recommendations for maintaining tidal circulation:

* Tidal prisms should not be reduced by fill within the intertidal zone.

* Unnatural sediment input should be controlled upstream. Various non-structural measures are available to reduce erosion, including prohibiting grading during the rainy season and requiring that graded slopes be stabilized prior to fall rains.

* An annual cycle of closure during the dry summer and reopening following winter rains is not necessarily unnatural for a wetland, unless that system historically maintained an open inlet. Signs of paramount concern are increasing duration of closure and decreasing water quality during the closed period.

* Tidal prisms can be increased by removing fill and dredging channels, discussed under section 4.

Altered Watershed Hydrology

Just as modification of water flow from the ocean side has a major impact on coastal wetland, so can modification of the stream drainage. Chapter 2 described how the release of reservoir water nearly eliminated a downstream salt marsh.

Unnaturally long periods of freshwater inundation killed halophytes, leached soil salts, and allowed freshwater marsh to replace salt marsh vegetation. Excessive freshwater input is detrimental to coastal wetlands. However, the impact of excluding freshwater flow is less clear. Fresh water is very important to salt marsh species because of the stimulus it provides for seed germination. Annual species and species which lack vegetative reproduction are particularly dependent on freshwater input. However, direct rainfall and local impoundments may be more important than runoff in an average year.

Experiences at the San Diego River marsh (Zedler 1981b) lead to an important recommendation:

* Management of coastal wetlands should be coordinated with management elsewhere in the watershed. The recommendation is particularly true for water and sand management, but it also holds for management of waterborne fertilizers, pesticides, and other toxins, whose impacts on southern California wetlands are little known.

Dredging

Major dredging projects have occurred in the harbors of Los Angeles, Long Beach and San Diego, and to maintain the ocean inlets to a number of lagoons. Nearly all of Agua Hedionda has been dredged to maintain a source of cooling water for the Encina Power Plant (Figure 49). Openwater fishing and boating activities have replaced marsh communities, but about 70 acres of eelgrass beds have developed where marsh used to occur (Bradshaw et al. 1976). Where dredging is not too frequent, the development of viable aquatic communities can lessen the overall reduction of natural resources.

Since dredging of existing channels is recommended as one way of increasing tidal prisms, and since dredging is necessary to create wetland habitat from filled or other upland topography, ecological guidelines are needed. Unfortunately, little research has been directed toward these needs. At least two current plans, which are attempts to mitigate losses of wetland habitat nearby, call for the construction of intertidal and subtidal habitats from higher topography. In Los Angeles Harbor, the Port District hopes to create a variety of channel, beach and marsh habitats within a five-acre parcel. On the west side of San

Diego Bay, creation of channel and intertidal marsh by removing sandy beach material is planned for a 0.7-ha (1.7-ac) area near Coronado Cays.

Concerns which should be addressed in developing guidelines for dredging include:

* It is desirable to salvage resources that are removed during the dredging process whenever possible. For example, eelgrass and marsh vegetation should be saved for future replanting or transplantation to other areas which would be enhanced by such vegetation.

* Disturbances to fish and bird life could be minimized by timing the dredging to avoid their reproductive periods. Late summer appears to be the least disruptive time for these species.

* Habitats designed to support intertidal marsh vegetation should be gently sloped (see the example of a natural profile in Figure 16, which averages 0.7%, or 0.8 m rise in 115 m). Marsh vegetation can be expected to grow from about 2 dm above mean sea level to extreme high water (cf. Figure 9).

* Habitats designed to support selected fish species should take into account their usual habitat features, especially bottom sediment types and current speeds.

Vehicle And Other Trampling Problems

The accessibility of upper marsh and transitional areas to vehicle and foot traffic subject them to denudation (Figure 30) and other abuses to the point where species become threatened by extinction (e.g. the salt marsh bird's beak). The corresponding popular view of marshlands as wastelands has likewise had a negative impact, as marsh habitats have been used as dumping grounds for refuse. It is a rare wetland that escapes deposition of a used couch, shopping cart, mattress, or garden trimmings.

In many cases, a single vehicle pass can have a lasting effect on marsh vegetation. When soils are wet, tires readily cut through root systems and bury plants in mud. The resulting ruts impede drainage when they are made across the slope, and accelerate drainage when they proceed downslope. Because marsh plants are sensitive to changes in elevation of as little as 10 cm, and because changes in drainage alter both soil moisture and salinity, such off-road vehicle use can cause dramatic changes in species composition. In addition to denudation and rut formation, off-road vehicles pose a noise problem.

Less damaging to the marsh, but still a potential cause for concern, is foot traffic. Effects of trampling pickleweed (Salicornia virginica) were studied by McIntyre (1977) in the San Diego River marsh. Both timing and intensity of trampling were investigated experimentally in winter, spring and summer of 1976. The soil and vegetation were both extremely sensitive to trampling, even in the least severe treatments. Soils became compacted and drainage was altered. Heavy trampling in winter decreased soil moisture, while trampling in summer led to higher soil moisture as the depressed topography trapped tidal water. Damage to vegetation tended to be greatest during the spring trampling experiments, which coincided with the period of greatest growth.

In developing recommendations for control of visitor usage of marsh habitats, it is important to recognize that there is an immediate impact to animals through noise and visual disturbance, and a lasting impact to soils and vegetation. Since off-road vehicles and dumping activities are detrimental,

* All wheeled vehicles should be excluded from coastal marshes.Since visitors on foot can derive

appreciation from wetland habitats, their detrimental effects should be lessened by several management practices.

* Where areas of wet soils are to be viewed, boardwalks could be constructed to confine visitors to selected routes and to prevent vegetation trampling, soil compaction and alteration of drainage.

* Traffic into the marsh should be limited during the bird nesting season.

* Spotting scopes or telescopes (perhaps the pay type) could be installed near blinds to encourage viewing from afar.

* Trails along the marsh periphery should be consolidated and marked with ropes and signs.

* Interpretive signs could instruct visitors on the detrimental effects of trampling and noise. Information should be provided in a constructive tone, rather than entirely prohibitive, to encourage a positive attitude.

Mosquito Control

Although the numbers of mosquitos which develop in southern California coastal wetlands are low, especially relative to more humid climatic regions, there is an active campaign to limit mosquito populations. This results from two factors: first, incidences of encephalitus and malaria, and second, the fact that naturally low mosquito densities make it feasible to control outbreaks. Public outcries in response to a few mosquito bites result from the usual absence of biting insects in the region and the lack of screens on many residences.

Problems in reducing vector and nuisance insect populations arise when control practices interfere with wildlife management. Ditching of ponds which provide habitat for insect larvae can interfere with drainage of the wetland as well as eliminate habitat known to be important for shorebirds. Use of pesticides may be toxic to non-target species. Spreading of oil on pond surfaces, once the common practice, often created more breeding habitat than it eliminated, as track vehicles crossed marshes and created ruts which impounded water. Current methods, at least in San Diego County, are to monitor larval densities and hand spray only those areas reaching danger levels. Where possible, mosquitofish (*Gambusia affinis*) are used as a biological control measure. However, in areas of dense vegetation they are ineffective. At San Elijo Lagoon, cattail (*Typha* spp.) vegetation is sometimes burned to open the habitat for mosquitofish.

In attempting to resolve the problems of pest control and wildlife management, the California Department of Parks and Recreation has drafted several recommendations, summarized as follows:

* Tidal flushing should be restored where man's activities have caused the impoundment of water.

* Horses should be excluded, since hoof depressions create additional mosquito habitat. Foot traffic in muddy areas should be controlled with boardwalks, as discussed in the previous section.

* Utilize mosquitofish where possible.

* Pump impounded waters at intervals to reduce larval habitat.

6.3 DEVELOPING PLANS FOR THE ESTABLISHMENT AND ENHANCEMENT OF WETLANDS

The California Coastal Conservancy is involved in a number of wetland projects throughout southern California. Each

project attempts to carry out the objectives of the Coastal Act while resolving the political, economical and ecological conflicts which surround each wetland. Scientists have been brought into the planning phase of these projects, and procedural guidelines are emerging. This section discusses several design concepts which should be considered in planning for wetland establishment or enhancement, and then summarizes the ecological capabilities and problems inherent in implementing such projects.

Ecological Concepts For Designing Wetlands

Developing priorities for the types of species and habitats which should be preserved or enhanced often leads to attempts to put values on natural resources. Those species which have become so reduced in numbers that they achieve endangered status often are given special consideration, and whole developments have been halted for concern over a single species. Yet it would seem that all native species deserve our concern, just as all natural ecosystems deserve consideration in our overall management outlook. Ehrenfeld (1976) has pointed out the fallacies of attaching various economic values to native species. Clearly, some have important economic ramifications, e.g. species valued in hunting, fishing, used in producing valuable natural products, etc. But many do not. These, he says, should be recognized for what they are: Valuable but "non-economic resources."

Because there are several endangered species which inhabit southern California coastal wetlands, much of the argument for preserving, conserving, restoring, and enhancing these wetlands focuses on selected species (Table 18). At the same time, the California Coastal Act calls for maintenance and enhancement of the wetlands as a whole. Most of the endangered species probably owe their reduced population size to reductions in habitat, so there would seem to be no conflict in managing for individual species or for wetland ecosystems. Where a functioning wetland exists, maintain its natural features. However, in designing modification of disturbed habitat and developing mitigation plans for wetland alterations, the first question is what type of habitat should be created. Should habitat for the most endangered species (if that could be determined) take precedence? Or, at the opposite extreme, should some of all types of habitats be incorporated in the "landscape design"? Like the new shopping center, should each wetland project have its fast food outlet (fly-over fish pond), supermarket (mud- or sandflat feeding ground), parking lot (roosting area), boutique (site for rare but interesting species), and department store (intertidal marsh complex)?

At this stage, some comments, but few conclusions, can be made. Critical to the discussion is understanding the optimum areal distribution of habitats for maintenance of native species. Management plans must take into account the management needs, not only of the local area, but also of the entire region and beyond. Plans should not be developed independently, without regard for other projects, but should proceed mutually with consideration of how both regional and local objectives can best be met. Once these objectives are understood, the question of area and distribution of areas can be considered. The principles of island biogeography (MacArthur and Wilson 1967) might assist the decision-making process. Generalizing from what we know about islands, we would expect big wetland areas to attract and support a larger number of species (especially birds), and that wetlands close to a source of species would have a higher probability of being colonized by those species than would distant wetlands.

Ecological Aspects of Restoring Marshes

Several plans for restoring wetlands have been proposed throughout California and a few are in the implementation phases. The biggest project in southern

Table 18. List of endangered species known to utilize southern California coastal wetlands (from USDI Fish and Wildlife Service 1980).

Common name	Scientific name	Usual habitat
American peregrine falcon	*Falco peregrinus anatum*	Over shorelines
Brown pelican	*Pelecanus occidentalis*	Deep water
Light-footed clapper rail	*Rallus longirostris levipes*	Lower marsh
California least tern	*Sterna albifrons browni*	Unvegetated flats
Belding's savannah sparrow*	*Passerculus sandwichensis beldingi*	Higher marsh
Salt-marsh bird's beak	*Cordylanthus maritimus* ssp. *maritimus*	Higher marsh

*Listed by State of California only.

California is the 32-ha (80-ac) artificial island constructed in south San Diego Bay under the direction of the Port of San Diego. This project was designed to provide wildlife habitat in an area where natural marshes have diminished substantially, while greatly reducing costs of dredge spoil disposal. Dredge spoils were pumped from a nearby marina development project to a diked area between the intake and outflow channels of the San Diego Gas & Electric Company power plant. Dredging and spoil deposition were completed in 1980, but the island is still settling to elevations suitable for the planned marsh habitat. [Determining the state of the art of California's wetland restoration projects is the topic of a February 1982 Restoration Workshop, for which proceedings will be available from the Tiburon Center for Environmental Studies, P. O. Box 855, Tiburon, California 94920.] The discussion here will focus on marsh restoration concepts and problems for southern California.

The term "restoration" is used rather loosely, since it is not clear what pre-disturbance marshes were like, either in structure or functioning. Since it is likely they were dynamic entities, as they are now, one would have to pick some arbitrary configuration to duplicate if the objective were to return marshes to their former, unimpaired condition. More realistic and more practicable is a looser application of the term, meaning to improve or enhance the marsh in ways that resemble ecologists' perception of pre-settlement wetlands. For this, less disturbed wetlands are used as a model, and the characteristics described in preceding chapters and summarized in Table 19 are the objectives.

General recommendations for restoring wetlands include:

* Enhancement plans should build on the assets of the modified wetland, maintaining those features of highest natural resource value, and planning for improvements which will require the least additional modification (because they are most likely to be successful). For example, if one type of natural community exists, it may be more feasible to expand this area (by providing suitable elevations, tidal circulation, or

Table 19. Attributes associated with more- and less-disturbed wetlands in southern California.

Wetland Feature	Less-disturbed wetlands	More-disturbed wetlands
Physiography	Small, confined to narrow river valleys, separated by coastal hills; most have small watersheds.	Size of marsh and channels has been reduced to a small fraction of original area.
Tidal flushing	Usually open to the ocean.	More frequently blocked than they would have been naturally.
Hydrology	Dominated by sea water most of the year; flooding occurs in wet years.	If closed to tides, lagoon water may become either hypersaline (>40 ppt) or brackish (0.5 to 30 ppt). Range of salinities exceeds natural conditions.
Intertidal soils	Hypersaline (>40 ppt), except during the wettest seasons or years. Soil moisture follows a seasonal pattern, caused by tides.	Can become more hypersaline or more brackish than natural, depending on lagoon hydrology. Moisture extremes are greater.
Channels	Well-circulated; good oxygen conditions, nutrients do not build up; planktonic and floating algae are diluted.	Become stagnant if closed to tides; temperatures increase; oxygen decreases; nutrients accumulate and lead to algal blooms; organic matter accumulates.
Low marsh elevations	Dominated by cordgrass (Spartina foliosa) which is used by the light-footed clapper rail.	Cordgrass is absent; rails are absent; pickleweed (Salicornia virginica) dominates.
Intermediate and upper marsh	About 12 to 14 species of vascular plants are common (See Table 4).	Some species may be eliminated by the extremes of salinity and moisture.
Transition to coastal scrub	Gradual change; depressions form salt pans which collect water and concentrate salts. Algae and insect larvae provide food for wetland consumers.	Largely gone due to development.
Primary productivity of the intertidal marsh	Vascular plants and algal mats are probably equally important in productivity; open marsh canopies allow light to penetrate to soils where algae become abundant.	Under brackish conditions, soil algae are less abundant due to denser overstory canopies. Under low-moisture conditions, soil algae are scarce.
Channel invertebrates	Abundant; high diversity of clams, crustaceans. Subject to temporary population reductions by heavy floods.	Clams and crustaceans are eliminated by stagnant conditions during lagoon closure.
Fish	Large number of fish species; breeding and nursery functions occur in channels & creeks.	Fish kills occur with stagnant conditions; only hardy species (e.g. Ca. killifish) persist.
Birds	Wide variety of water-related birds, both migrants and residents; several endangered species occur.	Fewer species but non-tidal areas are used by ducks and coots. Shorebirds are less abundant.

whatever) and allow species to spread from this source than to attempt to create a community which is absent at or near the site.

* Where two or more areas of high resource value occur within the degraded area, plans for enhancement should link the areas with a "corridor" of wetland habitat, rather than surrounding each area with development. Observations near the San Diego River suggest that birds moving back and forth between the river mudflat and Famosa Slough utilize a narrow connecting channel in preference to developed properties, even though the channel route is longer (Wetland Evaluation Class 1981).

* A modified wetland with no special features to enhance will provide more leeway in designing alterations. Determinations of the most desirable habitats to include should be made with both local and regional objectives in mind, as discussed in the previous section.

chniques for achieving specific jectives include:

* Where tidal flushing is impaired, breaching barriers are the usual first suggestion. Without tidal flushing for at least part of the year, the marsh would not develop its normal range of intertidal habitats nor support its full potential of plant and animal species. With tidal flushing, a variety of habitats, identifiable by elevation and substrate type but characterized by different degrees of submergence and salinity, becomes available for colonization.

In addition to creating the variety habitats, tides also provide many lonizers. Seeds of marsh plants, spores l colonies of algae, larvae and eggs of sh and invertebrates all disperse with e aid of tides. The earliest natural colonizers will be "opportunistic" species--species which usually have many seeds, eggs or larvae available for dispersal. Ubiquitous bacteria, fungi and protozoa, all tiny, rapidly dividing and readily floating individuals,will flourish first by feeding on the organic matter of the sediments. Algae species which grow well both in shallow water and on sediments will probably be the first producers to invade the new habitat. Among the marsh halophytes, pickleweed (Salicornia virginica), sea-blite (Suaeda californica), and perhaps annual pickleweed (Salicornia bigelovii) will arrive and begin growth, especially if the restoration site is near a well-established marsh. Species which are poorly dispersed or which are not well adapted to establish on bare substrates will be slow to invade. Artificial establishment may be desirable to speed their development.

* Where artificial marsh establishment is judged to be desirable, plantings can be undertaken, but environmental characteristics and sources of plants are both restrictive.

Elsewhere in the United States, marsh establishment has proven successful (Garbisch 1977, Environmental Laboratory 1978), although the value of the artificial marshes for wildlife takes much longer to determine. In southern California, guidelines are being developed for marsh establishment (Zedler in prep.), but no large-scale projects have been implemented.

A major consideration for large-scale artificial marsh establishment is where to obtain the plants. Many of the natural marsh habitats are protected from collecting, and the rest should be. As described here, the marshes are endangered ecosystems, and unnatural disturbances of all types should be carefully controlled. Two alternate sources, which should be explored first are: (1) other projects involving destruction of wetland vegetation, which can then be salvaged for

transplantation, and (2) commercial growers. The California Native Plant Society, Berkeley, should be contacted for information on availability of seeds and plants of native species.

* In locating material to plant, it is important to draw from local genetic resources, so that natural gene pools are not tampered with, and so that populations with the required degree of salt and drought tolerance are obtained. Plants from central and northern California have not been compared to southern California populations, so we are not certain how different they are genetically. However, the growing conditions are much more favorable in areas like San Francisco Bay, and genetic divergence is likely. Transplants and seeds should come from adjacent marshes wherever possible, and certainly not from outside the region.

* To reduce the amount of material required for transplantation or seeding, it is recommended that the marsh establishment program take place in phases. The initial planting should be done to create an on-site nursery for later plantings. This will reduce expenditures as well, because it will serve as a test plot and determine the establishment success before large areas are planted. The most suitable habitat should be selected for the nursery site so that growth is maximized (e.g. low salinity, protected from wave force, proper elevation for species to be transplanted). Plantings at two-meter intervals should allow easy harvesting of new offshoots during the following growing season. Planting in soils of higher sand content will allow easier collection.

The following constraints for marsh vegetation establishment have been identified in experimental studies near San Diego (Zedler 1981a). Where possible, solutions to the problems are suggested.

1. Hypersalinity of soils: Because the usual condition of intertidal soils is stressful, establishing plants is difficult.

Transplantation success will be greatest if planting occurs during periods of lower salinity or in places where soils are under 50 to 60 ppt. Freshwater irrigation during the early planting phase would probably be helpful, but such experiments have not been done.

2. Grazers pose serious problems to plantings on exposed soils. Several species are probably responsible for the damage to transplants, but small rodents seem to be the major offenders.

Protection of transplants from herbivores is usually required. Fences made of aviary wire (1/2-inch mesh) eliminate grazing, while fences of chicken wire (over 1-inch mesh) do not.

3. Competition with Salicornia virginica can reduce growth and expansion rates of Spartina foliosa (and probably other halophytes as well), but plantings done within established canopies experience less grazing. If grazing is likely to be a problem in the transplant area, and if Salicornia virginica has already invaded, it is advisable to leave the competing vegetation. Transplants will grow more slowly, but expensive grazing exclosures will not be required.

In designing the exact planting scheme for marsh halophytes, elevation and soil salinity are the most important features.

* For greatest success, species should be planted at their elevation of greatest natural abundance (as in Figure 9).

* Soil salinities at these elevations should not exceed those of the natural habitat (see Figure 11) for values at different times of the year). Salinities lower than those in Figure 11 would be preferable.

Plants can be obtained as seeds, sprigs or whole plants in cores of soil. The latter are the bulkiest to transport, but should have the highest survival, since the root systems are not disturbed.

* Sowing of seeds is not recommended in southern California. Experimental attempts with Spartina foliosa near existing stands of the species (with hypersaline soil) were unsuccessful.

* Seeds should be stored at 5°C (41°F) in fresh water for one month, then transplanted to 4-inch pots using greenhouse soil. Pots should be placed in standing fresh water and water levels maintained half-way up the pot. Large numbers of seeds are required, because many are not viable and germination of viable seeds is slow.

* Pots should be maintained in a sheltered environment, such as a greenhouse, which has reduced light and high humidity.

* Once seedlings are 10 to 20 cm tall, they can be transplanted to the site, preferably within grazing exclosures.

* Sprigs should be collected from mature plants which are rapidly expanding. Sandy soils are easiest to work in, and root systems are less disturbed in the digging process. Transfer sprigs to buckets of sea water for transport to the site. Plant at 2 m intervals.

* Cores can be collected using "clam guns," metal cylinders (approximately 20 cm diameter x 1 m) equipped with handles, a solid top and exhaust valve. These are pushed over the plant, into the soil about 20 cm, and extracted. Transport can be in dishpans or other flat containers. The same cylinders can be used to excavate holes for transplanting. This is very labor intensive but highly successful. The technique is recommended where few plants are available or where environmental conditions at the site are marginal for successful transplantation.

6.4 SUMMARY OF CHAPTER 6

Southern California's coastal wetlands are unique to the region, and because of a long history of disturbance, they are in danger of extinction as natural ecosystems. Restoration and enhancement, though probably possible, will be slow and difficult.

Our understanding of how various disturbances alter wetlands is incomplete, as is our knowledge of how to restore, enhance or establish wetland communities. Guidelines are emerging, and several recommendations are suggested in this chapter. However, in all cases, local wetland expertise would be invaluable in the planning and implementation processes. Each wetland has individual assets and potentials which could be identified and augmented. No single plan can deal with the variety of disturbances or the range of enhancement goals which might be proposed for a wetland.

The principal ecological concepts to be kept in mind in dealing with disturbances and planning for wetland enhancement are that:

* Tidal flushing maintains a variety of habitats which in turn support a broad range of intertidal species.

* Large units of habitat are likely to attract and maintain a larger number of species, much as large islands support more species than small islands.

* Habitats of value to mobile species should be connected by corridors to foster movements between nearby wetland habitats.

* Animals respond to movements and disturbances along the wetland periphery, and buffers (both visual and noise) are required to reduce the impacts. Species' sensitivities differ, so the width of buffers will depend on species to be protected and enhanced.

* Vegetation is damaged by vehicle and foot traffic. Access should be restricted to boardwalks above the marsh.

REFERENCES

Allen, L. G. 1980. Structure and productivity of the littoral fish assemblage of Upper Newport Bay, California. Ph.D. Dissertation, Univ. So. Calif., Los Angeles.

Allen, L. G. and M. H. Horn. 1975. Abundance, diversity and seasonality of fishes in Colorado Lagoon, Alamitos Bay, California. Estuarine Coastal Mar. Sci. 3:371-380.

Assis de Moraes, A. P. 1976. Flies (Diptera) attracted to blacklight at the Anaheim Bay salt marsh, California. M.S. Thesis, Calif. State Univ., Long Beach.

Barbour, M. G. 1970. Is any angiosperm an obligate halophyte? Am. Midl. Nat. 84:105-120.

Barbour, M. G. 1978. The effect of competition and salinity on the growth of a salt marsh plant species. Oecologia 37:93-100.

Barbour, M. G. and C. B. Davis. 1970. Salt tolerance of five California salt marsh plants. Am. Midl. Nat. 84:262-265.

Betz, F. F. 1978. Biological rhythms in the fiddler crab, Uca crenulata. M.S. Thesis, San Diego State Univ.

Boland, J. M. 1981. Seasonal abundances, habitat utilization, feeding strategies and interspecific competition within a wintering shorebird community and their possible relationships with the latitudinal distribution of shorebird species. M.S. Thesis, San Diego State Univ.

Bradshaw, J. S. 1968. The biological and ecological relationships in the Penasquitos Lagoon and salt marsh area of the Torrey Pines State Reserve Park. Contract No. 4-05094-033. Report prepared for the Calif. Division of Beaches and Parks.

Bradshaw, J., B. Browning, K. Smith and J. Speth. 1976. The natural resources of Agua Hedionda Lagoon. Coastal Wetlands Series #16. Calif. Dept. of Fish and Game, U. S. Fish and Wildlife Service.

Brenner, D., I. Valiela, C. D. van Raalte, and E. J. Carpenter. 1976. Grazing by Talorchestia longicornis on an algal mat in a New England salt marsh. J. Exp. Mar. Biol. Ecol. 22:161-170.

Brewer, G. 1975. Fish eggs and larvae in San Pedro Bay. Pages 1-12 in Report to U. S. Army Corps of Engineers on environmental investigations and analysis, Los Angeles Harbor, 1973-1975. Harbor Environmental Project, Allan Hancock Foundation. Univ. So. Calif., Los Angeles, Calif.

Brewer, G. 1979. Fish egg and larval surveys. Pages 199-226 in Ecological changes in outer Los Angeles-Long Beach Harbors following initiation of secondary waste treatment and cessation of fish cannery waste effluent. Marine Studies of San Pedro Bay, California. Part 16. Allan Hancock Foundation and the Office of Sea Grant Programs, Institute for Marine and Coastal Studies. Univ. So. Calif., Los Angeles, Calif.

Brothers, E. B. 1975. The comparative ecology and behavior of three sympatric California gobies. Ph.D. Dissertation, Univ. Calif. San Diego.

Browning, B. and J. Speth. 1973. The natural resources of San Diego Bay: their status and future. Coastal Wetlands Series #5. Calif. Dept. of Fish and Game.

California Coastal Zone Conservation Commission. 1975. California Coastal Plan. Sacramento, Calif.

Cameron, G. N. 1972. Analysis of insect trophic diversity in two salt marsh communities. Ecology 53:58-73.

Cameron, G. N. 1976. Do tides affect coastal insect communities? Am. Midl. Nat. 95:279-287.

Carpelan, L. H. 1961. Salinity tolerances of some fishes of a southern California coastal lagoon. Copeia 1961(1):32-39.

Carpelan, L. H. 1969. Physical characteristics of southern California coastal lagoons. Pages 319-334 in A. A. Castañares and F. B. Phleger, eds. Lagunas Costeras, Un Simposio. Universidad Nacional Autonoma de Mexico.

Caswell, H., F. Reed, S. N. Stephenson, and P. A. Werner. 1973. Photosynthetic pathways and selective herbivory: a hypothesis. Am. Nat. 107:645-473.

Clark, J. R. 1978. Natural science and coastal planning: the California experience. Pages 177-206 in R. G. Healy, J. S. Banta, J. R. Clark, and W. J. Duddleston, eds. Protecting the golden shore, chapter V. The Conservation Foundation, Washington, D.C.

Clark, J. 1979. Ballona wetlands study. Faculty and Master's Degree Candidates, Univ. Calif. Los Angeles Urban Planning Program.

Collier, G. 1975. The Pacific flyway. Environ. Southwest 471:3-9.

Coulombe, H. N. 1965. An ecological study of a southern California salt marsh rodent fauna. M. S. Thesis, Univ. Calif. Los Angeles.

Coulombe, H. N. 1970. The role of succulent halophytes in the water balance of salt marsh rodents. Oecologia 4:223-247.

Cox, M. C. 1969. The biology of the euryhaline water boatman Trichocorixa reticulata (Guerin-Meneville) (Hemiptera: Corixidae). M.S. Thesis, San Diego State Univ.

Crisp, D. J. 1975. Secondary productivity in the sea. Pages 71-89 in Productivity of world ecosystems. National Academy of Sciences, Washington, DC.

Darley, W. M., C. T. Ohlaman and B. B. Wimpee. 1979. Utilization of dissolved organic carbon by natural populations of epibenthic salt marsh diatoms. J. Phycol. 15:1-5.

Davis, L. V. and I. E. Gray. 1966. Zonal and seasonal distribution of insects in North Carolina salt marshes. Ecol. Monogr. 36:275-295.

Dawes, J. C. 1975. Avian ecology of Los Penasquitos Lagoon. M. S. Thesis, San Diego State Univ.

Dickert, T. G., J. Nybakken, G. M. Caillet, M. S. Foster, G. V. Morejohn, and G. Page. 1981. Wetlands management in coastal zone planning: a prototype framework for relating natural science and land use planning. Pages 37-48 in Biennial Report, Calif. Sea Grant College Program, 1978-80. Scripps Institution of Oceanography, La Jolla, Calif.

Dillingham Environmental Company. 1971. Section V: Vegetation. Pages V-1 to V-64 in An environmental evaluation of the Bolsa Chica area. Submitted to Signal Properties, Inc.

Dock, C. F. and R. W. Schreiber. 1981. The birds of Ballona. Pages Bi-1 to Bi-88 in R. W. Schreiber, ed. Biota of the Ballona region, Los Angeles County. Los Angeles County Natural History Museum Foundation.

Dunn, P. 1981. Field observations of Cordylanthus maritimus Nuttall ssp. maritimus at Tijuana Estuary, California. Draft report to the U.S. Dept. of the Navy. Naval Air Station, North Island, San Diego, Calif.

Ehrenfeld, D. W. 1976. The conservation of non-resources. Am. Sci. 64:648-656.

Eilers, H. P. 1980. Ecology of a coastal salt marsh after long-term absence of tidal fluctuation. Bull. So. Calif. Acad. Sci. 79:55-64.

Eilers, H. P. 1981. Production in coastal salt marshes of southern California. Environmental Protection Agency, National Technical Information Service. Tech. Rep. EPA-60013-81-023.

Environmental Laboratory. 1978. Wetland habitat development with dredged material: engineering and plant propagation. Dredged Material Research Program, U. S. Army Corps of Engineers Waterways Experimental Station, Vicksburg, Miss. Tech. Rep. DS-78-16.

Ford, R. F., G. McGowen and M. V. Needham. 1971. Biological inventory: investigations of fish, invertebrates and marine grasses in the Tijuana River Estuary. Pages 39-64 in Environmental impact study for the proposed Tijuana River Flood Control Channel. Tech. Rep., Ocean Studies and Engineering, Long Beach, Calif.

Foster, W. A. and J. E. Treherne. 1976. Insects of marine salt marshes: problems and adaptations. Pages 5-42 in L. Cheng, ed. Marine insects. American Elsevier Pub. Co., N.Y.

Frey, R. W. and P. B. Basan. 1978. Coastal salt marshes. Pages 101-169 in R. A. Davis, Jr., ed. Coastal sedimentary environments. Springer-Verlag, New York.

Friesen, R. D, W. K. Thomas and D. R. Patten. 1981. The mammals of Ballona. Pages M-1 to M-57 in R. W. Schreiber, ed. The biota of the Ballona region, Los Angeles County. Los Angeles County Natural History Museum Foundation.

Fritz, E. S. 1975. The life history of the California killifish, Fundulus parvipinnis Gerard, in Anaheim Bay, California. Pages 91-106 in E. D. Lane and C. W. Hill, eds. The marine resources of Anaheim Bay. Calif. Dept. of Fish and Game Fish Bull. 165.

Gallagher, J. L. and F. C. Daiber. 1974. Primary production of edaphic algal communities in a Delaware salt marsh. Limnol. Oceanogr. 19:390-395.

Gallagher, J. L., W. J. Pfeiffer and L. R. Pomeroy. 1976. Leaching and microbial utilization of dissolved organic carbon from leaves of Spartina alterniflora. Estuarine Coastal Mar. Sci. 4:467-471.

Garbisch. E. W., Jr. 1977. Recent and planned marsh establishment work throughout the contiguous United States: a survey and basic guidelines. Environmental Effects Laboratory, U.S. Army Corps of Engineers Waterways Experimental Station. Vicksburg, Miss. Contract Rep. D-77-3.

Haaker, P. L. 1975. The biology of the California halibut Paralichthys californicus (Ayres) in Anaheim Bay. Pages 137-152 in E. D. Lane and C. W. Hill, eds. The marine resources of Anaheim Bay. Calif. Dept. of Fish and Game Fish Bull. 165.

Haines, E. B. 1979. Interactions between Georgia salt marshes and coastal waters: a changing paradigm. Pages 35-46 in R. J. Livingston, ed. Ecological processes in coastal and marine systems. Plenum Press, N.Y.

Hayes, M. P. and C. Guyer. 1981. The herpetofauna of Ballona. Pages H-1 to H-80 in R. W. Schreiber, ed. The biota of the Ballona region, Los Angeles County. Los Angeles County Natural History Museum Foundation.

Hopkinson, C. S., J. G. Gosselink and R. T. Parrondo. 1978. Aboveground production of seven marsh plant species in coastal Louisiana. Ecology 59:760-769.

Horn, M. H. and L. G. Allen. 1981. Comparison of the structure and function of estuarine and harbor fish communities in southern California [Abstract]. Estuaries 4:243.

Huff, R. J. 1981. Areawide water quality management plan: Penasquitos Lagoon watershed management plan. San Diego Association of Governments, Board of Directors Agenda Rep. No. R-26, San Diego, Calif.

Hunt, C. B. 1967. Physiography of the United States. W. H. Freeman and Co., New York.

Inman, D. L. and B. M. Brush. 1973. The coastal challenge. Science 181:20-32.

Inman, D. L. and J. D. Frautschy. 1966. Littoral processes and the development of shorelines. Pages 511-536 in Coastal engineering - Proceedings of the Santa Barbara Specialty Conference, 1965. American Society of Civil Engineers.

Inman, D. L. and C. E. Nordstrom. 1977. Opening of coastal lagoons by sand fluidization. Pages 35-39 in Ann. Rep., Univ. Calif. Sea Grant College Program, 1976-1977. Univ. Calif. IMR Ref. No. 78-101, Sea Grant Publ. No. 61, La Jolla, Calif.

Isaacs, J. 1979. Introduction. In California's coastal wetlands. Calif. Sea Grant College Program. Institute of Marine Resources, La Jolla, Calif.

Jorgensen, P. D. 1975. Habitat preferences of the light-footed clapper rail in Tijuana Estuary Marsh, California. M. S. Thesis, San Diego State Univ.

Keefe, C. W. 1972. Marsh production: a summary of the literature. Contrib. Mar. Sci. 16:163-181.

Kirby, C. J. and J. G. Gosselink. 1976. Primary production in a Louisiana Gulf Coast *Spartina alterniflora* marsh. Ecology 57:1052-1059.

Kutilek, M. J. 1968. Social behavior and feeding of the fiddler crab, *Uca crenulata* (Lockington) M.S. Thesis, San Diego State Univ.

Lane, E. D. and C. W. Hill, eds. 1975. The marine resources of Anaheim Bay. Calif. Dept. of Fish and Game Fish Bull. 165.

Leithiser, R. M. 1977. The seasonal abundance and distribution of larval fishes in Anaheim Bay, California. M. A. Thesis, Calif. State Univ., Long Beach.

Lohmar, J. M., K. B. Macdonald and S. A. Janes. 1980. Late Pleistocene-Holocene sedimentary infilling and faunal change in a southern California coastal lagoon. Quaternary Depositional Environments of the Pacific Coast, Pacific Coast Paleography Syposium 4:231-240. Pacific Section, Society of Economic Paleontologists and Mineralogists, Los Angeles, Calif.

Lopez, G. R., J. S. Levinton and L. B. Slobodkin. 1977. The effect of grazing by the detritivore *Orchestia grillus* on *Spartina* litter and its associated microbial community. Oecologia 30:111-127.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J.

MacDonald, C. K. 1975. Notes on the family Gobiidae from Anaheim Bay. Pages 117-122 in E. D. Lane and C. W. Hill, eds. The marine resources of Anaheim Bay. Calif. Dept. of Fish and Game Fish Bull. 165.

Macdonald, K. B. 1967. Quantitative studies of salt marsh mollusc faunas from the North American Pacific Coast. Ph.D. Dissertation, Univ. Calif., San Diego.

Macdonald, K. B. 1969. Quantitative studies of salt marsh mollusc faunas from the North American Pacific Coast. Ecol. Monogr. 39:33-60.

Macdonald, K. B. 1971. Variations in the physical environment of a coastal slough subject to seasonal closure [Abstract]. Page 141 in D. S. Gorsline, ed. Second National Coastal and Shallow Water Research Conference sponsored by Geography Programs, Office of Naval Research. University Press, Univ. of So. Calif., Los Angeles.

Macdonald, K. B. 1976a. The natural resources of Carpenteria Marsh: their status and future. Coastal Wetlands Series #13. Calif. Dept. of Fish and Game, U. S. Fish and Wildlife Service.

Macdonald, K. B. 1976b. The natural resources of Mugu Lagoon. Coastal Wetlands Series #17. Calif. Dept. of Fish and Game, U. S. Fish and Wildlife Service.

Macdonald, K. B. 1977a. Coastal salt marsh. Pages 263-469 in M. G. Barbour and J. Major, eds. Terrestrial vegetation of California. John Wiley and Sons, New York.

Macdonald, K. B. 1977b. Plant and animal communities of Pacific North American salt marshes. Pages 167-191 in V. Chapman, ed. Wet coastal ecosystems. Elsevier Scientific Pub. Co., N.Y.

MacGinitie, G. E. and N. MacGinitie. 1949. Natural history of marine mammals. McGraw-Hill, New York. 472 p.

MacMillen, R. E. 1964. Water economy and salt balance in the western harvest mouse, Reithrodontomys megalotis. Physiol. Zool. 37:45-56.

Mahall, B. E. and R. B. Park. 1976a. The ecotone between Spartina foliosa Trin. and Salicornia virginica L. in salt marshes of northern San Francisco Bay. I. Biomass and production. J. Ecol. 64:421-433.

Mahall, B. E. and R. B. Park. 1976b. The ecotone between Spartina foliosa Trin. and Salicornia virginica L. in salt marshes of northern San Francisco Bay. II. Soil water and salinity. J. Ecol. 64:793-810.

Mahall, B. E. and R. B. Park. 1976c. The ecotone between Spartina foliosa Trin. and Salicornia virginica L. in salt marshes of northern San Francisco Bay. III. Soil aeration and tidal immersion. J. Ecol. 64:811-820.

Manahan, D. T. 1980. Autoradiographic studies on the uptake of dissolved glycine from seawater by bivalve larvae [Abstract]. Am. Zoology. 20(4):869.

Mason, H. 1980. Techniques for creating salt marshes along the California coast. Pages 23-24 in J. C. Lewis and E. W. Bunce, eds. Rehabilitation and creation of selected coastal habitats: proceedings of a workshop. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C. FWS/OBS-80-27.

Massey, B. W. 1979. Belding's Savannah sparrow. So. Calif. Ocean Studies Consortium, Calif. State Univ. Contract. No. DACW09-78-C-0008, U. S. Army Corps of Engineers, Los Angeles District.

Massey, B. W. and R. Zembal. 1979. A comparative study of the light-footed clapper rail, Rallus longirostris levipes in Anaheim Bay and Upper Newport Bay, Orange County, California. U. S. Fish and Wildlife Service Endangered Species Office, Sacramento, Calif.

McCloy, M. J. 1979. Population regulation in the deposit feeding mesogastropod Cerithidea californica as it occurs in a San Diego salt marsh habitat. M. S. Thesis, San Diego State Univ.

McGowen, G. E. 1977. Ichthyoplankton populations in south San Diego Bay and related effects of an electricity generating station. M. S. Thesis, San Diego State Univ.

McIllwee, W. R. 1970. San Diego County coastal wetlands inventory: Tijuana Slough. State of Calif., Dept. of Fish and Game, Game Habitat Development. Unpub. rep.

McIntyre, M. B. 1977. The biotic and physical effects of trampling salt marsh (Salicornia virginica L.). M. S. Thesis, San Diego State Univ.

Metz, E. 1978. San Diego regional coastal wetlands workshop, revised draft working paper - Los Penasquitos Lagoon. Calif. Coastal Commission, San Francisco, Calif.

Miller, D. S. and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Dept. of Fish Game and Fish Bull. 157.

Miller, J. N. 1966. The present and past molluscan faunas and environments of four southern California coastal lagoons. M. S. Thesis, Univ. Calif., San Diego.

Minnesang, D. 1980. Abiotic factors influencing the number of Coleoptera taken at blacklight in a southern California salt marsh. M. S. Thesis, Calif. State Univ., Long Beach.

Moore, I. 1956. Notes of some intertidal Coleoptera with descriptions of the early stages (Carabidae, Staphylinidae, Malachiidae). Trans. San Diego Soc. Nat. Hist. 12:207-230.

Moore, I. 1964. The Staphylinidae of the marine mud flats of southern California and northwestern Baja California (Coleoptera). Trans. San Diego Soc. Nat. Hist. 13:269-284.

Moore, I. and E. F. Legner. 1972. A bit about beach beetles and habitat destruction. Environ. Southwest 445:7.

Moore, I. and E. F. Legner. 1974. Seashore entomology, a neglected fruitful field for the study of biosystematics. Insect World Digest, July-August:20-24.

Mudie, P. J. 1969. A survey of the coastal wetland vegetation north of San Diego County. Wildlife Management Admin. Report No. 70-4, Calif. Dept. of Fish and Game.

Mudie, P. J. 1970. A survey of the coastal wetland vegetation of San Diego Bay. No. W26 D25-51. Calif. Dept. of Fish and Game.

Mudie, P. J. and R. Byrne. 1980. Pollen evidence for historic sedimentation rates in California coastal marshes. Estuarine Coastal Mar. Sci. 10:305-316.

Mudie, P. J., B. Browning and J. Speth. 1974. The natural resources of Los Penasquitos Lagoon. Recommendations for use and development. Coastal Wetlands Series #7. Calif. Dept. of Fish and Game.

Mudie, P. J., B. Browning and J. Speth. 1976. The natural resources of San Dieguito and Batiquitos Lagoons. Coastal Wetland Series #12. Calif. Dept. of Fish and Game.

Murray, S. N., M. M. Littler and I. A. Abbott. 1980. Biogeography of the California marine algae with emphasis on the southern California islands. Pages 325-339 in D. M. Power, ed. The California islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, Calif.

Nagano, C. D. 1981. California coastal insects: another vanishing community. Terra 19(4):27-30.

Nagano, C. D. In press. Population status of the tiger beetles found along the sea coast of southern California. Atala.

Nagano, C. D. and J. Hogue. In press. The insects and related terrestrial arthropods of Mugu Lagoon, Ventura County, California. Interim Rep. Tech. Publ. U. S. Navy, Point Mugu Naval Air Station.

Nagano, C. D., C. L. Hogue, R. R. Snelling, and J. P. Donahue. 1981. The insects and related terrestrial arthropods of the Ballona Creek region. Pages E1-E89 in R. Schreiber, ed. The biota of the Ballona region, Los Angeles County, California. Report to the Los Angeles County Dept. of Regional Planning.

Nardin, T. R, R. H. Osborne, D. J. Bottjer, and R. C. Scheidemann, Jr. 1981. Holocene sea-level curves for Santa Monica Shelf, California continental borderland. Science 213:331-333.

National Oceanic and Atmospheric Administration (NOAA). 1980. Climates of the states. 2nd ed. Gale Research Co., Detroit, Mich.

Neuenschwander, L., T. H. Thorsted, Jr. and R. Vogl. 1979. The salt marsh and transitional vegetation of Bahia de San Quintin. Bull. So. Calif. Acad. Sci. 78:163-182.

Nixon, S. 1980. Between coastal marshes and coastal waters--a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. Pages 437-525 in P. Hamilton and K. Macdonald, eds. Estuarine and wetlands processes. Plenum Press, New York.

Nordby, C. In preparation. Comparative ecology of ichthyoplankton within and outside Tijuana Estuary, California. M. S. Thesis, San Diego State Univ.

Nordby, C., J. Zedler, P. Williams, and J. Boland. 1980. Coastal wetlands restoration and enhancement: final report. U. S. Dept. of the Navy, Naval Air Station, North Island, San Diego, Calif.

Nordstrom, C. E. and D. L. Inman. 1973. Beach and cliff erosion in San Diego County, California. Pages 125-132 in A. Ross and R. Dowles, eds. Studies of the geology and geological hazards of the greater San Diego area, California. San Diego Association of Geologists Field Trip Guidebook.

Nybakken, J. and J. Oliver. In preparation. The ecology of intertidal flats of central California: a community profile. U.S. Fish and Wildlife Service, Office of Biological Services.

Nybakken, J., G. Cailliet and W. Broszukow. 1977. Ecological and hydrographic studies of Elkhorn Slough, Moss Landing Harbor and nearshore coastal waters. Moss Landing Marine Laboratories, Moss Landing, Calif.

Odum, E. P. 1971. Estuarine ecology. Pages 352-362 in Fundamentals of ecology. W. B. Saunders, Philadelphia, Penna.

Onuf, C. P., ed. 1979. Guidelines for the protection of the natural resources of California's coastal wetlands: proceedings of a workshop held at Univ. Calif. Santa Barbara, 24-26 May 1979. California Coastal Commission, San Francisco, Calif.

Onuf, C. P. 1980. Science and plans: California's coastal wetlands. Coastal Zone '80. Am. Soc. Civil Engr., New York.

Onuf, C. P. Unpublished. Demography and production of Salicornia virginica L. in a southern California salt marsh.

Onuf, C. P, M. L. Quammen, G. P. Shaffer, C. H. Peterson, J. W. Chapman, J. Cermak, and R. W. Holmes. 1978. An analysis of the values of central and southern California coastal wetlands. Pages 189-199 in P. W. Greeson, J. R. Clark and J. E. Clark, eds. Wetlands functions and values: the state of our understanding. American Water Resources Assoc., Minneapolis, Minn.

Onuf, C. P., R. W. Holmes and C. H. Peterson. 1981. Coastal wetlands management: application of biological criteria. Pages 61-63 in California Sea Grant College Program 1978-1980 Biennial Report. Institute of Marine Science, La Jolla, Calif.

Pamatmat, M. M. 1968. Ecology and metabolism of a benthic community on an intertidal sand flat. Int. Rev. ges. Hydrobiol., Bd. 53, S. 211-298.

Peterson, C. H. 1975. Stability of species and of community for the benthos of two lagoons. Ecology 56:958-965.

Peterson, C. H. 1977. Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. Mar. Biol. 43:343-359.

Phleger, C. F. 1971. Effects of salinity on growth of a salt marsh grass. Ecology 52:908-911.

Phleger, F. B. 1970. Foraminiferal populations and marine marsh processes. Limnol. Oceanogr. 15:522-534.

Phleger, F. B. 1977. Soils of marine marshes. Pages 69-77 in V. Chapman, ed. Wet coastal ecosystems. Elsevier Scientific Pub. Co., New York.

Phleger, F. B. and J. S. Bradshaw. 1966. Sedimentary environments in a marine marsh. Science 154:1551-1553.

Pomeroy, L. R., K. Bancroft, J. Breed, R. R. Christian, D. Frankenberg, J. R. Hall, L. G. Maurer, W. J. Wiebe, R. G. Wiegert, and R. L. Wetzel. 1976. Flux of organic matter through a salt marsh. Pages 270-279 in M. Wiley, ed. Estuarine processes II. Academic Press, New York.

Porter, K. G. and J. D. Orcutt, Jr. 1980. Nutritional adequacy, manageability, and toxicity as factors that determine the food quality of blue-green algae for Daphnia. Pages 268-281 in W. C. Kerfoot, ed. Evolution and ecology of zooplankton communities. Special Symp. Vol. 3, Am. Soc. Limnol. Oceanogr. Univ. Press of New England, Hanover, N.H.

Poulson, T. L. and G. A. Bartholomew. 1962. Salt balance in the savannah sparrow. Physiol. Zool. 35:109-119.

Purer, E. 1942. Plant ecology of the coastal salt marshlands of San Diego County. Ecol. Monogr. 12:82-111.

Quammen, M. 1980. The impact of predation by shorebirds, benthic feeding fish and a crab on the shallow living invertebrates in intertidal mudflats of two southern California lagoons. Ph.D. Dissertation, Univ. Calif., Irvine.

Riznyk, R. Z., J. I. Edens and R. C. Libby. 1978. Production of epibenthic diatoms in a southern California impounded estuary. J. Phycol. 14:273-279.

Sanders, R. 1964. Contributions from the Los Angeles Museum. Biological Survey 38. Diptera from San Nicholas Island and Pt. Mugu, California. Bull. So. Calif. Acad. Sci. 63:21-25.

Scott, D. 1976. Quantitative studies of marsh Foraminiferal patterns in southern California and their application to Holocene stratigraphic problems. Pages 153-170 in 1st Int. Symp. on Benthonic Foraminifera of Continental Margins. Part A. Ecology and Biology, Maritime Sediments. Spec. Publ. 1.

Seapy, R. R. 1981. Structure, distribution, and seasonal dynamics of the benthic community in Upper Newport Bay, California. Calif. Dept. of Fish and Game, Sacramento, Calif. Marine Resources Tech. Rep. No. 46.

Seapy, R. R. and M. M. Littler. 1980. Biogeography of rocky intertidal macroinvertebrates of the southern California islands. Pages 307-323 in D. M. Power, ed. The California islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, Calif.

Seneca, E. D. 1974. A preliminary germination study of Spartina foliosa, California cordgrass. Wasmann J. Biol 33:215-219.

Shenker, J. M. and J. M. Dean. 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity and temporal variation. Estuaries 2:155-163.

Smalley, A. E. 1959. The growth cycle of Spartina and its relation to the insect populations in the marsh. Proc. Salt Marsh Conf., Pages 96-100. Univ. Georgia Mar. Inst.

Speth, J. W. 1969a. Status report on the coastal wetlands of southern California as of February 1, 1969. Calif. Dept. of Fish and Game.

Speth, J. W. 1969b. The fuss over coastal wetlands. Outdoor Calif. 30(4):6-7.

Speth, J. W., B. Browning and K. Smith. 1976. The natural resources of Anaheim Bay-Huntington Harbour. Coastal Wetlands Series #18. Calif. Dept. of Fish and Game, U. S. Fish and Wildlife Service, Office of Biological Services.

Stevenson, R. E. and K. O. Emery. 1958. Marshlands at Newport Bay. Allan Hancock Foundation Publications. Occasional Paper No. 20. Univ. So. Calif. Press, Los Angeles, Calif.

Sully, J. 1977. Avian uses of Huntington Harbor and Outer Bolsa Bay. M.S. Thesis, Calif. State Univ., Los Angeles.

Swift, C. C. and G. D. Frantz. 1981. Estuarine fish communities of Ballona. Pages F-1 to F-31 in R. Schreiber, ed. The biota of the Ballona region, Los Angeles County, California. Report to the Los Angeles County Dept. of Regional Planning.

Tasto, R. N. 1975. Aspects of the biology of Pacific staghorn sculpin, Leptocottus armatus Girard in Anaheim Bay. Pages 123-135 in E. D. Lane and C. W. Hill, eds. The marine resources of Anaheim Bay. Calif. Dept. of Fish and Game Fish Bull. 165.

Teal, J. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43:614-624.

Thorsted, T. H. 1972. The salt marsh vegetation of Bahia de San Quintin, Baja California, Mexico. M. S. Thesis, Los Angeles State College.

Turner, R. E. 1976. Geographic variations in salt marsh macrophyte production: a review. Contrib. Mar. Sci. 20:47-68.

U.S. Coast and Geodetic Survey (USC & GS). 1978. Tide tables for the west coast of North and South America.

USDI (U.S. Dept. of Interior) Fish and Wildlife Service. 1980. Republication of lists of endangered and threatened species and correction of technical errors in final rules. Federal Register, Part II, Vol. 45, No. 99. Pages 33768-33781.

Van Raalte, C. D., I. Valiela and J. M. Teal. 1976. Production of epibenthic salt marsh algae: light and nutrient limitation. Limnol. Oceanogr. 21:862-872.

Vedder, J. G. and D. G. Howell. 1980. Topographic evolution of the southern California borderland during late Cenozoic time. Pages 7-31 in D. M. Power, ed. The California islands. Santa Barbara Museum of Natural History, Santa Barbara, Calif.

Vogl, R. 1966. Salt marsh vegetation of Upper Newport Bay, California. Ecology 47:80-87.

Waisel, Y. 1972. Biology of halophytes. Academic Press, New York.

Warme, J. E. 1969a. Live and dead molluscs in a coastal lagoon. J. Paleontol. 43:141-150.

Warme, J. E. 1969b. Mugu Lagoon, coastal southern California: origin sediments and productivity. Pages 137-154 in A. A. Castañares and F. B. Phleger, eds. Lagunas Costeras, Un Simposio. UNAM-UNESCO, MEXICO, D.F.

Wetland Evaluation Class. 1981. The Famosa Slough Channel: resource evaluation and recommendations for enhancement. Unpub. class report. San Diego State Univ.

White, W. S. 1977. Taxonomic composition, abundance, distribution and seasonality of fish eggs and larvae in Newport Bay, California. M. A. Thesis, Calif. State Univ. Fullerton.

White, W. S. and R. C. Wunderlich. Unpublished. The natural resources of the Tijuana Estuary. Preliminary draft. U. S. Fish and Wildlife Service.

Whitlatch, R. and S. Obrebski. 1980. Feeding selection and coexistence in two deposit feeding gastropods. Mar. Biol. 58:219-226.

Whittaker, R. H. 1975. Communities and ecosystems. 2nd ed. MacMillan Publ. Co., Inc., N.Y.

Willason, S. W. 1980. Factors influencing the biology and coexistence of Grapsid crabs, Pachygrapsus crassipes Randall and Hemigrapsus oregonensis (Dana) in a California salt marsh. M. A. Thesis, Univ. Calif. Santa Barbara.

Williams, P. 1981. Detritus utilization by Mytilus edulis. Estuarine Coastal Shelf Sci. 12:739-746.

Wilson, C. J. 1980. The effect of substrate type on the survival and recruitment of epibenthic diatoms in Mugu Lagoon, California. M. A. Thesis, Univ. Calif. Santa Barbara.

Winfield, P. 1980. Dynamics of carbon and nitrogen in a southern California salt marsh. Ph.D. Dissertation, Univ. Calif. Riverside and San Diego State Univ.

Zedler, J. B. 1975. Salt marsh community structure along an elevation gradient [Abstract]. Bull. Ecol. Soc. Amer. 56(2):47.

Zedler, J. B. 1977. Salt marsh community structure in the Tijuana Estuary, California. Estuarine Coastal Mar. Sci. 5:39-53.

Zedler, J. B. 1980. Algal mat productivity: comparisons in a salt marsh. Estuaries 3:122-131.

Zedler, J. B. 1981a. Coastal wetlands management: restoration and establishment. California Sea Grant College Program 1978-80 Biennial Report, Pages 56-60. Institute of Marine Science, La Jolla, Calif.

Zedler, J. B. 1981b. The San Diego River marsh: before and after the 1980 flood. Environment Southwest 495:20-22.

Zedler, J. B. 1981c. Arid region wetlands: susceptibility to disturbance [Abstract]. Estuaries 4:262.

Zedler, J. B. Unpublished a. Salt marsh algal composition: spatial and temporal comparisons.

Zedler, J. B. Unpublished b. Freshwater impacts in normally hypersaline marshes.

Zedler, J. B., T. Winfield and D. Mauriello. 1978. Primary productivity in a southern California estuary. Coastal Zone '78, Vol. II:649-662. American Society of Civil Engineers, New York.

Zedler, J. B., C. Nordby and P. Williams. 1979. Clapper rail habitat: requirements and improvement. Project final report to U. S. Fish and Wildlife Service.

Zedler, J. B., T. Winfield and P. Williams. 1980. Salt marsh productivity with natural and altered tidal circulation. Oecologia (Berl.) 44:236-240.

Zembal, R. L. and B. W. Massey. 1981. Continuation study of the light-footed clapper rail Rallus longirostris levipes, 1981. Final Report. Calif. Dept. of Fish and Game, Sacramento, Calif.

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16. Abstract (Limit: 200 words)

Southern California coastal wetlands are small and disturbed. The intertidal marshes are generally hypersaline, because of low rainfall and high evaporation. Tidal marshes are dominated by cordgrass (low elevations) and a variety of succulents, notably pickleweed (higher elevations). Hypersalinity reduces halophyte growth, allowing soil algae to develop and at times produce as much as the canopy vegetation.

Halophytes probably decompose before being consumed by marsh animals, thereby funneling much of their carbon to microbes, while algae are grazed directly by snails, crabs, and topsmelt. The major carnivores are fishes, shorebirds, raptors, and two endangered marsh-dependent birds.

Marsh vegetation provides a refuge and food for the native invertebrates, birds and small mammals. Some organic matter moves to consumers in intertidal creeks and flats, and tides return their wastes as nutrients which promote marsh plant growth.

Most of the region's wetland acreage has been destroyed. Management problems include continuing development, reduced tidal circulation, depauperate species lists, and the need to create marsh communities on newly exposed substrates. The constraints of hypersaline soils, scarce sources of propagules, and poor establishment ability of southern California halophytes make marsh enhancement a slow and difficult process.

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