THE ECOLOGY OF TIJUANA ESTUARY:

An Estuarine Profile

Fish and Wildlife Service

California Sea Grant College Program

U.S. Department of the Interior

U.S. Department of Commerce

THE ECOLOGY OF TIJUANA ESTUARY, CALIFORNIA: AN ESTUARINE PROFILE

by

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This report should be cited as follows:

Zedler, J. B., and C. S. Nordby. 1986. The ecology of Tijuana Estuary, California: an
   estuarine profile. U.S. Fish Wildl. Serv. Biol. Rep. 85 (7.5). 104 pp.

PREFACE

Throughout the history of wetland studies, people have argued about the similarity of wetlands — with views ranging from "all wetlands are alike" to "every wetland is unique." The truth lies somewhere in between, such that wetlands share many features (e.g., the importance of hydrology in controlling habitat type) but also have unique qualities. In this Estuarine Profile, we try to point out how the various properties of Tijuana Estuary compare to those of other estuaries within the region as well as within the nation. The designation of Tijuana Estuary as one of the National Oceanic and Atmospheric Administration's National Estuarine Sanctuaries shows that it is one of a class of ecosystems worthy of research and education, yet different enough to warrant selection as a regional type.

What makes Tijuana Estuary eligible for national recognition? It functions as a coastal water body that is influenced by both marine and river waters. It supports a range of natural plant and animal communities that are especially adapted to withstand the variable salinities that occur when sea and fresh waters mix. It has persisted through human history as a natural ecosystem that retains many of its natural qualities despite disturbance from urban and agricultural land uses. Unique to Tijuana Estuary is its international setting, with three-fourths of its watershed in Mexico; its diversity of ecological communities, which provide habitat for a variety of rare and endangered species; and its history of ecological study, with extensive data from years with and without catastrophic disturbances.

What sets California's estuaries apart from others in the nation is the degree of variability in the physical environment. During most of the year, they are marine-dominated systems, i.e., extensions of the ocean. During the winter rainy season, they may become completely fresh. In addition, there is substantial annual variation from years with no streamflow to years with major floods. The extremely variable nature of southern California's coastal habitats is not evident from short-term observation. Indeed, many visitors enjoy weeks of warm, cloud-free days and deny that we even have "weather." But from over a decade of study, there have been repeated opportunities to witness extreme events within Tijuana Estuary, ranging from catastrophic flooding to unprecedented drought. These events have in turn allowed us to identify how physical factors influence biotic communities, and to quantify the dynamics of estuarine organisms as they respond to environmental extremes.

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CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimenters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m²)	10.76	square feet
square kilometers (km²)	0.3861	square miles
hectares (ha)	2.471	areas
liters (l)	0.2642	gallons
cubic meters (m³)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	$1.8(°C) + 32$	Fahrenheit degrees

U.S. Customary to Metric

Multiply	By	To Obtain
inches (in)	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft²)	0.0929	square meters
acres	0.4047	hectares
square miles (mi²)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft³)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees	$0.5556(°F - 32)$	Celsius degrees

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CHAPTER 1

INTRODUCTION — AN OVERVIEW

The story of Tijuana Estuary is complex. Ecologically, it has been influenced by its highly variable environment. Historically, it has shifted from a natural to a highly modified system. Politically, its fate has been hotly debated and competing interests continue to influence its management.

This is the first attempt to synthesize and interpret a rapidly growing data base on the estuary's diverse biota — its vegetation, algae, birds, fishes, and invertebrates. Because so many changes have occurred in response to recent catastrophic events, we describe how each aspect of the estuary appeared before 1980 and how it has responded to several perturbations. The experimental tests of these cause-effect relationships have not been completed, and there is little reason to expect that environmental conditions have stabilized or that new types of disturbances won't occur. Thus, this profile should be viewed as a stage in the process of understanding Tijuana Estuary. Like the estuary itself, our knowledge is continuously evolving.

1.1 THE INTERNATIONAL SETTING

Tijuana Estuary is entirely within San Diego County, California, although three-fourths of its watershed is in Mexico (Figure 1). The Tijuana River originates in the mountains of Baja California. Water from the United States portion of its watershed flows down Cottonwood Creek and joins the Tijuana River in Mexico. The river then crosses the border just north of the city of Tijuana, Baja California.

On old maps, Tijuana Estuary is called Oneonta Lagoon or Slough. The Tijuana River, which feeds it, has been variously called Rio Tecate, Rio Tiajuana, Tia Juana River, and Tiajuana River. In 1968, the U.S. Board on Geographic Names approved the name Tijuana River (D. Orth, Executive Secretary, U.S. Board on Geographic Names, letter). Somewhat later, the name Tijuana began to replace Oneonta, but not everyone recognizes the term "Tijuana Estuary." A number of scientists still doubt that it qualifies as an estuary. Yet, this southwesternmost estuary of the continental United States is not only a "coastal water body that is substantially diluted by fresh water" (Pritchard 1967), but one of national and international significance.

As discussed throughout this profile, the estuary is very much a function of its watershed. The land uses and management practices on both sides of the border greatly influence the quantity and quality of water entering Tijuana Estuary. Thus, it is important to characterize the regional environmental conditions that have shaped and continue to shape this international estuary (Chapter 2 and Chapter 3, respectively).

1.2 ESTUARY TYPE CLASSIFICATION

Pritchard (1967) developed an estuarine classification scheme based on geologic origin and physiography. In this frame of reference, Tijuana Estuary is very much like most of the world's estuaries, because it is a flooded river valley, also known as a coastal plain estuary. As sea level rose during the last postglacial period, marine waters submerged the Tijuana River valley. Sediments that were brought downstream from the watershed spread out between the coastal mountains to create a small but well-defined coastal plain (Figure 2). The action of wind and waves gradually built up a sandbar and dune system parallel to the coast, and formed a semienclosed body of water. The area where marine waters are intermittently mixed with fresh water from Tijuana River is a small estuary immediately adjacent to the coast.

In other respects, Tijuana Estuary is very different from most of the world's estuaries. It does not fit well within the salinity characterization

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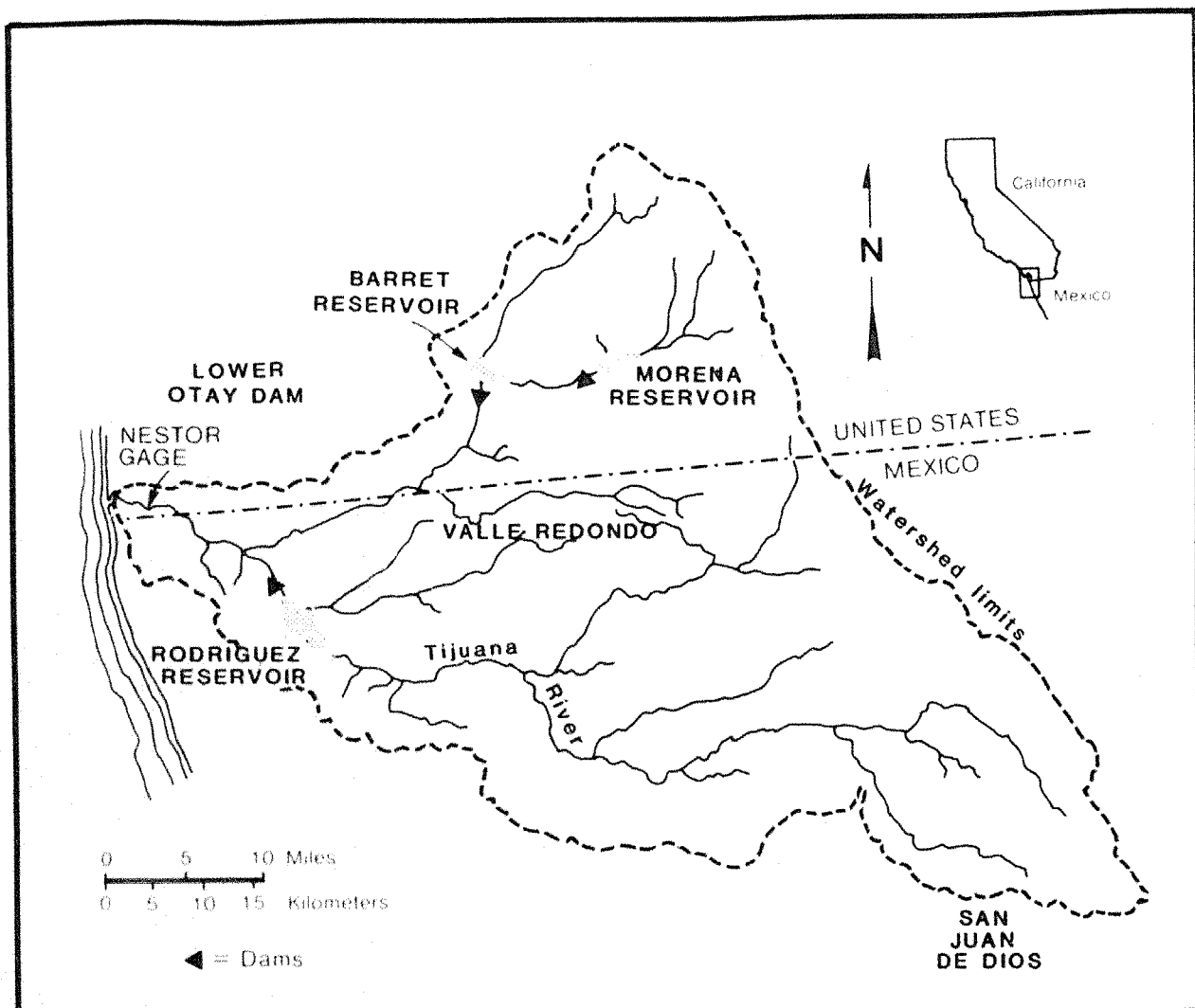
Figure 1. Location of Tijuana Estuary and map of watershed. Stations are indicated where rainfall and precipitation were measured (from IBWC 1983).

schemes that have been developed to describe estuarine embayments (Davis 1978). Estuaries can be divided into salt-wedge (river-dominated), partially mixed (salinity gradient downstream), or vertically homogeneous (brackish water throughout) types. They can also be distinguished by their salinity profiles as either positive (fresh water floating over saline water) or negative (warm saline water floating over cool fresh water). As we describe in Chapter 3, Tijuana Estuary is sometimes river dominated, sometimes partially mixed, and usually vertically homogeneous, although with marine, rather than brackish, water. Its vertical salinity profile can become positive or negative, depending on weather and tidal flushing conditions.

Because most of the estuary has shallow-water habitat, the wetland classification of Cowardin et al. (1979) is also applicable. The intertidal portion of the system fits within the California Province, estuarine system, intertidal subsystem, emergent wetland class, persistent subclass, dominated by common pickleweed (Salicornia virginica) and Pacific cordgrass (Spartina foliosa).

Tijuana Estuary is a highly variable system that may best be termed an "intermittent estuary." During the winter wet season, its waters are diluted by rainfall and streamflow; during the rest of the year, it is an extension of the ocean. As streamflow and wetland soil salinities suggest (Chapter 3), it may be one of the nation's most variable estuaries.

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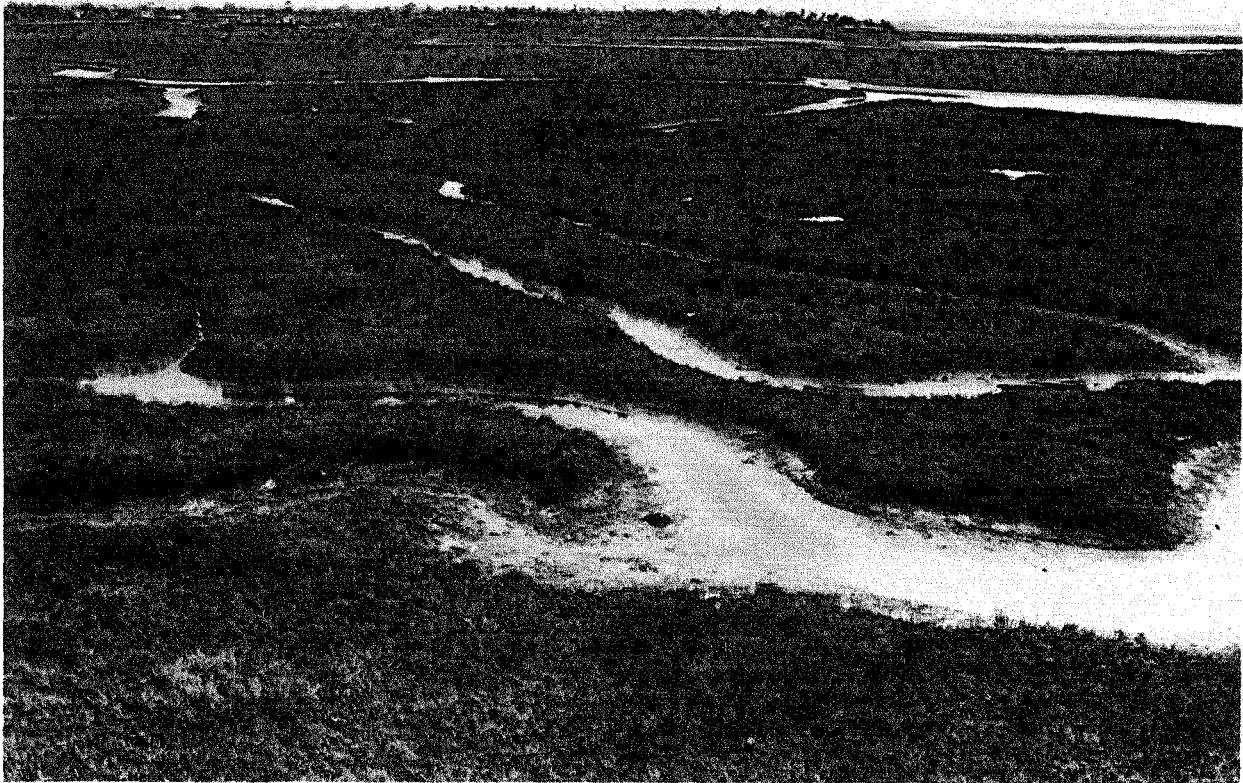
Figure 2. The northern arm of Tijuana Estuary, looking east (photo by D. Fink).

1.3 THE ESTUARINE HABITATS

Tijuana Estuary is a wetland-dominated estuary (Figures 2-3). There is no major embayment, but rather a series of channels and a relatively narrow ocean connection. In most years, the mouth has been open, and tidal flushing has prevailed. The intertidal area supports mostly salt marsh vegetation, while mudflats and sandflats occupy only a small fraction of the site. Inland, the upper salt marsh grades into transitional vegetation, which in turn grades into coastal scrub and chaparral.

Many features of the estuary have been substantially influenced by disturbances of both natural and human origin. Natural flooding in 1980 broadened the riverbed and changed its course. Winter storms in 1983 washed the dunes into the main channels and obliterated two salt marsh islands. In the early 1900's, sewage disposal practices led to the dredging of an east-west channel to connect the estuary to an adjacent lagoon. Dikes were later constructed to subdivide that lagoon into three wastewater receiving ponds, which were subsequently abandoned and the dikes

breached to improve tidal flushing. Gravel extraction for street and dike construction left isolated ponds within the estuary. Long-term dumping and filling altered most of the peripheral topography, and off-road vehicles denuded many roads and paths. Scars remain throughout the southern half of the estuary from former military, agricultural, and horse-raising activities. Present-day sewage spills from Mexico change the quantity, and certainly the quality, of inflowing waters.

Can any area that has experienced such extensive assaults still be considered a naturally functioning estuary? The closest we can come to answering that question is to compare it with more disturbed systems near Los Angeles and with less disturbed systems in Baja California. Tijuana Estuary ranks with the latter.

1.4 NATIONAL SIGNIFICANCE

In 1982, the National Oceanic and Atmospheric Administration (NOAA) designated Tijuana Estuary a National Estuarine Sanctuary, in recognition of its value as a research and educational resource. A long record of use in estuarine research and the

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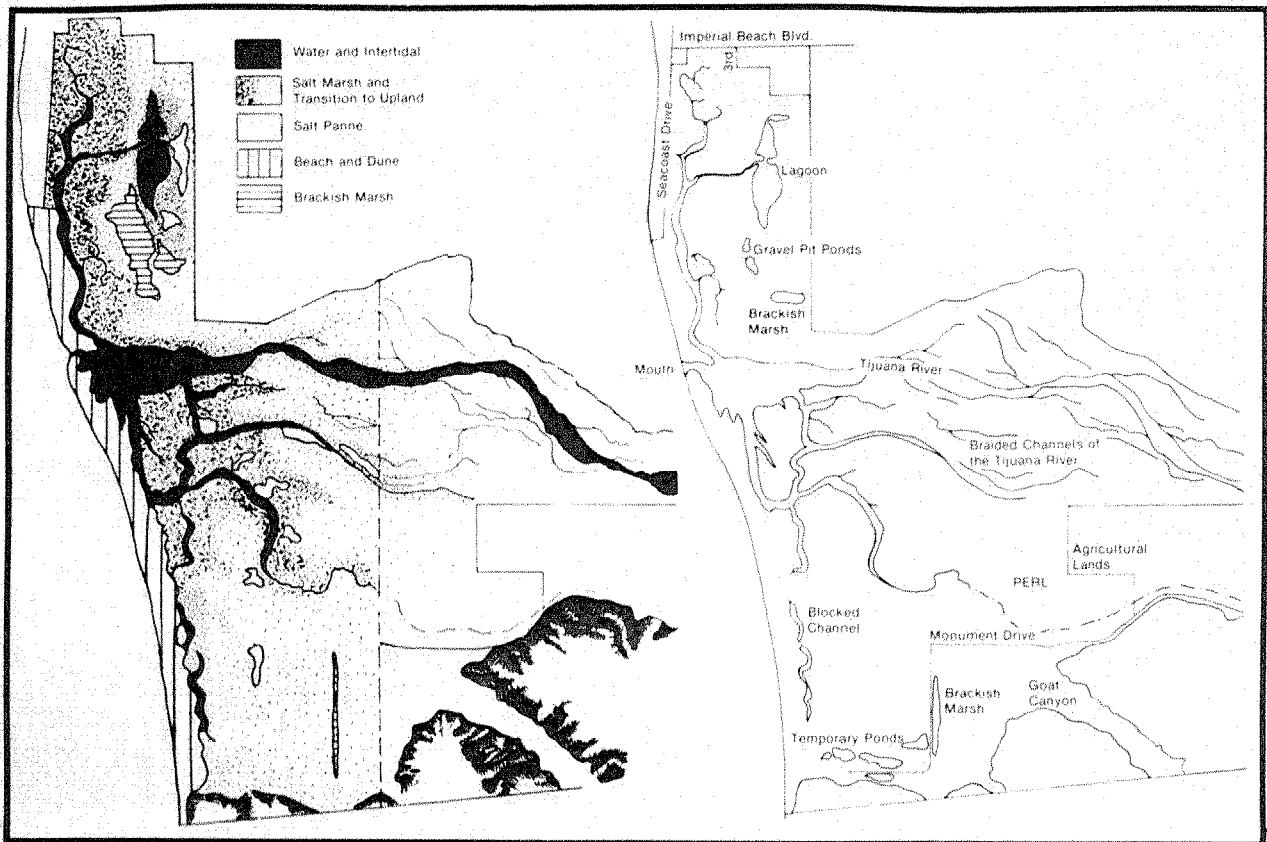
Figure 3. Maps of Tijuana Estuary showing selected habitats (from a January 1985 aerial photo) and place names used in this profile.

presence of distinctive estuarine features were essential attributes for selection. Approximately 1,024 ha were set aside for resource protection, research, interpretation, land acquisition, and facility development. Management of the sanctuary is a cooperative effort that involves many agencies and individuals (Chapter 6) in accordance with a detailed management plan (Dobbin Associates 1985). Only three of the Nation's other 14 sanctuaries are located along the Pacific coast: Elkhorn Slough on Monterey Bay, California; South Slough on Coos Bay, Oregon; and Padilla Bay in Washington.

Before its designation as a sanctuary, a large part of the estuary was purchased by the U.S. Fish and Wildlife Service for protection of endangered species and their habitat. Significant populations of the California least tern (*Sterna antillarum browni*) and the salt marsh bird's beak (*Cordylanthus maritimus* ssp. *maritimus*) remain at Tijuana Estuary. In addition, the State-listed Belding's Savannah sparrow (*Passerculus sandwichensis beldingi*) nests in the salt marsh. These and other rare and threatened species have declined in numbers as their habitats have succumbed to the pressures of development. Their persistence at Tijuana Estuary documents the importance of the area for wildlife. The plight of other species, such as the light-footed clapper rail (*Rallus longirostris levipes*), illustrates the need to enhance and maintain the area. A large population of this endangered bird inhabited the lower salt marsh of Tijuana Estuary until 1984. The story of its local extinction is detailed in Chapter 3.

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CHAPTER 2

MAJOR FACTORS THAT HAVE SHAPED THE ESTUARY

2.1 GEOLOGIC HISTORY

The geologic history of Tijuana Estuary and its adjacent coast is poorly studied. Yet it is so different from most of the Nation's estuaries that even the most general descriptions are useful. In his review of sea level and coastal morphology during the late Pleistocene, Bloom (1983a,b) characterized the Pacific Coast as "a total contrast to the trailing continental margin with coastal plains of the Atlantic and Gulf coasts. Active tectonics associated with regional strike-slip faulting characterize the California coast."

As continental drift shifted North America toward the west, a steep coastline and narrow continental shelf developed (Figure 4). Marine terraces were gradually carved along the shores. Then, in the late Cenozoic, tectonic uplift raised alluvial terraces to several hundred meters above modern sea levels; the lowest of these terraces were laid down 125,000 to 80,000 years ago (Ku and Kern 1974; Kern 1977; Lajoie et al. 1979). In some places, the youngest terraces have been thrust 40 m above current shorelines.

Because the shelf has a steep decline, Pleistocene glaciation and receding sea levels did not expose large expanses of coastal land. What is now the Tijuana River presumably cut through these terraces, although the narrow floodplain suggests that flows were not consistently large. The cut that frames Tijuana Estuary is only a few kilometers wide.

The picture emerges of a sharp, steeply inclined coast with vertically active terraces. Then, in the Holocene, a rising sea began to reclaim the exposed margins of the coastal shelf. As Bloom (1983a) goes on to say, "the last 15,000 years of California coastal evolution have been dominated by submergence coincident with deglaciation." The rivers were drowned and lagoons formed as longshore drift created sandy barriers along the coast. With flooding, most of the coastal embayments filled with sediment, and, without continuous river flow and scouring, their mouths closed between flood seasons.

The recent geologic factors that have shaped the estuary are thus the competing forces of rising sea level, which promotes inland migration of the estuary, and tectonic uplift, which reverses that trend. The location of the shore and the configuration of the mouth are additional variables that influence the size and condition of the estuary. Longshore drift is generally southward in southern California, with flows interrupted by submarine canyons. However, the precise patterns and seasonal shifts at Tijuana Estuary have not been quantified. What is clear is that catastrophic beach erosion has shifted the shoreline landward in the past few years. How much of that shift is due to recent storms and how much is a general trend due to rising sea level are yet to be determined.

The recent history of sea level rise has been summarized by Flick and Cayan (1984) and Cayan and Flick (1985). Data from 1906 to the present, taken in San Diego Bay, indicate an average rise of about 20 cm/century (Figure 5). During recurrent El Niño events, the rate of sea level rise has been even higher. The highest sea level on record occurred in January 1983, when predicted sea levels were exceeded by 26 cm due to the coincidence of El Niño, high spring tides, and a major sea storm. Still, the water levels might have been even higher if these three events had also coincided with the highest point in the 19-year tidal cycle (Cayan and Flick 1985). The future location and configuration of the shoreline will depend on both the chronic and catastrophic increases in sea level. While the former will shift estuarine habitats inland, the latter will lap away at the marine margins.

The 1904 map of Tijuana Estuary (Figure 6) provides the earliest indication of historic conditions. Three features that are clearly mapped are not evident in later photographs. First, there is
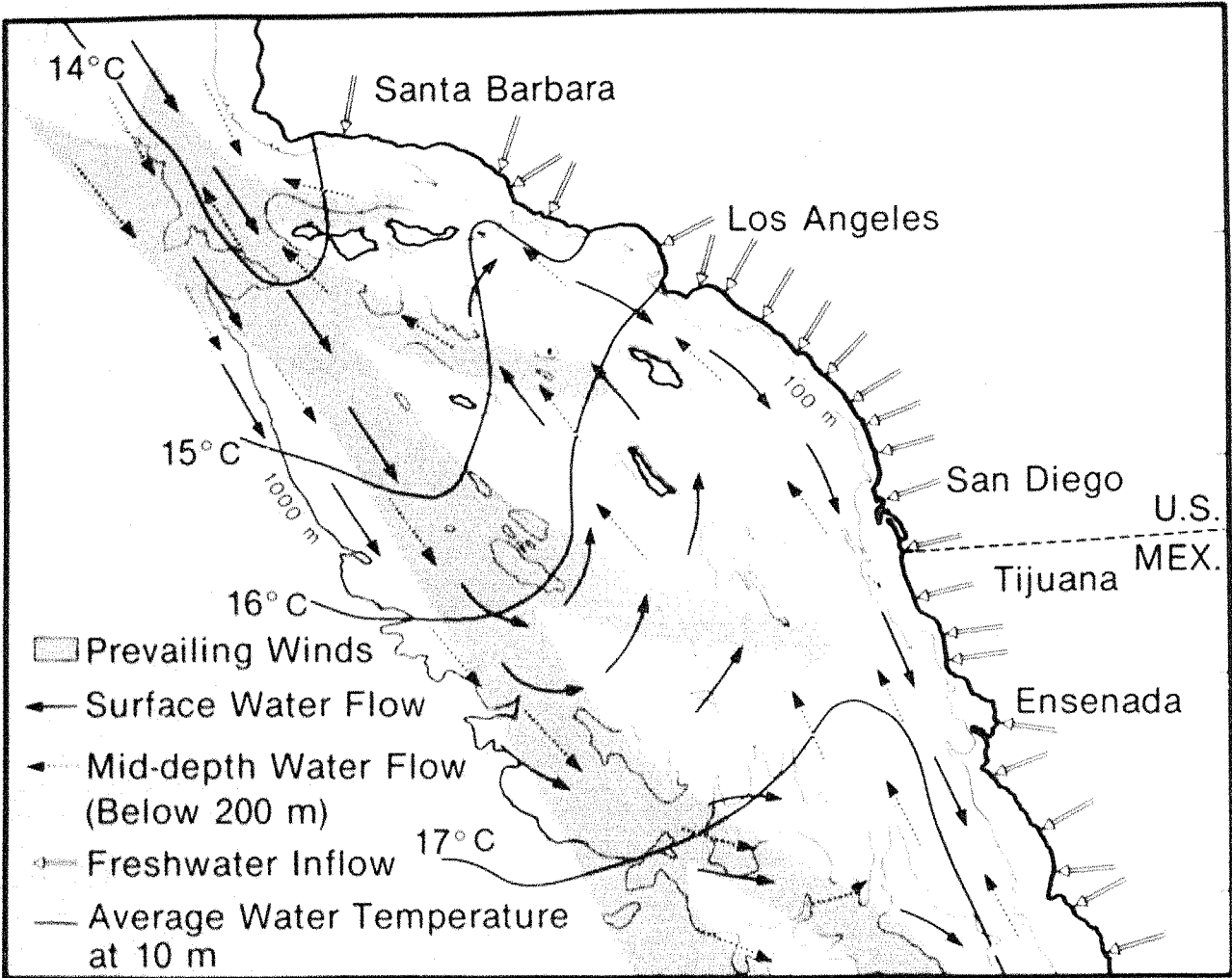
Figure 4. Nearshore patterns of bathymetry, wind, and ocean circulation (redrawn from Resources Partnership 1979).
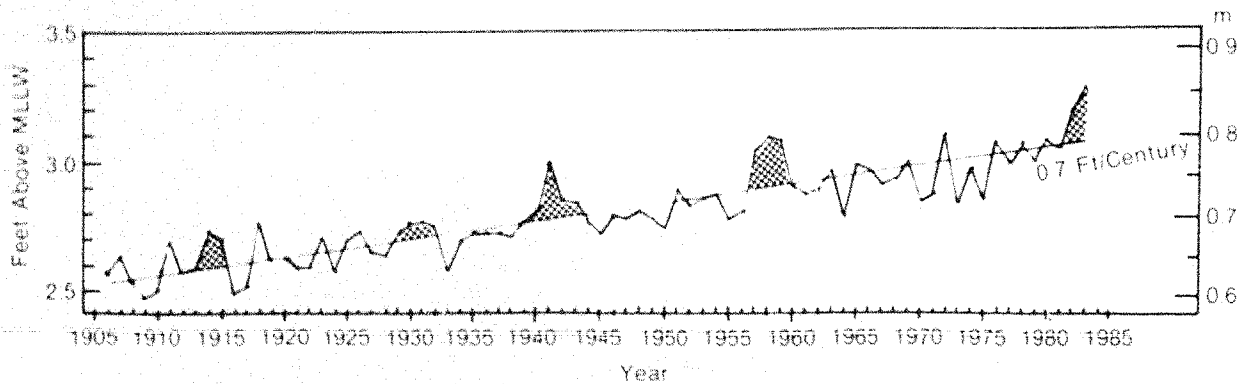
Figure 5. Data on sea level rise for San Diego Bay, 10 km north of Tijuana Estuary. Yearly mean sea level is referred to the 1960-78 datum for mean lower low water (MLLW). The linear increase is 21 cm (0.7 ft) per century. Shaded areas indicate periods of or near major El Niño episodes (reprinted with permission from Cayan and Flick 1985).
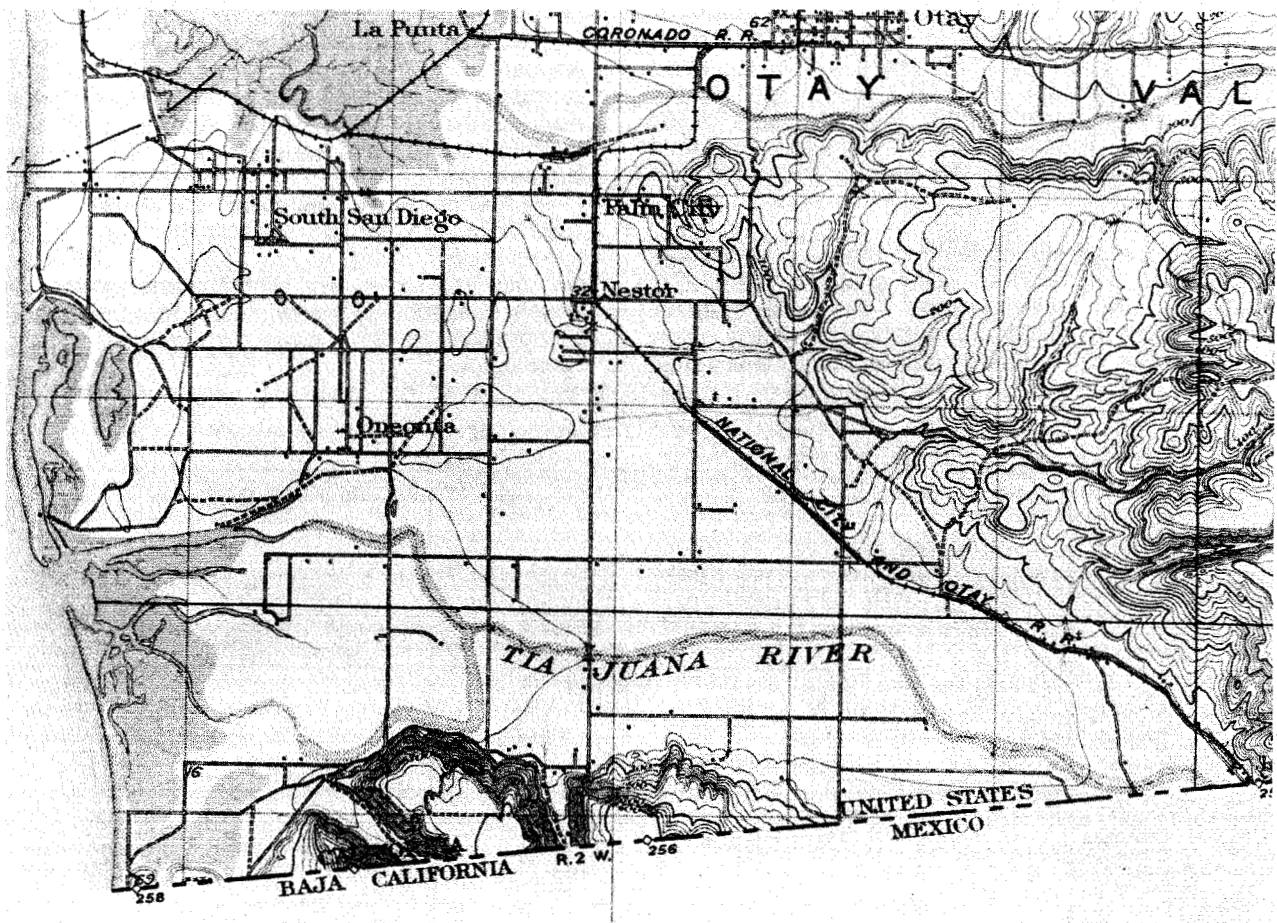
Figure 6. The 1904 map of Tijuana Estuary (from U.S. Coast and Geodetic Survey).

an isolated, land-locked lagoon in the northeastern part of the estuary. Without a natural connection between the lagoon and the rest of the estuary, this habitat must have been a highly variable wetland that filled in the rainy season and dried out in summer. Second, the mouth of the Tijuana River is represented as a minor bay, rather than a narrow channel. If this map does not represent an unusually high tide, then there was a much larger subtidal area than exists at present, and major sedimentation occurred after 1904. Third, there are two river courses, one entering the center of the estuary and one toward the southern end. The latter no longer connects with the river.

2.2 MEDITERRANEAN-TYPE CLIMATE

Cool, wet winters and warm, dry summers characterize the climate of southern California. Most days are sunny, although morning fog is common along the coast. Solar radiation data for Chula Vista (the station nearest Tijuana Estuary)

were collected in 1976 and 1977; the average was 411 calories/cm²/day, ranging from an average of 561 for June to 217 for December (Taylor 1978). Griner and Pryde (1976) state that San Diegans enjoy about 73% of the maximum possible sunshine. Daily temperatures average 17° C (63° F), with monthly highs in July or August (26° C, 78° F) and lows in January (7° C, 45° F). Frost is rare along the coast.

The coastal climate of southern California is reminiscent of the Mediterranean region (Barbour and Major 1977), and the coastal vegetation is similar to that of France, southern Africa, and southwestern Australia, all of which have Mediterranean-type climates. For coastal wetland vegetation, average rainfall on the coast is unlikely to be the direct determining factor; rather, the timing and amounts of rainfall and river flows within the entire watershed set limits on species distribution and growth. For intertidal organisms, conditions that cause high evaporation rates are

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also limiting. Hot, dry desert winds can be devastating, especially when they coincide with low tide. It is a climate with many extremes; some years and decades have little rainfall and runoff; other years have winter storms that cause tremendous floods. However, precipitation data indicate that storms are always of brief duration.

Data for six stations within the Tijuana Estuary watershed (Figure 7) show the seasonal patterns of rainfall and evaporation. At all stations, evaporation exceeds precipitation in nearly every month. The more inland stations have lower ratios of evaporation and precipitation, as is typical of the western sides of mountain ranges (Table 1). Annual rainfall averages are about 25 cm (10 inches), most of which falls between November and April. Although some winter months have heavy rainfall, monthly averages are less than 5 cm (2 inches). Annual evaporation rates are very high. Averages at Chula Vista for 1919-1981 (IBWC 1981) are 161 cm (64 inches) per year, with the maximum occurring in July (19 cm = 7.6 inches per month). Even in winter, substantial water losses can occur. The minimum monthly average evaporation is for December, with 7 cm (2.8 inches).
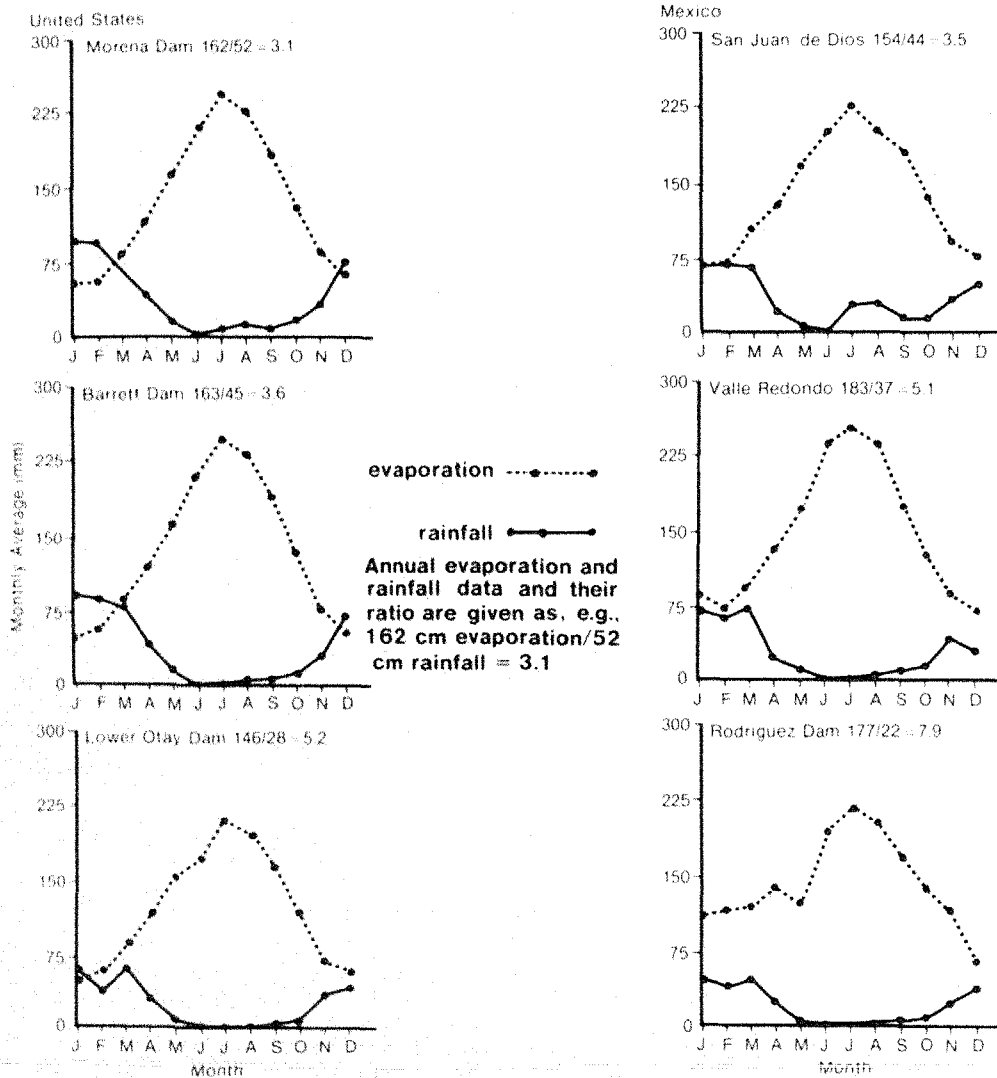
Figure 7. Monthly averages of evaporation and rainfall at six Tijuana River watershed locations in the United States and Mexico (see map, Figure 1, and elevations, Table 2; data from IBWC 1983).

Table 1. Locations and history of weather records for environmental stations within the Tijuana River watershed (Figure 7).

Station	Lat.	Long.	Elev. m	Evaporation records	Rainfall records
UNITED STATES					
Morena Dam	32°41'	116°31'	938	1916-1983	1906-1983
Barrett Dam	32 41	116 40	495	1921-1983	1907-1983
Lower Otay Dam	32 37	116 56	156	1950-1983	1906-1983
MEXICO					
San Juan de Dios	32 59	116 00	1280	1956-1983	1956-1983
Valle Redondo	32 31	116 45	242	1939-1942, 1946-1983	1938-1983

Although rainfall patterns influence the intertidal portions of the estuary, temperature and salinity data for channel waters show that the subtidal habitats are much less variable (Table 2). When Tijuana Estuary is open to tidal flushing, monthly water temperatures vary only slightly, and water salinities change primarily with major river flows.

The rainfall data for San Diego extend back to 1880 and indicate that periods of relative drought were interrupted by wet years in 1883, 1921, 1940, 1951, 1978, 1980, and 1983. Rainfall patterns differed greatly for each of those years. In some years, there were summer storms (5 cm of rain fell at Chula Vista in August 1977); in some years

there were winter droughts (almost no rain fell from late December 1983 through summer of 1984). Again, the factors most important to the estuary are not necessarily annual rainfall totals. Rather, from recent studies of estuarine dynamics, the amounts and times of rainfall and streamflow within the entire Tijuana River watershed appear to be critical. The extremes of wet and dry years are apparent in the frequency histogram for rainfall years (Figure 8) and in the high coefficient of variation (438%).

Table 2. Mean temperature (°C) and electrical conductivity (mmho/cm, a measure of salinity; sea water is approx. 50 mmhos/cm) at Winfield's (1980) tidal creek sampling stations in Tijuana Estuary. Data for two stations are averaged.

Date	Temperature		Conductivity	
	Flood	Ebb	Flood	Ebb
5/31/77	19	18	50	51
6/29/77	19	16	51	40
7/26/77	20	19	46	47
8/26/77	22	20	46	45
9/13/77	21	25	46	46
10/25/77	17	23	53	56
11/13/77	20	20	54	54
1/10/78	16	17	38	38
3/7/78	14	18	no data	no data
4/5/78	18	20	57	63
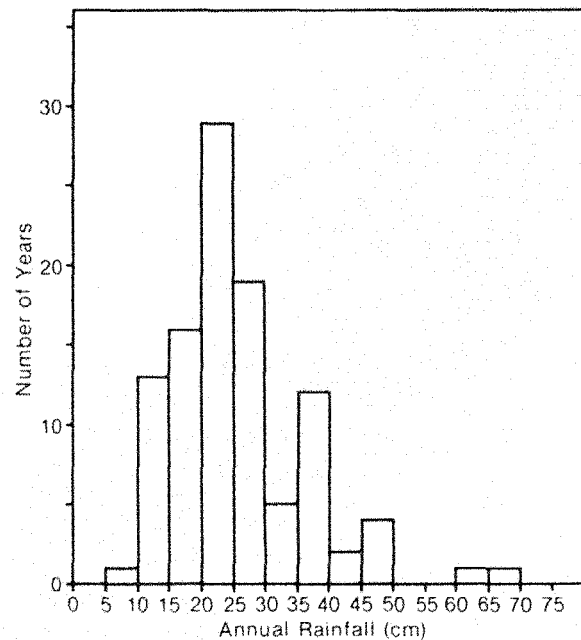
Figure 8. Histogram of annual rainfall for San Diego (Lindbergh Field) 1880-1984. Mean annual rainfall for this period = 25.7 cm (n = 105).

2.3 LAND USE HISTORY

Through examination of maps, photographs, and historical records, it has been possible to identify critical events that have shaped Tijuana Estuary. The physiography of 1985 differs substantially from that of the earliest maps and air photos. The many changes in land use reflect attitudes about the landscape. The estuary has been used and abused by a variety of human activities. These disturbances have intensified the effects of natural catastrophic events.

The 1904 map (Figure 6) of southwestern California shows Tijuana Estuary as having a minor bay and a broad mouth. The Tijuana River has two channels, one near the southern bluffs that border Mexico and another due east of the mouth. An isolated, land-locked lagoon is located in the northeastern part of the estuary. These three features persist to date, but in highly modified form.

The earliest aerial photographs of Tijuana Estuary were taken in the 1920's. The history of adjacent land uses and their impact on the estuary become apparent on inspection of the condition of the river mouth, barrier dunes, channel edges, high marsh habitats, wetland-upland transitions, inland lagoon, and the adjacent upland. By 1928 (Figure 9a), Imperial Beach had been settled with more than 50 dwellings, most of which were within 3 blocks of the beach. Several roads were present

a   b
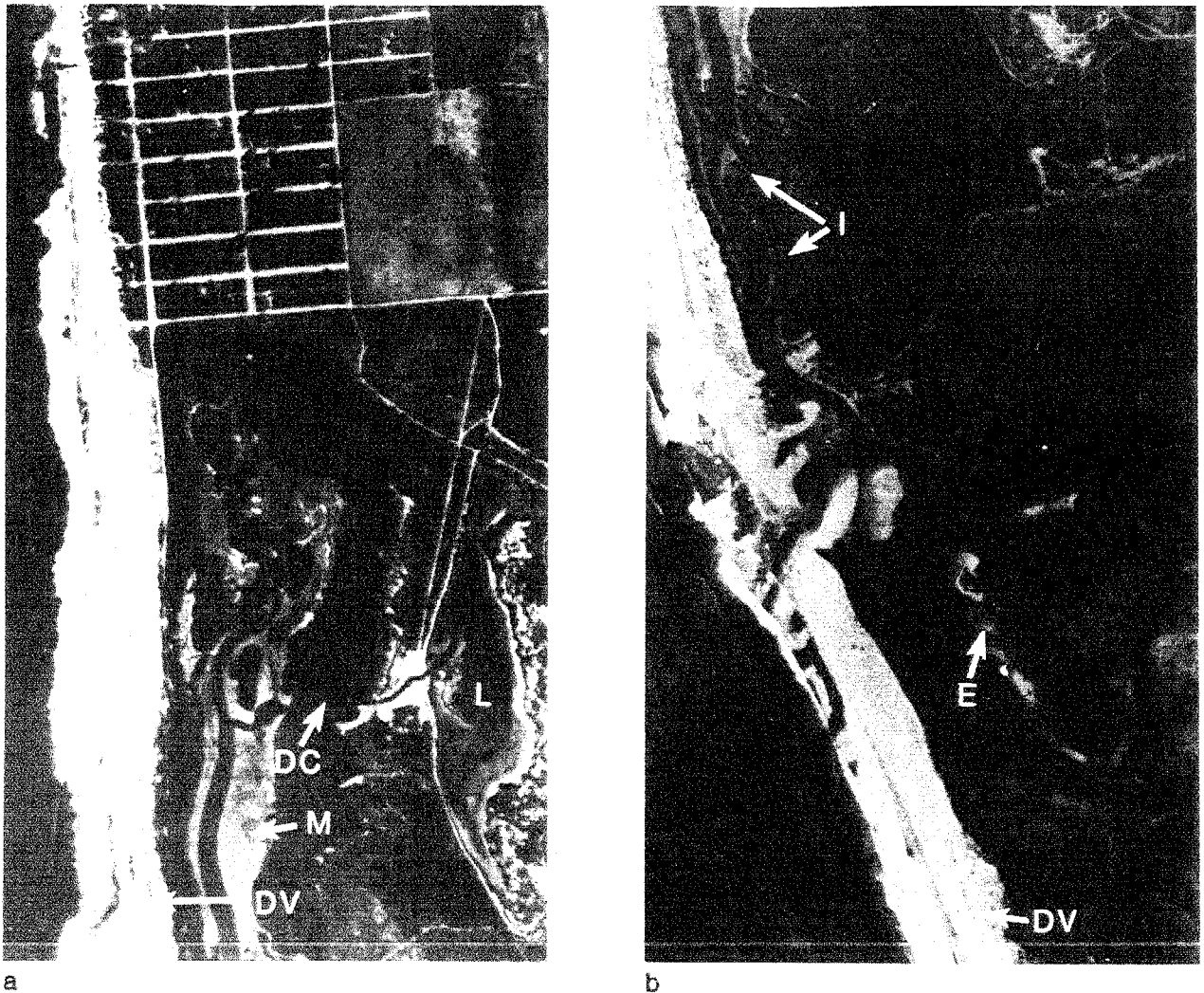
Figure 9. The 1928 aerial photograph of Tijuana Estuary (from County of San Diego). Panel a shows the northern arm of the estuary; panel b shows the central embayment (E). Note dune vegetation (DV), mudflats (M) along tidal channels, islands (I), inland lagoon (L), and dredged channel (DC).

around the periphery of the wetland. However, there was only a path and no houses on the barrier dune adjacent to the salt marsh. Signs of agriculture in the floodplain are evident upstream of the estuary and north of what is now Monument Road.

Several physiographic features that changed in later years are noted in the photos of 1928, 1953, 1964, 1970, 1984, and 1985. In 1928, the dune had intermittent vegetation extending from what is now Imperial Beach Blvd. south to the estuary mouth. This is consistent with Purer's (1936) description of a rich flora that included shrubs such as lemonadeberry (*Rhus integrifolia*). Channels had major bare mudflats along their periphery. The inland lagoons clearly contained marsh vegetation throughout. Only a small area of channel is visible, and that was dredged to link the lagoon with the estuary. Two islands were present in the main north-south channel. The mouth (Figure 9b) had tidal flushing through an opening that angled southwest. A relatively large embayment was located south of the mouth, although it may have been shallower than indicated on the 1904 map (Figure 6). What appear to be large salt pannes were present east of the the inland lagoon.

By 1953 (Figure 10), many changes had occurred both in the periphery of the estuary and within the area of tidal influence. Imperial Beach was a well-populated community: a military airport had been built east of the estuary; military activity was evident along the southernmost portion of the beach; and agricultural activities had proceeded to within a few blocks of the beach.

Within the estuary, several habitats had changed dramatically. The barrier dune had begun to be developed for housing along the northwestern part of the estuary, although dune vegetation was still present farther south. Salt marsh vegetation had established along the edges of the channels. A sewage-treatment plant had been built north of the inland lagoon, and the northernmost depression had been diked to create a sewage pond. Presumably, the dredged channel carried the overflow to the ocean. A bridge had been built over the dredged channel, probably to truck gravel from shallow pits just south of the inland lagoon. The mouth was still open to tidal flushing through an opening that had migrated south of its 1928 location. Much of the area that was deep-water habitat appeared to have filled in with beach sand, and the southern channel had become constricted. Salt pannes were still evident east of the inland lagoon, but a brackish marsh had appeared at the terminus of urban drainage from the airport, perhaps in a depression caused by excavation. Additional disturbance caused by gravel extraction was evident just west of the new wetland area.

Changes that took place in the 1960's and 1970's were described using additional air photos; for the most part, changes remained visible in the 1978 photo (Figure 11). By 1964, apartment buildings had been constructed along the beach, extending south to their present limit. Dune vegetation remained relatively dense south of the apartments. Near the mouth were disturbed areas and areas of bare sand toward the main estuary channel. A second dike had been built within the inland lagoon. Sewage was then discharged to two oxidation ponds before overflowing to the estuary.
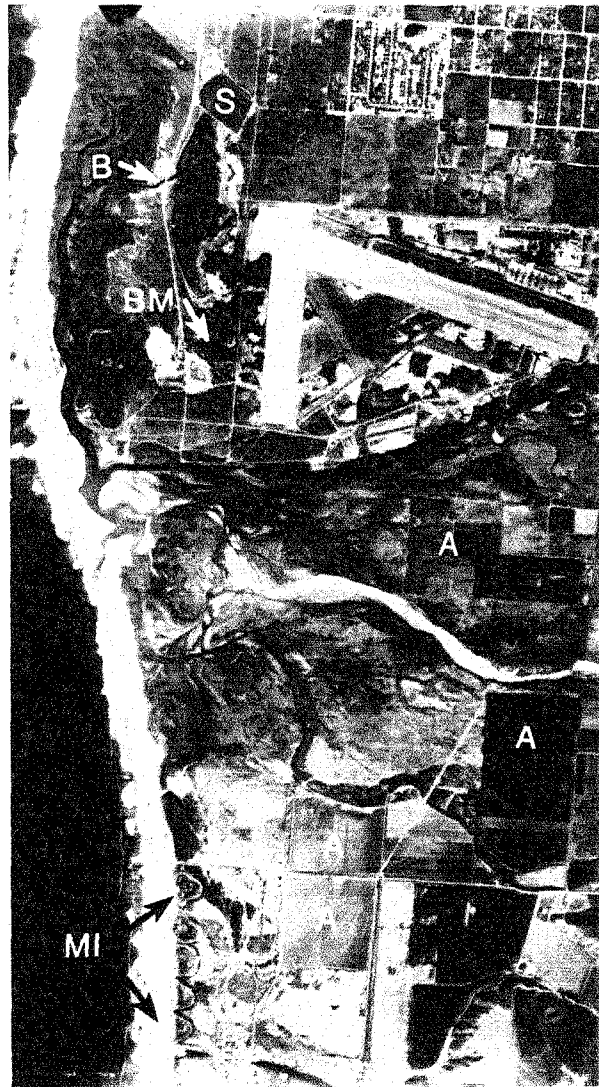
Figure 10. The 1953 aerial photograph of Tijuana Estuary (from U.S. Department of Agriculture). Note bridge (B) over the dredged channel, sewage oxidation pond (S), brackish marsh (BM), military installations (MI), and agricultural uses (A).

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The nearby bridge remained, and extensive disturbance by vehicle traffic had occurred.

By 1970 several new disturbances were visible. Additional apartments had been built along the coast, and the barrier dune no longer supported good vegetative cover. Large areas of dune washover had developed both north and south of the estuary mouth. As is obvious from events of the 1980's, this relatively gradual loss of dune vegetation ultimately had an estuary-wide impact. The sewage operation at the inland lagoons had been abandoned, and saline pannes were obvious during the July, dry-season photo. Tidal flushing was lacking behind the diked areas. The mouth had shifted southward. East of the sewage impoundments, a channel had been dug to direct street runoff into the southernmost lagoon.

In January and again in February of 1980, floods that exceeded all previous flow records simultaneously eroded and filled different parts of the estuary. The flooding shifted the course of the Tijuana River from its southern channel (Figure 11) across several parcels of agricultural land, carving a diagonal channel toward the airport, where it connected with the central estuarine channel. A much broader coastal embayment was created at the river mouth. Major sedimentation occurred in the southern half of the estuary. Monument Road was buried by half a meter of silt that flowed down Goat Canyon.

In January 1983, concurrent high tides and heavy surf flooded Sea Coast Drive and washed sand between the apartment buildings into the street and onto the edge of the salt marsh. Where

Figure 11. The February 18, 1978, aerial photograph of Tijuana Estuary (from Aerial Fotobank). Note development on beach (D), abandoned sewage oxidation ponds (S), gravel excavation (G), agriculture (A), and location of main river channel (R).

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dune vegetation had been disturbed, there were major washovers. The photo from March 1984 (Figure 12) documents the effects of the winter storms on the barrier beach, while that of August 1984 (Figure 13) shows the delayed effect on the estuary mouth. Dune sands were washed into the main estuary channel, substantially reducing the tidal prism and ultimately causing the closure of Tijuana Estuary to tidal flushing. Closure occurred on or about April 8, 1984, after which a dredging plan was developed and implemented by the U.S. Fish and Wildlife Service. Excavation of the sand from the main channel began after a long permit process, but the estuary was not reopened to tidal

Figure 12. The March 19, 1984, aerial photograph of Tijuana Estuary (U.S. Army Corps of Engineers). Note washovers (W), macroalgal blooms (M), breached dikes (BD), and southerly location of mouth just prior to closure.

Figure 13. The August 30, 1984, aerial photograph shows the estuary after nearly 5 months of closure to tidal flushing (from U.S. Army Corps of Engineers). Note patches of cordgrass mortality (C) near tidal creeks.

flushing until mid-December 1984. Eight months of closure had devastating effects on the estuary.

While the reduction of tidal flushing is in itself a catastrophic event for a marine-dominated system, the situation was made worse by its coincidence with a year of near-zero rainfall. Channels became hypersaline (60 ppt in fall 1984; R. Rudnicki, SDSU, pers. comm.), shallow creek bottoms desiccated and turned to brick, and marsh soils became so dry and hypersaline (over 100 ppt in September 1984) that large areas of low-marsh vegetation died out (Figure 14). Bare patches within the salt marsh were obvious from the air in August 1984 (Figure 13).

Tidal flushing was reinstated in December 1984 after dredging of the main estuary channel from the end of Sea Coast Drive south to the mouth, and tidal flushing has continued to the present. Sand that washed eastward was bulldozed back to recreate dunes, which are now part of a dune revegetation program. Additional dredging in the south arm of the estuary is scheduled for 1986, and similar dune rebuilding activities are planned.

In comparison with earlier estuary conditions, several changes had occurred by 1985 (Figure 15). Native dune vegetation was almost entirely gone both north and south of the mouth. Along the channels, salt marsh vegetation that died back in 1984 had begun to recover in 1985, although species composition had changed (Chapter 5). Dikes that once separated the sewage lagoons had been breached and widened (Chapter 6). The islands in the main channel were obliterated by the sand washover of 1983. The mouth was artificially cut; and south of the new mouth, it is clear that the beach line had moved inland. What was once a
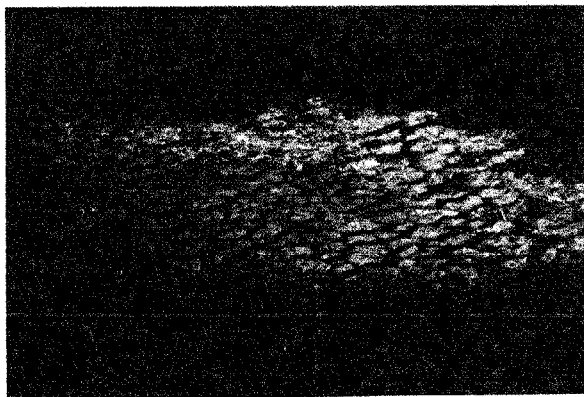
Figure 14. Cordgrass mortality during nontidal conditions in 1984 (photo by J. Zedler).

shallow embayment became the beach line, and only a narrow channel remained. Control of vehicle traffic along the urban periphery of the estuary had allowed some vegetation regrowth.

Disturbances that occurred south of the estuary mouth in the 1960's left scars that were still apparent in 1985. Near the Border Field State Park overlook, areas used to corral horses and an exercise track used to rehabilitate race horses have been slow to recover. Twenty years later, the highly compacted soils support only limited vegetation. Military installations, shown as irregular circles in the 1953 aerial photo (Figure 10) were filled with sands washed from the beach and dune during the 1983 storm. Standing water accumulated east of the road to the overlook, allowing establishment of brackish marsh vegetation in that area. Reduced soil salinities and nutrient-rich sewage spills stimulated the invasion of weedy wetland species, such as brass buttons (*Cotula coronopifolia*).

2.4 STREAMFLOW HISTORY

Streamflow in the San Diego region is the most variable in the United States, and differences between wet and dry years are greater than in any other part of the country (Pryde 1976). Even small variations in streamflow affect the coastal wetlands, because floodplains are narrow, and there is little volume of estuarine water present to ameliorate the impacts of increased or decreased flows.

The Tijuana River drains a watershed of 448,323 ha, three-fourths of which is in Mexico (Figure 1). Of that watershed, 78% is behind dams (IBWC 1983). The effects of reservoirs on streamflow are undetermined, because all three dams were installed before streams were gaged. Morena Dam dates to 1912, Barrett to 1922, and Rodriguez to 1936. Their respective capacities are 62 million m^3 (50,210 acre-ft), 55 million m^3 (44,760 acre-ft), and 138 million m^3 (111,880 acre-ft). The largest and closest to Tijuana Estuary is Rodriguez Dam, just upstream of the city of Tijuana. It is likely that dry-season flows are lower and that flood flows are delayed by the presence of these reservoirs.

Flows of the Tijuana River have been measured since 1937 at the Nestor gage, which includes 99.6% of the watershed (Figure 1). On the average, the Tijuana River has its peak flow in March (Figure 16). However, as with rainfall data, averages tell little of the relationship between streamflow and estuarine dynamics. Year-to-year flows are highly variable (coefficient of variation = 325%), as are monthly flows (c.v. = 690%). With

such a streamflow history, Tijuana Estuary may be the Nation's most variable estuary. It is marine-dominated on a seasonal basis (sometimes for several years in succession); it is occasionally fresh during catastrophic flooding, such as occurred in 1980.

Monthly flow volumes at Nestor (Figure 17) show that major floods occurred in 1978 and 1980

after a 35-year period with little flow. Log-transformations of the monthly streamflows enhance the years of low flow and deemphasize high-flow years. Seasonal patterns become much clearer with such transformation, and the winter-flow, summer-drought pattern becomes obvious. Note, however, that several entire years had zero flow at the Nestor gage. During these times, the estuary is presumed to have been filled entirely

Figure 15. Tijuana Estuary on January 1, 1985 (from Aerial Fotobank). Compare locations of main river channel (R) and agricultural activities (A) with Figure 11. Traces of horse-raising activities (H) are visible near the Border Field State Park overlook (O). Estuarine habitat types, drawn from this photo, are mapped in Figure 3.

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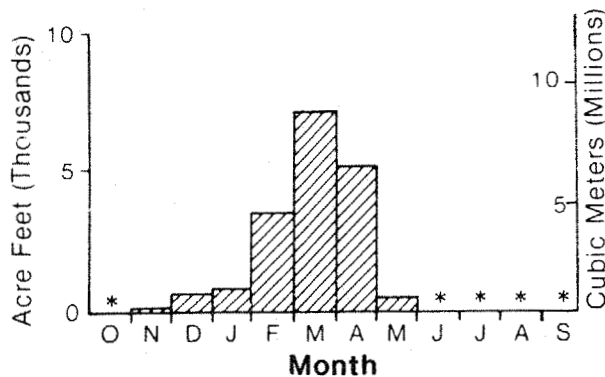
Figure 16. Average monthly streamflow at Tijuana River. Asterisks indicate months with average flows <100 acre-ft (Nestor gage; data from USGS 1937-1978).

with seawater. Even in years with seasonal streamflow, the predominant influence has been marine.

While floods are the exception in the streamflow record, they have an enormous influence on the estuary. The estuary has been characterized as having a low tidal prism, with a range of from 0.1 to 3.7 million m^3 (100-3,000 acre-ft; IBWC 1976). As a result, freshwater input during storm events can have far-reaching effects on the system. From the floods of 1978 and 1980, we have learned how dramatically water salinities change, how rapidly the invertebrate populations shift, and how extensively the marsh soils and vegetation are affected by these unusual events. Though brief, they are catastrophic in their effect. What we see at any given time is the estuary's cumulative response since the last catastrophic event.
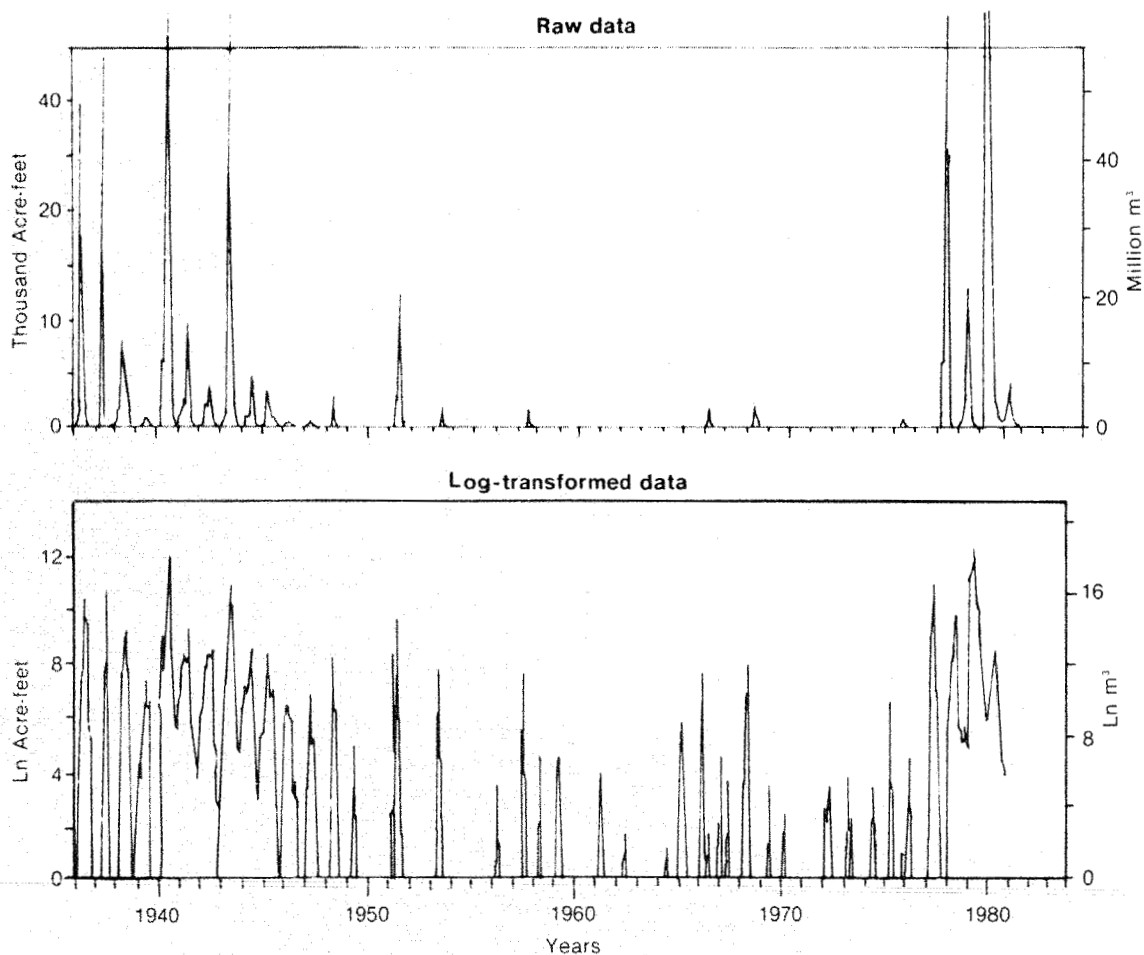
Figure 17. Streamflow data for Tijuana River (Nestor gage). Log-transformed data are given to emphasize low-volume flows (data from USGS 1937-1981 and IBWC 1950-1983).

CHAPTER 3

ECOLOGICAL COMMUNITIES AT TIJUANA ESTUARY

The diversity of habitats at Tijuana Estuary results from the variability in topography, tidal influence, and streamflow inputs. This chapter describes the major communities of organisms at the estuary; additional information on their relationships to other wetlands in southern California is provided in Zedler (1982b).

3.1 PHYSIOGRAPHIC DIVERSITY

Tijuana Estuary includes seven major habitat types that we have designated as: transition from upland to wetland, salt marsh, salt panne, brackish marsh, estuarine channels and tidal creeks, intertidal flats, and dunes and beach. They are listed in order of their occurrence as one proceeds southwest across the estuary (Table 3). Of the wetland habitats, the three that cover the largest area are salt marsh, channels and tidal creeks, and dunes and beach (Table 3). Most of the estuarine research has focused on the salt marsh habitat; regional comparisons of salt marshes appeared in Zedler (1982b). In this chapter, we characterize the dominant species of plants and animals for each habitat and highlight species of special concern.

Table 3. Areal comparisons of habitat types at Tijuana Estuary based on computer-assisted image processing of the 1985 aerial photograph. See Figure 3 for area included in the comparison.

Habitat type	% of Total	Hectares	Acres
Transition, upper marsh and upland species	41.9	255.1	630.3
Lower and mid-marsh areas	13.6	82.6	204.0
Salt pannes	4.1	25.2	62.4
Brackish marsh	7.1	43.4	107.2
Channels and intertidal flats	20.9	127.0	313.8
Beach and dunes	12.4	75.6	186.7
Total area considered in this analysis		608.9	1504.4

Small variations in hydrology and elevation are responsible for the physiographic diversity of Tijuana Estuary. Unfortunately, detailed surveys have been carried out only in the salt marsh; topographic mapping and hydrologic analysis of the entire estuary are underway (P. Williams, SDSU, in prog.). Even though the natural physiography has been substantially altered by catastrophic events and human disturbances, most of the habitats present today probably represent variations on what existed at the turn of the century. One likely exception is the brackish marsh habitat, which appears to be directly dependent on urban runoff. Another is the transition zone, which has borne the brunt of urban and agricultural encroachment. Just how closely it resembles the natural condition will never be known, because there are no sites where undisturbed coastal scrub grades into undisturbed coastal wetland.

With or without human disturbance, none of the estuarine communities is viewed as static in either species composition or population sizes. Our knowledge of community change is limited by the lack of consistent sampling of most habitats. However, for the most extensive community, the salt marsh, there is now a 7-year record that allows discussion of vegetation dynamics (Chapter 5). This data base, plus the record of variable climatic conditions and streamflow regimes, makes it clear that Tijuana Estuary is continually subject to environmental variation. The result is a mosaic of populations that are constantly shifting in space and time.

These long-term patterns of habitat change have been revealed only recently; they are emphasized here because they are not obvious upon short-term observation. Other dynamic aspects of the estuary are more easily documented. These are the daily and seasonal fluctuations in tidal height, the alternation of wet and dry seasons that creates pools in winter and salt pannes in summer, the seasonal patterns of temperature that stimulate development of macroalgae in the inland lagoons and tidal creeks, and the migration of birds that use the intertidal

flats in winter but not in midsummer. Each community must be viewed as a function of its changing physical environment, as well as a complex mixture of interacting species.

3.2 TRANSITION FROM UPLAND TO WETLAND

By definition, transitions are areas where one community type (e.g., upland) shifts to another (e.g., wetland). The most extensive wetland habitat at Tijuana Estuary is the intertidal salt marsh. It is a spatially heterogeneous community that occurs from the highest influence of sea water to the lowest limit of vascular plants (usually cordgrass) along mudflats and tidal creeks. Its exact upper boundary is difficult to discern, because the vegetation blends into that of the upland. The two communities overlap in a transitional area that has elements of both.

Most of the peripheral upland has been disturbed at Tijuana Estuary. The best information on what these areas might have been like naturally comes from Baja California (Neuenschwander 1972). At Bahia de San Quintin, (30° 25' N., 116° 00' W.), we analyzed the transitional vegetation in detail to determine at what point one leaves the upland and enters the wetland (Zedler and Cox 1984). There, the wetland plants that occurred highest along the slope were alkali heath (*Frankenia grandifolia*), sea lavender (*Limonium californicum*), and sea-blite (*Suaeda esteroa*). The upland plants that were found farthest downslope were two species of box-thorn (*Lycium* spp.) and *Frankenia palmeri*. In California, the latter occurs only in San Diego Bay; whether or not it ever occurred at Tijuana Estuary is unknown. The box-thorn (*Lycium californicum*), however, is common in several of the remnants of transitional vegetation at Tijuana Estuary. It is easily recognized by its thorny, stiff-twigged appearance and small red berries. Like many shrubs of the coastal scrub community, box-thorn is drought deciduous. It is leafless during summer when the salt marsh vegetation is at peak biomass.

A small remnant of the transition community persists in a sloped corner of the northern end of Tijuana Estuary. Because the slope is one of the most frequently used entry points for visitors to the estuary, a detailed description of upland-wetland compositional shifts has been developed. The area was sampled in 1984 (Table 4) with 396 quadrats spanning elevations from the street into the marsh. In this transition area, the upland community is coastal sage scrub with several shrub species, some of which are evergreen (e.g., laurel sumac, *Rhus laurina*; lemonadeberry, *R. integrifolia*; jojoba, *Simmondsia chinensis*), and some of which are drought-deciduous (e.g., golden bush, *Haplopappus venetus*; and California sagebrush, *Artemisia californica*).

The data in Table 4 indicate a relatively abrupt boundary between upland and wetland plants. The band of overlap is narrow. While many exotic plants have invaded the coastal scrub, few have sufficient tolerance of inundation and salt stress to invade the coastal wetlands. One weedy species, the Australian salt bush (*Atriplex semibaccata*), has an extremely wide range of tolerance. It occurs throughout the transition zone and well into the upper salt marsh. It withstands the dry saline upland as well as occasional inundation by seawater.

The marsh species that grows highest up the slope is saltgrass (*Distichlis spicata*). Also found in sandy areas near the dunes, this marsh plant is easily mistaken for Bermuda grass (*Cynodon dactylon*) in vegetative form. Insects, however, know the difference. The saltgrass is the sole host plant for larvae of the wandering skipper (*Panoquina errans*, Lepidoptera: Hesperidae; Figure 18). The first occurrences of alkali weed (*Cressa truxillensis*) and alkali heath are additional indicators that you have moved from the upland down into the wetland. At the sloped corner, they first appear at approximately 3 m (9.2 ft) above MSL. While the habitat where the highest marsh plants occur is often dry, it becomes inundated when storms coincide with the highest spring tides (Cayan and Flick 1985).

The animals of the transition community (snakes, lizards, rodents, songbirds) are primarily from more terrestrial habitats. Species of special interest at Tijuana Estuary include the short-eared owl (*Asio flammeus*) and black-shouldered kite (*Elanus caeruleus*), which prey upon the smaller animals. Due to the scarcity of the habitat type, no studies have quantified the animal communities.

3.3 INTERTIDAL SALT MARSH

While the salt marsh appears to be a plant-dominated community, it provides habitat for a wide variety of animals, including resident and migratory species. Judging by the amount of time that birds spend foraging and resting in the marsh, this habitat may be as important as channels and intertidal flats for the shorebirds and waterfowl of the estuary. Insects and benthic invertebrates are likewise abundant in the intertidal marsh. The plants structure the community and support a complex food web.

The gradually changing composition of the intertidal plant community is shown graphically (Figure 19) as a series of overlapping distributional curves. Almost every species has its peak occurrence at a different elevation band, and the vegetation forms a continuum rather than a set of zones. Still, the presence of shrub-like succulents

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Table 4. Percent occurrence of the more abundant species in the transition from upland to wetland at the northernmost part of Tijuana Estuary. Data are from 0.25 m² circular quadrats (numbers sampled in parentheses) taken per 40-cm elevation class (Zedler unpubl. data).

Species	Elevation Class[a]										
	1 (29)	2 (99)	3 (52)	4 (25)	5 (33)	6 (30)	7 (31)	8 (34)	9 (22)	10 (33)	11 (8)
Artemisia californica						7		15			
Eriogonum fasciculatum			2	4		17	19	21	27	3	12
Haplopappus venetus			6	4		3	10	9			
Rhus laurina					39		13	6			
Atriplex semibaccata		14	15	16	12	3	52	3	27	39	75
Cressa truxillensis	34	19	8	12		3					
Distichlis spicata	66	68	75	64	33	13	3				
Frankenia grandifolia	59	40	27	44	15						
Lycium californicum	14	3	12								
Monanthochloe littoralis	59	37	6	4							
Salicornia subterminalis	41	44	23								
Salicornia virginica	52	17	14	24							
Limonium californicum		10									
Atriplex watsonii		4	6	4							

[a]Elevation classes each included a 40-cm (16-inch) elevation range; they are numbered from low to high elevation.
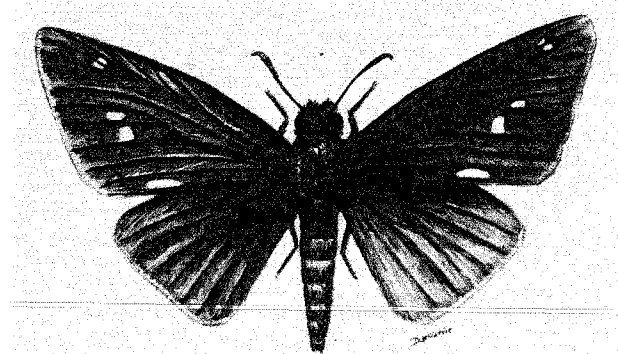
Figure 18. The wandering skipper. Body 14 mm long. McIntire collection, copyright 1986 by Zedler.

at the uppermost elevations and the taller cordgrass (Spartina foliosa) at the lowest elevations helps to designate higher and lower marsh habitats. Unlike the drought-deciduous coastal scrub species, the plants of the salt marsh grow through the summer and early fall. Presumably, this is because the wetland plants have access to moisture from tidal waters throughout the dry summer and fall.

The higher salt marsh (Figure 20) is one of the most complex wetland communities, because it is subject to alternating environmental extremes of drought and inundation, because disturbance is frequent, and because its topography is sometimes mounded. Eighty-six mounds that ranged from 9 to 57 cm in height and 5.6 to 18.6 m in diameter were characterized in 1984 (Cox and Zedler, in press).

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Each "island" of higher topography allows species of the higher marsh to extend farther into the wetland. The marsh periphery is thus patchy and diverse; the larger the mound, the longer the plant species list. In addition, the mounds provide habitat for several herbivorous mammals that in turn influence mound and intermound vegetation.

Cox attributes the mound formation to ground squirrels and other burrowing mammals that utilize the high ground. He suggests that over centuries, they gradually transport soils toward a central burrow opening until a pattern of mounds and intermound areas is created. Whether the concentration of squirrels on mounds is cause or effect, however, is hard to demonstrate in short-term studies. What is clear is that the mounds of high ground, which are surrounded by wetter marsh, add small-scale habitat diversity to the wetland. Where adjacent areas have been filled or developed, these islands provide the only clue to the higher-elevation communities that might have occurred in the transition zone. The invasion process can be seen in wet winters, such as 1983, when high spots are leached of their salts and upland weeds (e.g., the wild radish, *Raphanus sativum*) germinate and grow. Such salt-intolerant species rarely persist beyond the next dry season.

Herpetofauna are likewise limited to these areas of high ground. The San Diego horned lizard (*Phrynosoma coronatum blainvillei*; Figure 21) is declining because of frequent collection, but a few remain in isolated areas. Snakes are not common, and their rarity partly explains the abundance of rodents such as ground squirrels (*Spermophilus beechyii*) and rabbits (*Lepus californicus* and *Sylvilagus audubonii sactidiegi*) that populate the upper marsh.

Birds that nest in the high marsh include the white-crowned sparrow (*Zonotrichia leucophrys*), song sparrow (*Melospiza melodia*), western meadowlark (*Sturnella neglecta*), and killdeer (*Charadrius vociferus*). Other birds use the area extensively for foraging. Raptors, such as the northern harrier (*Circus cyaneus*), American kestrel (*Falco sparverius*), and golden eagle (*Aquila chrysaetos*), exploit the populations of small mammals; while Belding's Savannah sparrows, horned larks (*Eremophila alpestris*), and loggerhead shrikes (*Lanius ludovicianus*) feed on insects and other small prey (A. White, SDSU, pers. comm.).

Characteristic plants of the higher marsh are the perennial glasswort (*Salicornia subterminalis*), the shore grass (*Monanthochloe littoralis*), alkali heath, sea lavender, and *Atriplex watsonii*. All of these species are perennials that reproduce vegetatively, and seedlings are rare. Only during the long rainy season of 1983 were there conspicuous episodes of seedling establishment.
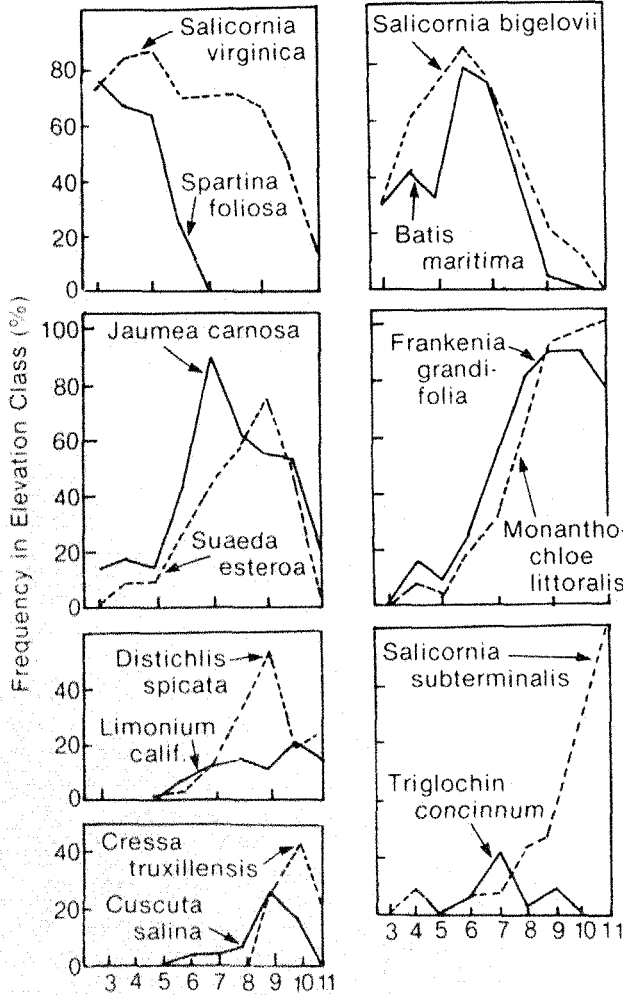
Explanation of X axis

Class number	Elevation (cm MSL)	Quadrats in class	Class number	Elevation (cm MSL)	Quadrats in class
3	30-39	7	8	80-89	35
4	40-49	12	9	90-99	30
5	50-59	22	10	100-109	35
6	60-69	113	11	110-130	8
7	70-79	95			

Figure 19. The frequency of occurrence of abundant plant species in the salt marsh of Tijuana Estuary (from Zedler 1977).

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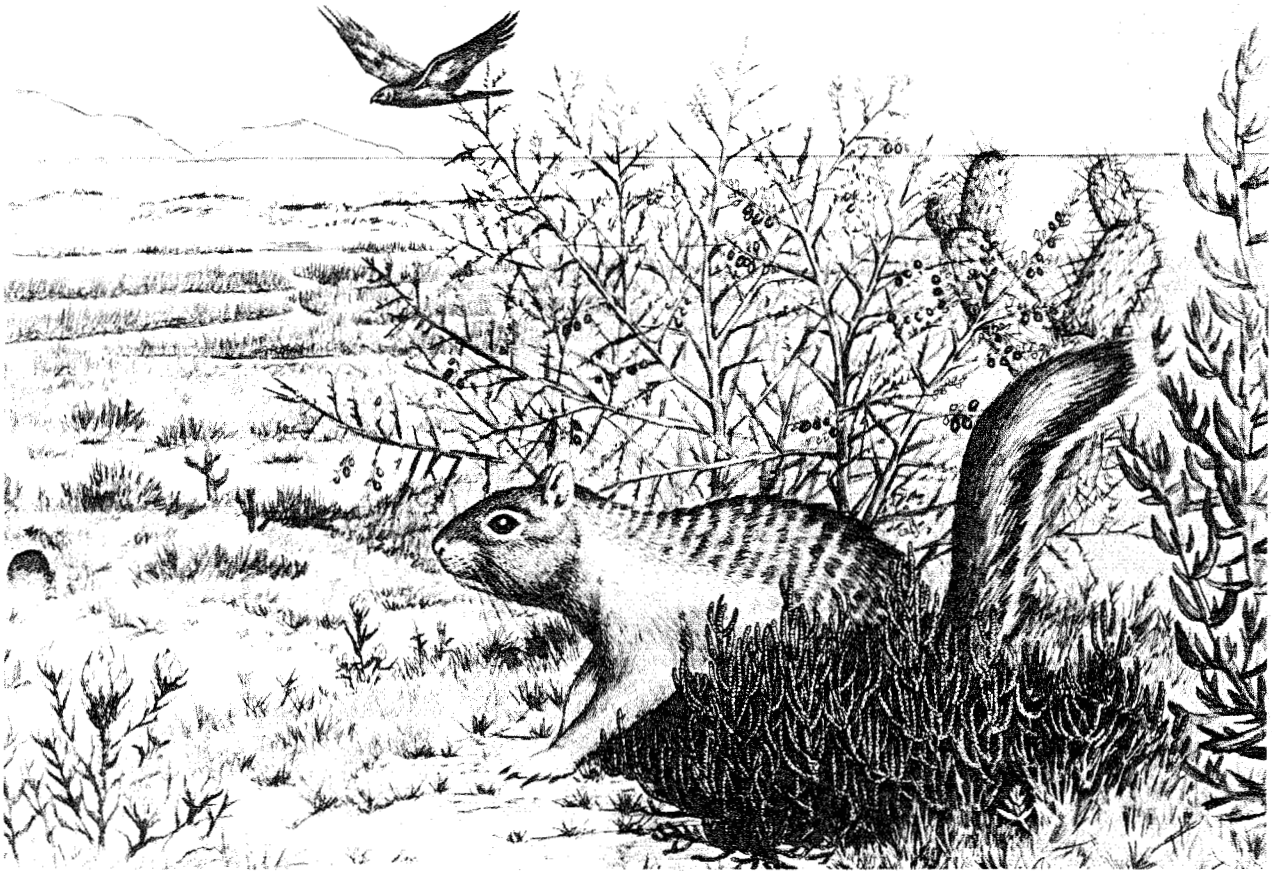
Figure 20. The upper marsh habitat with the California ground squirrel, salt marsh bird's beak (lower left), box-thorn, prickly pear, golden bush (behind the ground squirrel), and glasswort and shore grass (in front of the ground squirrel). A northern harrier is silhouetted above the horizon. McIntire collection, copyright 1986 by Zedler.

In a few places at Tijuana Estuary, the endangered salt marsh bird's beak (*Cordylanthus maritimus* ssp. *maritimus*; Figure 20) occurs in the higher marsh. Because it is an annual, it is evident only for a short time during the spring and summer growing season, and because the plants are small, it is easiest to spot when in bloom (April-June). It is thought that this annual plant can survive the warm dry summer without frequent tidal submergence because it is hemiparasitic. Its roots develop haustoria that penetrate a variety of other species to gain water and nutrients. Subpopulations of bird's beak are highly dynamic, sometimes spreading, sometimes disappearing for a year or more. A little disturbance appears to open habitat for seedling establishment (Vanderweir 1983), and the activities of mammals may be an important part of the plant's ecology. However, too much disturbance (e.g., repeated trampling, soil compaction) prevents survival, and habitat destruction near urban development is probably a major cause of its endangered status.
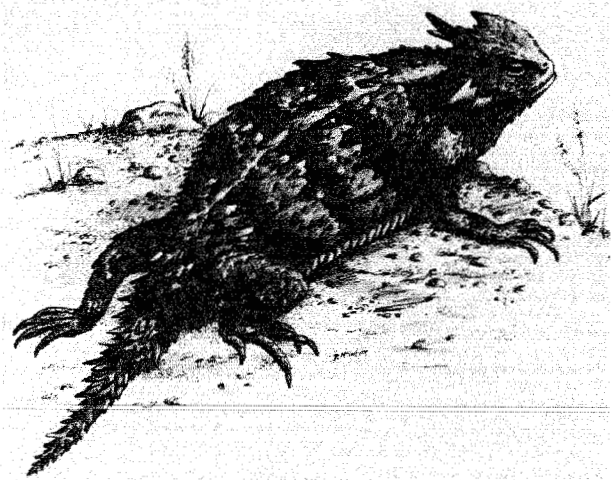
Figure 21. The San Diego horned lizard. McIntire collection, copyright 1986 by Zedler.

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The vegetation and soils of the upper marsh support many insects, spiders, and mites, but few other invertebrates (Figure 22). *Tachys corax*, literally the swift raven, is the most prevalent species of carabid beetle found at Tijuana Estuary. This small insect (to 3.5 mm) occurs in all marsh habitats and feeds primarily on other small arthropods. Another beetle, *Eurynephala maritima*, is found on the stems of pickleweed. Two spiders that inhabit this zone are *Tetragnatha laboriosa* and *Pardosa ramulosa*. The former is often found extended along the narrow leaves of cordgrass, while the latter is abundant on algal mats.

Intermediate elevations of the salt marsh are much more frequently wetted by the tides. Higher inundation tolerance is required of both the plants and infauna. The dominant plant is the perennial pickleweed (*Salicornia virginica*; Figure 23), which has the broadest elevational range of all the salt marsh species. It is also a species of broad geographic range, occurring on the Pacific Coast
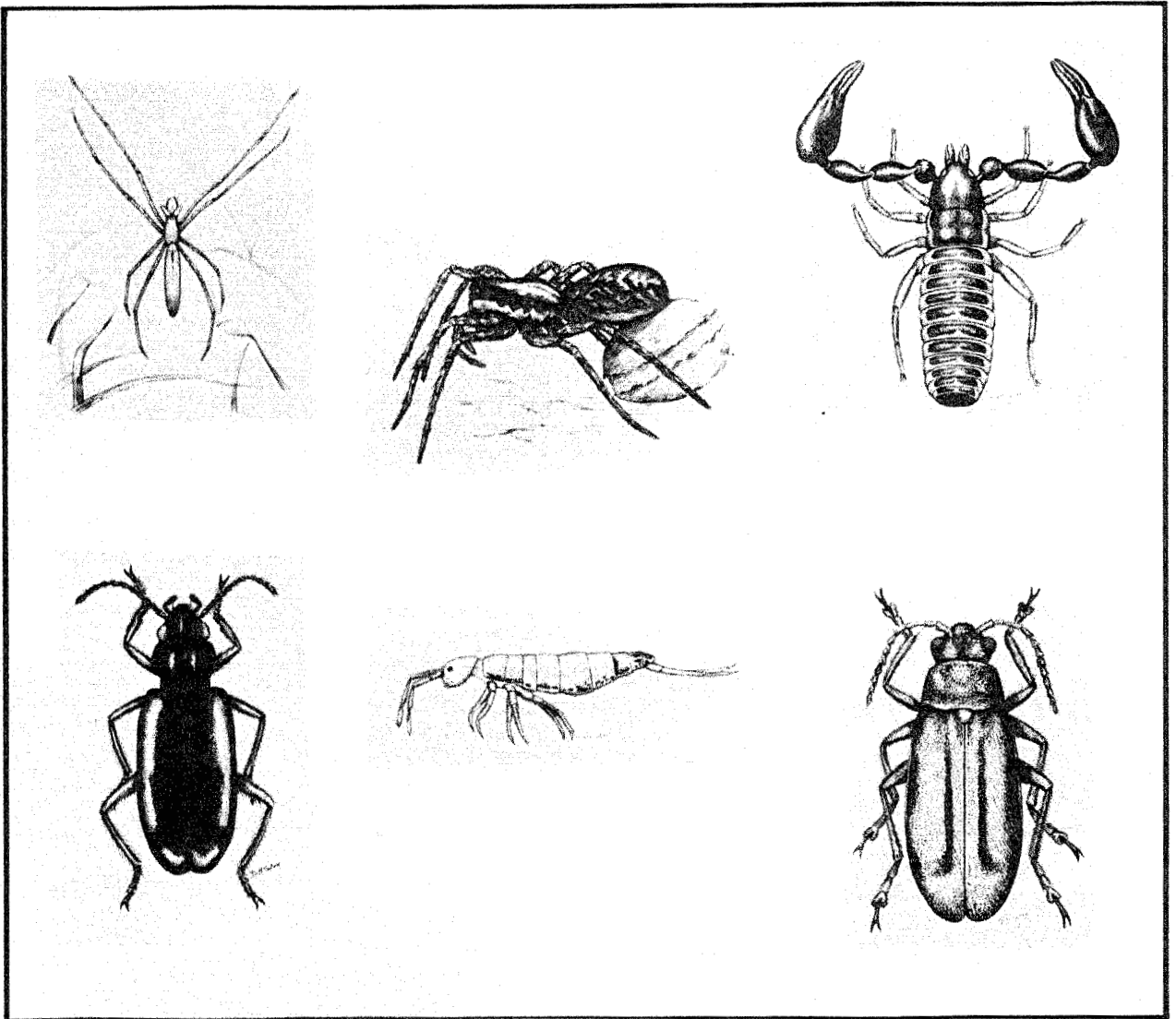
Figure 22. Selected insects and arachnids of the salt marsh. Illustrated are two spiders, *Tetragnatha laboriosa* (upper left, body 10 mm long) and *Pardosa ramulosa* (body 10 mm long; shown with eggs); the pseudoscorpion (*Halobisium occidentale*; Chelonethida), which is found with pickleweed; the springtail (Collembola: Isotomidae, *Isotoma* sp.; bottom center), a very small but abundant species, especially in plant detritus; and two beetles, *Tachys corax* (lower left) and *Eurynephala maritima* (lower right, body 6 mm long). McIntire collection, copyright 1986 by Zedler.

Figure 23. Salt marsh vegetation of the intermediate elevations. Illustrated are sea lavender (left), arrow grass (foreground), sea-blite (background), perennial pickleweed (right), and Jaumea (lower right, in flower). McIntire collection, copyright 1986 by Zedler.

from Puget Sound, Washington, to the southern tip of Baja California, Mexico (Macdonald and Barbour 1974), and on the Atlantic Coast.

A small but significant bird finds its preferred habitat within pickleweed-dominated marshes. Belding's Savannah sparrow (Figure 24) is listed by the State of California as an endangered species. It builds its nest low to the ground, often under a pickleweed canopy but sometimes in saltgrass (*Distichlis spicata*) or shore grass. In 1985, there were 81 pairs of Belding's Savannah sparrow nesting in the middle marsh areas north of the Tijuana River. Censuses in 1973 and 1977 indicated that there were 100 and 95 nesting pairs, respectively, for the entire estuary. From the 1977 census data of 1,610 breeding pairs in the State, it appears that Tijuana Estuary supports a substantial fraction of the remaining population. Only 5 of the 28 wetlands censused that year had larger
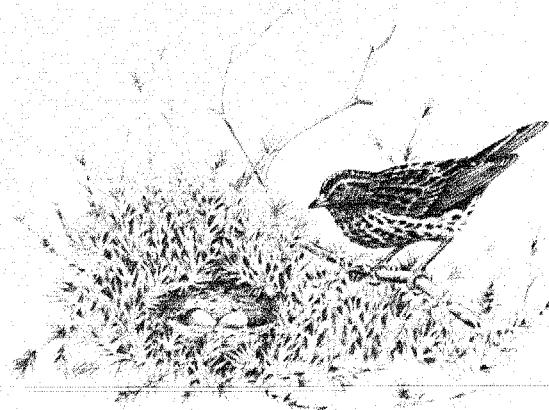
Figure 24. Belding's Savannah sparrow with ground nest in shore grass. McIntire collection, copyright 1986 by Zedler.

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populations (Massey 1979). The birds perch on the taller plants and defend territories throughout most of the summer. They eat insects in the marsh, but often fly to creek or channel banks or even to the beach to feed (B. Massey, private consultant, pers. comm.; and White, pers. comm.). Studies of their behavior, responses to disturbance, and habitat preferences are underway at Tijuana Estuary (White, in prog.).

Although pickleweed forms monotypic canopies in many of the region's lagoonal wetlands, i.e., those that close to tidal flushing on a fairly regular basis, it is usually mixed with several other succulents at Tijuana Estuary. Before 1984, arrow-grass (*Triglochin concinnum*) and sea-blite (*Suaeda esteroa*) were common cohabitants, and saltwort (*Batis maritima*) and annual pickleweed (*Salicornia bigelovii*) dominated areas that were poorly drained. The latter two species were most

abundant around intertidal pools of the middle marsh (Figure 25). Composition in this part of the marsh has changed greatly since 1980 (Chapter 5).

The animals of the midmarsh elevations are abundant and rich in species. Part of the reason is dependable moisture, and part is the availability of food. Algae are everywhere, in pools and under the salt marsh canopy (Zedler 1980, 1982a). In winter, filamentous green algae dominate the epibenthos, and in summer, filamentous blue-greens form dense tufted mats over the soil and plant stem bases (Figure 26). Over 70 species of diatoms occur within these filamentous mats (Zedler 1982a). The animals that utilize these foods include Ephydrid flies, whose larvae occur on decaying plant matter; California horn snails (*Cerithidea californica*); amphipods; and snails (*Assiminea* and *Melampus*, Figure 26). High
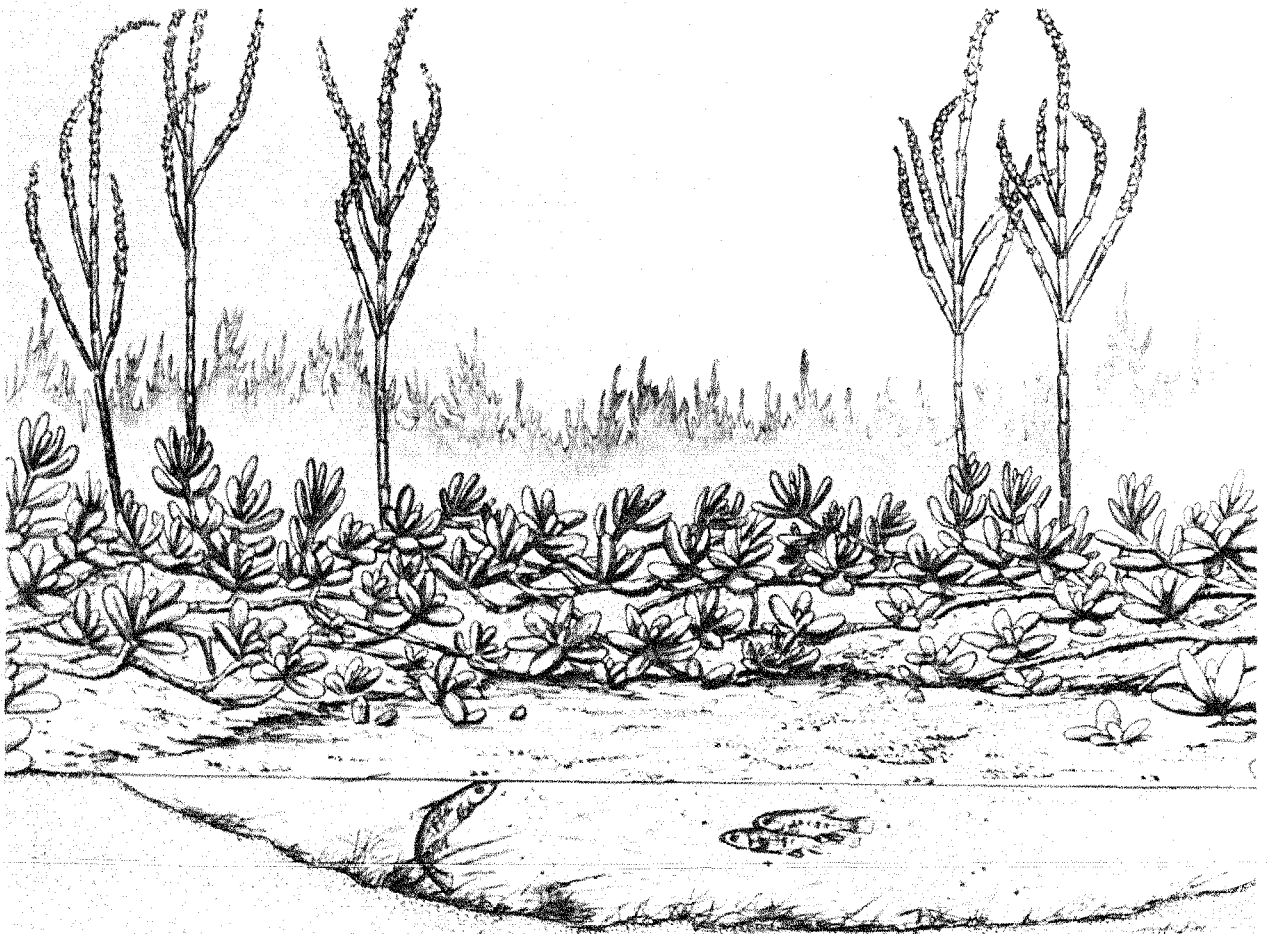
Figure 25. Intertidal pool with annual pickleweed (background) and saltwort (surrounding the pool). McIntire collection, copyright 1986 by Zedler.
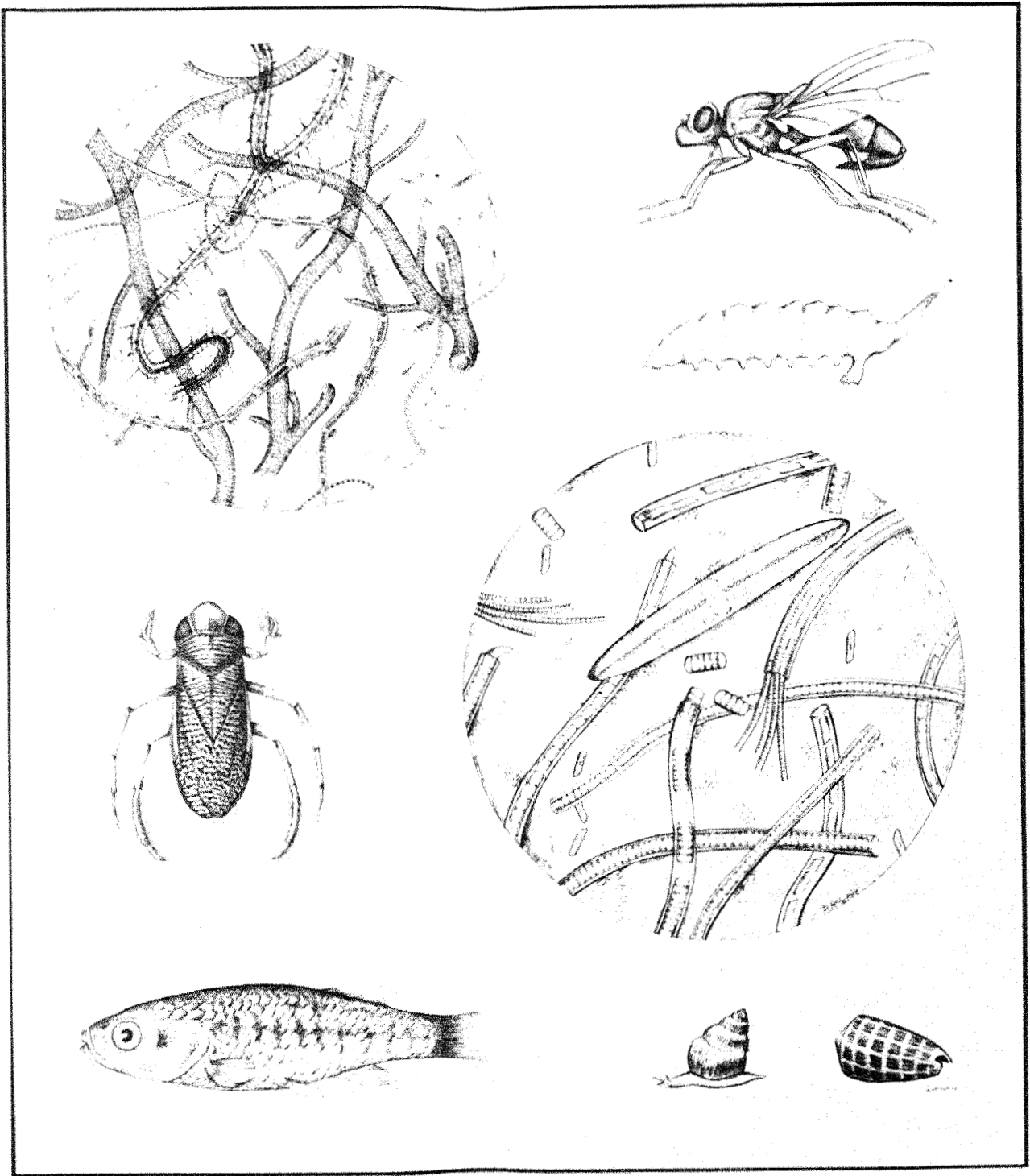
Figure 26. Organisms of the tidal pools include the green algae (upper left circle), *Enteromorpha* sp. (multicellular, branched tubes) and *Rhizoclonium* spp. (filaments) several blue-green algae (lower right circle), *Microcoleus lyngbyaceus* (wide filaments) and *Schizothrix* spp. (narrow filaments), and the diatoms *Gyrosigma obliquum* (in tubes) and *Trachyneis aspera* (lower left). The fly (*Ephydra*, Ephydridae; upper right), is abundant; adults feed on diatoms, the larvae on algae. The water boatman (*Trichcocorixia reticulata*, left middle) can be extremely dense in the pools. The small molluscs, *Assiminea* and *Melampus* (lower right), feed upon the algae and detritus; the California killifish (lower left) feeds on arthropods. McIntire collection, copyright 1986 by Zedler.

concentrations of insects, especially water boatmen (*Trichocorixia* spp.), occur in the pools. They feed on the algae and in turn provide food for the California killifish (*Fundulus parvipinnis*), which spawn and develop in these pools (Fritz 1975).

A variety of birds are often seen foraging in the midmarsh habitat. Common are the willet (*Catoptrophorus semipalmatus*), marbled godwit (*Limosa fedoa*), long-billed curlew (*Numenius americanus*), great blue heron (*Ardea herodias*), common egret (*Casmerodius albus*), and Belding's Savannah sparrow (White, pers. comm.).

The lower marsh of Tijuana Estuary is the most well-studied habitat of the entire system. The dominant plant, Pacific cordgrass (*Spartina foliosa*),

typifies this community (Figure 27). Cordgrass has proven easy to monitor (Zedler 1983b), amenable to transplantation (Zedler 1984), and responsive to manipulative experimentation (Covin 1984). Still, our knowledge of the total community is incomplete. Insects that live in and on the cordgrass are just beginning to be studied (Figure 28; Covin 1986). With new investigations, species that are new to science are discovered (e.g., *Incertella* sp. and *Cricotopus* sp., Figure 28). Both of these tiny insects have larvae that live within the leaves of cordgrass (J. Covin, SDSU, pers. comm.). Horn snails, lined shore crabs (*Pachygrapsus crassipes*), and yellow shore crabs (*Hemigrapsus oregonensis*) are abundant, but their habits are not well known. They feed on the algal mats and detritus and are themselves eaten by the larger marsh birds.
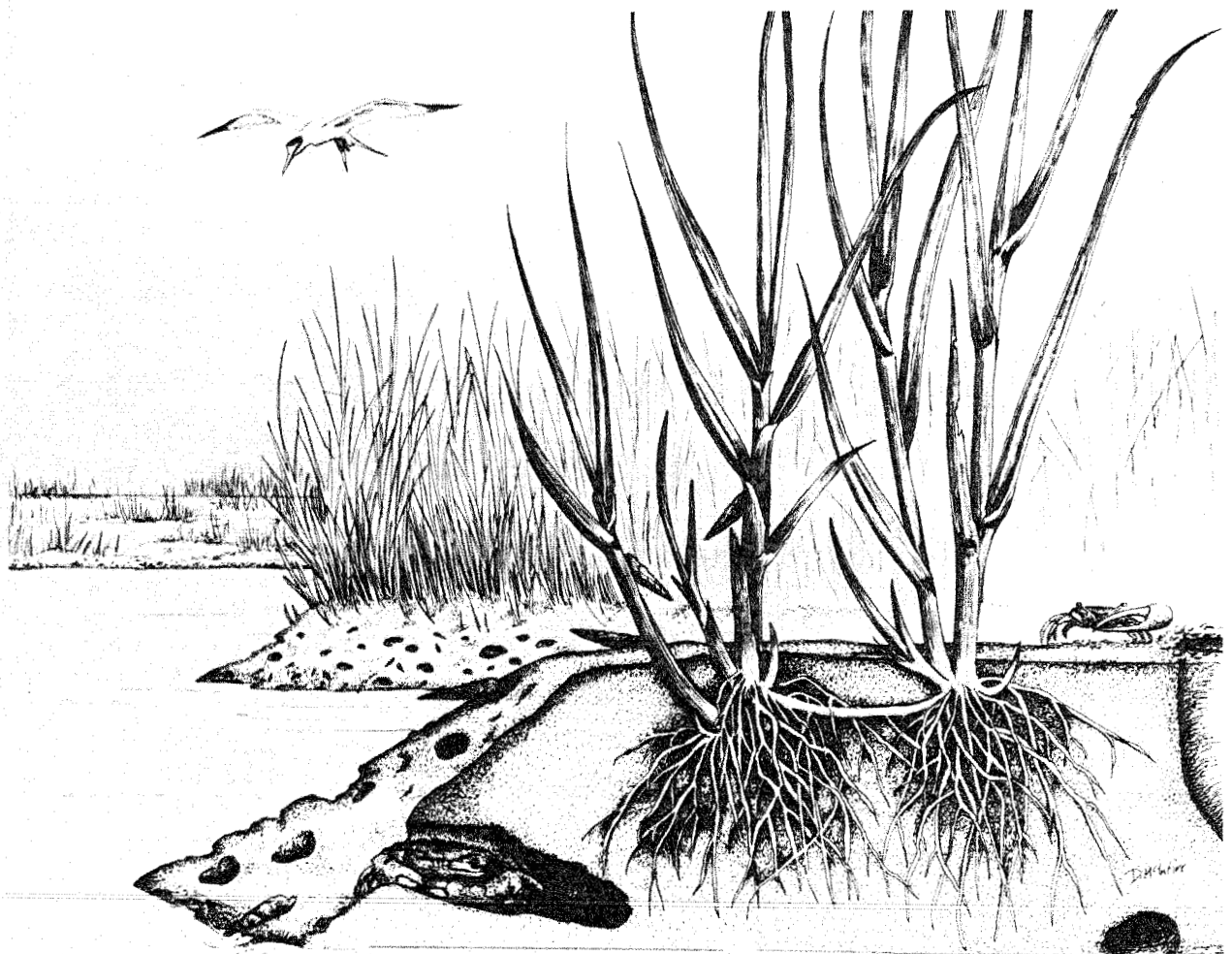
Figure 27. The cordgrass community, showing the fiddler crab (right) and the lined shore crab (in burrow). California horn snails are attached to the cordgrass stems and on the mud. A California least tern is poised, ready to dive for fish in the channel. McIntire collection, copyright 1986 by Zedler.
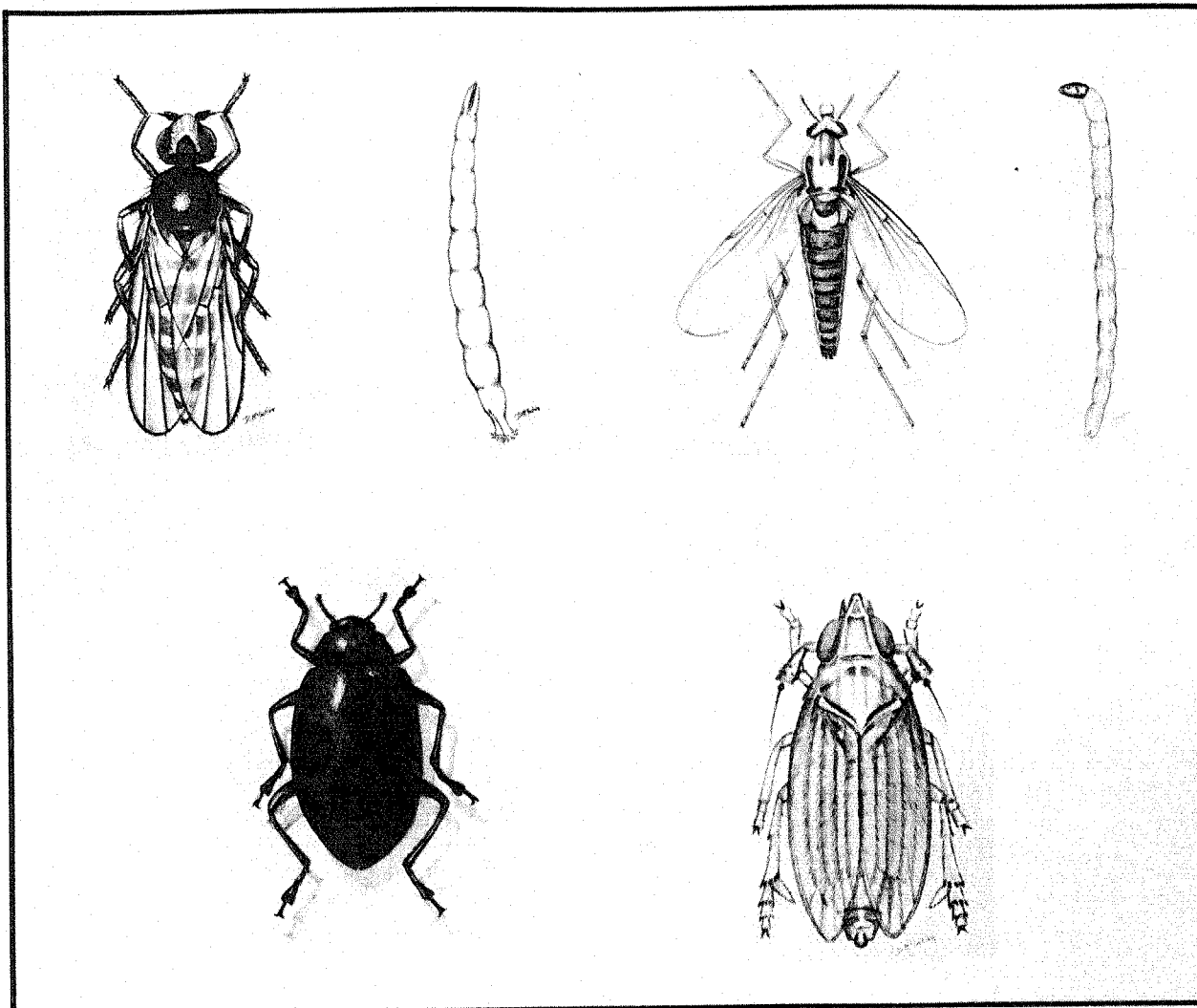
Figure 28. Insects of the cordgrass community. Two tiny dipterans, *Incertella* sp. (Chloropidae) and *Cricotopus* (Hydrobaeninae), have larvae that live in and feed on cordgrass stems; the beetle (*Coleomegilla fuscilabris*; Coleoptera: Coccinelidae) is abundant only on cordgrass; and the plant-hopper (*Prokelisia*; Homoptera: Delphacidae) is found on cordgrass in all the marshes of this region. McIntire Collection, copyright 1986 by Zedler.

No animal characterizes the lower marsh better than the light-footed clapper rail (Figure 29; Jorgensen 1975; Zembal and Massey 1981a,b). Jorgensen's (1975) study at Tijuana Estuary assessed the birds' occupancy, nesting, and foraging in five habitat types (high marsh, middle marsh, saltwort-annual pickleweed, short cordgrass, and tall cordgrass). Rails were censused in winter when tides exceeded 2.2 m (7.3 ft) MLLW and in summer using taped vocalizations. Thirty-four breeding pairs were identified in 1974, of which 18 were in tall cordgrass, 11 in middle marsh, 4 in short cordgrass, and 1 in high marsh. Nesting density (number per area of habitat type)

was greatest (about 3/ha or 1.3/acre) in tall cordgrass. The average elevation at which nests occurred was 1.6 m (5.1 ft) MLLW, which corresponded to the mean daily higher high tide (MHHW). The highest density of nests was observed in the northern arm of the estuary, where the single highest winter census count was 55 individuals. In comparison, a maximum of nine birds was counted in the area near the mouth of the estuary, and at most four in the southern arm of the estuary, where cordgrass is absent.

Jorgensen (1975) has suggested several advantages of cordgrass-dominated marshes for
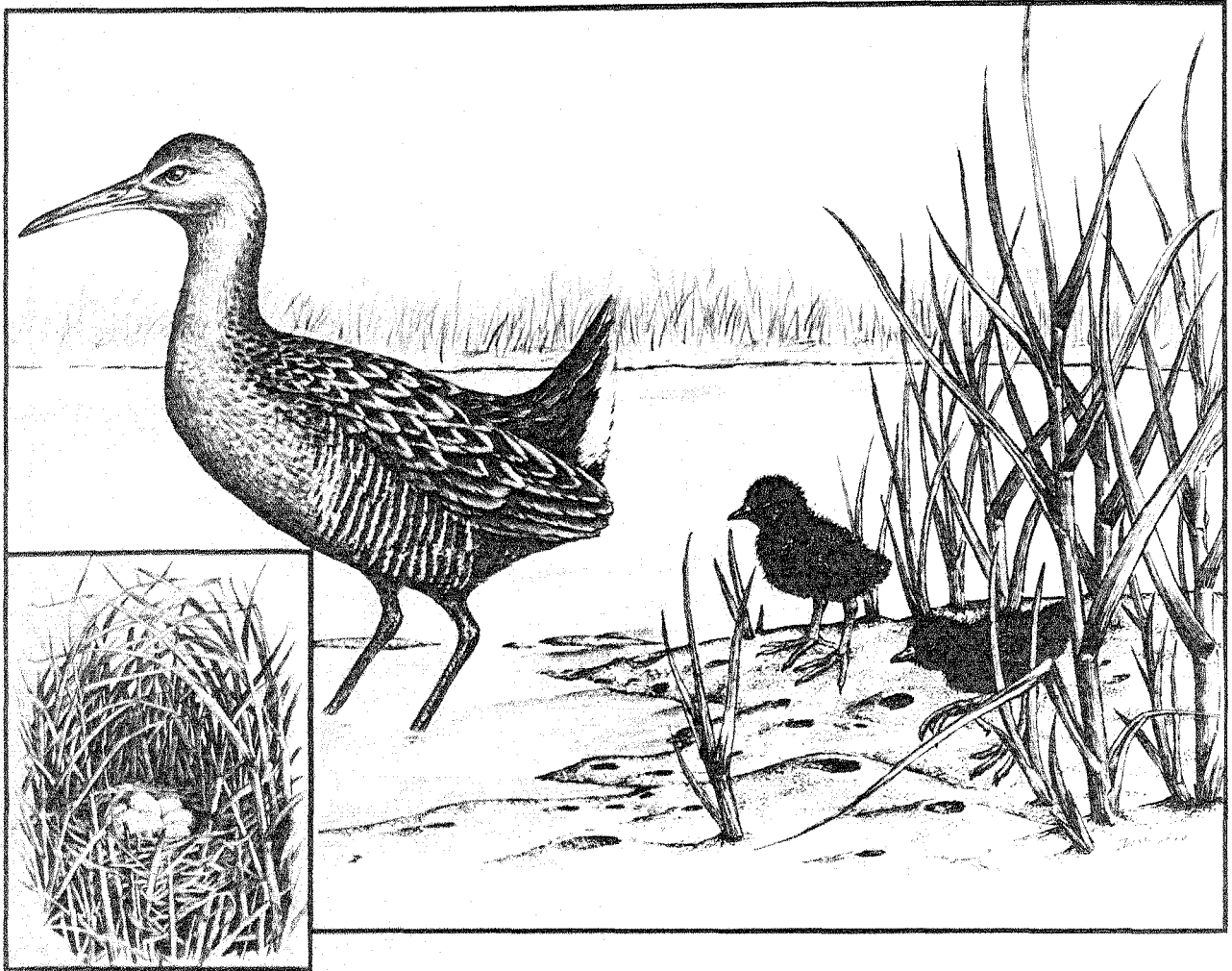
Figure 29. The light-footed clapper rail finds cover, food, and nesting material in the cordgrass marsh. Its nest is a masterpiece of construction, with a floating platform and protective arch, commonly made of cordgrass. McIntire collection, copyright 1986 by Zedler.

the rails. The tall grass provides cover for protection against predators and the birds weave a canopy of live stems over their nests (Figure 29). Both the egg and brood nests are woven of dead cordgrass stems. The nests that are anchored to vertical cordgrass stems can float, thereby preventing submergence; the nests in cordgrass can be more firmly anchored than elsewhere; the lower marsh areas are wetter and less accessible to terrestrial predators, and the black-colored chicks are camouflaged against the black substrate of the lower marsh. Finally, their most common foods occur in or near areas where cordgrass is abundant. Yellow shore crabs and lined shore crabs were the dominant items in regurgitated pellets analyzed by Jorgensen (1975). Further evidence of the species' relationship with tidal cordgrass marshes developed in 1984 when

cordgrass died and the Tijuana Estuary population of rails became extinct (Chapter 5).

The population of light-footed clapper rails at Tijuana Estuary has been censused frequently (Jorgensen 1975; Zembal and Massey 1981a,b; P. Jorgensen, Estuarine Sanctuary Manager, pers. comm.). Before 1985, the population fluctuated between 25 and 41 breeding pairs (Table 5). The year with peak population density was 1983, when cordgrass vegetation was luxuriant (Chapter 5). At that time, Tijuana Estuary supported 17% of the State's 249 breeding birds. Then, following the closure of the estuarine mouth in 1984, the March-April census of 1985 failed to locate any rails. Recorded bird calls were used to locate territorial pairs, but no breeding was indicated. Only four birds have been seen since then

Table 5. History of changes in the number of pairs of light-footed clapper rails at Tijuana Estuary. Data from Clapper Rail Recovery Team (unpubl.) and Jorgensen (pers. comm.).

Year	Tijuana Estuary No. of Pairs	California Total Pairs
1980	26	203
1981	31	173
1982	25	221
1983	41	249
1984	38	277
1985	0[a]	142

[a]Two individuals were sighted in 1985 at times other than the annual census: four birds were found in March 1986.

(Jorgensen, pers. comm.). Where they came from is unknown; some of the preclosure population may have emigrated upstream and survived in brackish marsh habitats.

For California as a whole, there was a major decline in light-footed clapper rails from 249 to 176 pairs in 1984 (Table 5), with heavy losses in other wetlands that remained open to tidal flushing. Reasons for the general decline are not clear. However, the 1984 extinction of the Tijuana Estuary population was probably due to a combination of stresses: reduced food supplies, poor cover, and lack of predator protection.

Light-footed clapper rails are considered to be generalists in terms of feeding, but direct observation and dissection of regurgitated pellets shows that the majority of foods come from channel and tidal creek habitats: marine decapods, isopods, snails, crabs, fishes, and some insects and spiders (Massey and Zembal 1979). With the 1984 drought, invertebrate populations declined, rails had few prey available, and starvation is a likely cause of bird mortality. Declining cover during the nesting season may have led to nesting failure by reducing the area of dense cordgrass for nest construction and by making nests and birds more visible to predators. Finally, the absence of tidal flushing greatly reduced protection from predators. Few mammals frequent habitats where tides saturate the soils twice a day, but in summer and fall 1984, there were few natural deterrents to terrestrial predators. Birds that had little cover and low food supplies would no doubt have been highly susceptible to predation; chicks would have been easy prey for dogs, cats, rats, and raptors.

It is likely that most of the rail populations throughout the region were reduced by mortality, rather than emigration, as alternative habitats are few and far from the coastal wetlands. The birds are found in the marshes of Estero de Punta Banda near Ensenada, Mexico. Habitat has also declined at this wetland, with a large part of the bay being dredged for construction of an oil-platform factory. Prospects for reestablishment of a genetically diverse population at Tijuana Estuary are slim, given the declines throughout the region (R. Zembal, USFWS, pers. comm.).

3.4 SALT PANNES

The salt pannes are upper intertidal areas that are devoid of vegetation. During winter, they accumulate rainfall and saline water from high spring tides in December through February; in summer, they are covered by a salt crust that forms with evaporation of salt spray and tidal water from high spring tides in May through July. Soil salinities of 200 ppt are common at the end of the dry season. Two contrasting communities can thus be found (Figure 30). During the winter aquatic phase, algae flourish and aquatic insects become abundant. Ducks utilize the shallow waters for feeding and resting. During the summer dry season, the habitat appears barren, because most of the resident insects and other arthropods live in the soil.

Because the dry season is longer than the winter inundation period, barren conditions prevail, hence, the habitat is called a salt panne, rather than a temporary tidal pond. The ephemeral nature of the inundated phase makes it difficult to appreciate how productive and complex these communities can be. It is often recommended in mitigation proposals that salt pannes be converted to some other use, because their wetland values are assumed to be low. Very little research has been done in salt pannes, so their habitat values have not been quantified.

Species that are characteristic of salt pannes have developed adaptations to extreme conditions such as prolonged inundation and high salt accumulation. Many soil-dwelling insects utilize "plastrons," or air traps, that allow them to respire when the water or soil is anaerobic (Foster and Treherne 1976). In addition, many have developed waterproof integuments and mechanisms for secreting hypertonic rectal fluids to regulate osmotic and ionic balance.

The most detailed study of salt panne insects conducted at Tijuana Estuary concerned rove beetles (Staphylinidae, Genus *Bledius*; Figure 31; Nordby 1984). Several species of these small beetles inhabit complex underground labyrinths that are evidenced at the surface by excavated

Figure 30. During winter (above) the salt pannes accumulate water from high spring tides and rainfall; during summer they dry and are covered by a white salt crust. Algae and ditch grass (*Ruppia maritima*) grow during the aquatic phase; pintails and other aquatic birds feed and rest there. In summer, abundant burrows of a diverse insect community are present. McIntire collection, copyright 1986 by Zedler.

"middens." The density of middens reaches 500/m^2; the tunnels beneath them are about 20 cm in depth. Densities of beetles were highest in March 1984, when 8 adults and 22 juveniles were recorded per 1,650 cm^3 core. Reproduction occurred in the spring with eggs attached to the sides of burrows by means of a clear, threadlike material.

Intertidal elevation is the most important physical variable that characterizes rove beetle distribution patterns. They are densest in a narrow belt at about the high tide line. The beetles appear to prefer soil dampened by tidal inundation but not covered by standing water. A typical biweekly fluctuation of midden densities occurs with the high summer tides: as a high tide recedes, midden mounds appear as the beetles begin to burrow, more densely at the region where the soils have begun to dry and less densely at the water's edge; as the soil dries, the middens accumulate as excavation activities continue; then, an ensuing high tide erases the surface middens, and the pattern is repeated. It is not known what happens
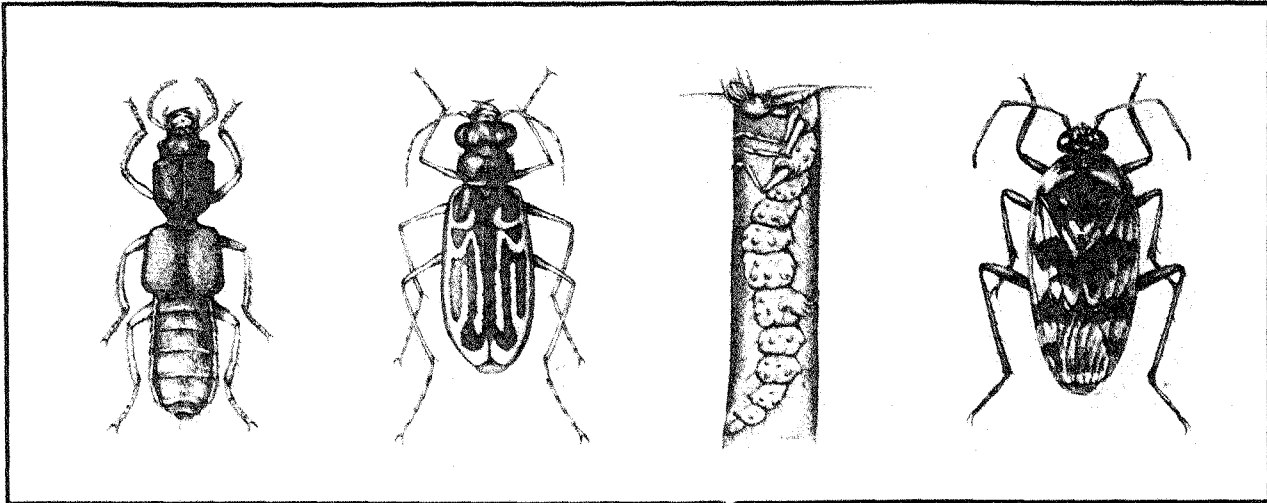
Figure 31. The salt panne insects include several species of rove beetle (*Bledius*; Coleoptera: Staphylinidae, on left), tiger beetle (adult shown in center is *Cicindela gabbi*; larva is *C. oregona*; Coleoptera: Cicindelidae), and bugs. The saldid bug (*Pentacora signoreti*; Hemiptera: Saldidae, 8 mm long), a very important predator, is abundant on all salt and mudflats from lower to higher marsh. McIntire collection, copyright 1986 by Zedler.

to the beetles during high tide. In studies of a Scandinavian species of *Bledius*, Larson (1953) found that these rove beetles evacuated tunnels during high tide and could be found beneath debris at the wrack line during such periods. This did not occur at Tijuana Estuary. Very few beetles were ever observed outside a burrow, regardless of tidal cycle.

Some insects that inhabit the salt pannes are considered "threatened." Threatened species are those whose range is declining due to loss of habitat and/or have been proposed as candidates for State or Federal listing. Among such insects are the tiger beetles (genus *Cicindela*). Tijuana Estuary supports the highest diversity and abundance of tiger beetles of any coastal locality in southern California and possibly all of California (C. Nagano, UC Santa Barbara Museum, pers. comm.). There are at least four species of this genus that occur here, two of which inhabit the salt pannes, although they have been observed there only in low numbers. These are the mudflat tiger beetle (*Cicindela trifasciata sigmoidea*) and Gabb's tiger beetle (*C. gabbi*, Figure 31).

Tiger beetles are predaceous; they feed upon any arthropods they can overpower. Adults are found on mud or sand near permanent bodies of water. Larvae inhabit burrows in the soil in the same area as the adults. The larvae (Figure 31) are also predaceous, using hooklike mandibles to capture and kill their prey, which is then consumed within the burrow. Because their prey includes insects that are harmful to man, these beetles are

considered beneficial. Tiger beetles are preyed upon by other salt panne and tidal flat insects including robber flies (Diptera: Asilidae) and dragonflies (Odonata: Anisoptera), and numerous vertebrates such as birds, reptiles, and mammals (D. McIntire, naturalist, pers. comm.).

Tiger beetles are considered to be good indicators of the disturbance to coastal systems (Nagano 1982); the least disturbed habitats have several species of tiger beetles. Although quantitative data from the period before closure of the estuary mouth are lacking, qualitative estimates indicate that populations increased significantly after the mouth was reopened (McIntire, pers. comm.).

Another group of insects that can be regarded as good indicators of disturbance are the true bugs of the order Hemiptera, family Saldidae. Several taxa of these insects occur on the least disturbed salt pannes. They have a wide salinity tolerance and are carnivorous, feeding on springtails, mites, and other insects and spiders. One member of this family, *Pentacora signoreli* (Figure 31), is very abundant at Tijuana Estuary. Individuals coated with salt crust have been observed on salt pannes, but the mechanism for tolerating such high salinities is not known (McIntire, pers. comm.).

Salt pannes are often used as foraging areas for Belding's Savannah sparrows, which feed on the insects there. California least terns and snowy plovers are both known to nest on salt pannes. Both species use preformed depressions, such as

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animal footprints, in the hardpan for nest scrapes. If there are patches of other substrate, such as sand or small wrack, the birds will create their own scrapes on these. When the pannes are inundated, snowy plovers also use them as feeding areas (White, pers. comm.).

3.5 BRACKISH MARSH

Habitats that typically have reduced water salinities (between 0.5 and 30 ppt) are considered brackish or mixohaline (Cowardin et al. 1979). In southern California, such habitats occur next to seepages or where rainfall or runoff is impounded. Evaporation then concentrates salts. Water levels fluctuate widely but irregularly. Due to differences in salinity and water levels, the plants and animals of the salt marsh are generally not found here. Instead, a community more characteristic of the region's freshwater marshes is found (Figure 32). Cattails (*Typha domingensis*) and bulrushes (*Scirpus californica*) are the usual dominants among the emergent species, while the submergent ditchgrass (*Ruppia maritima*) is abundant seasonally. Red-wing blackbirds (*Agelaius phoeniceus*) commonly set up territories in the tall, dense vegetation, and dragonflies (Odonata: Anisoptera; Figure 32) are obvious insect inhabitants.

At Tijuana Estuary, the areas of brackish marsh appear to have formed artificially following hydrologic and topographic modifications. The 1928 air photo (Figure 9) indicates that natural brackish marsh may have been present at the inland lagoon before a channel was dredged to make the area tidal. Before 1900, the area would have supported brackish marsh if sufficient rainwater accumulated or if seepages were present. In the absence of continual brackish or freshwater inputs, the depression would probably have been an alkali sink colonized by brackish species during wetter periods.

Brackish marshes are now found at the south end of the inland lagoon in an area fed by urban and airfield runoff; at the abandoned gravel pits, where rainfall accumulates, and at the southern end of the estuary, where sewage spills from Mexico through Goat Canyon provide an intermittent water source. The braided channels of the Tijuana River support ephemeral patches of brackish marsh, but their location and longevity relate to recent flooding and to spills of sewage or irrigation water.

The function of these brackish habitats relative to the estuarine ecosystem is under debate. Further north, there is evidence that springs were frequent around the intertidal wetlands, and various restoration plans have called for the creation of large areas of fresh-to-brackish marshes (e.g., State Coastal Conservancy plans for Orange County wetlands and for restoration of Los Cerritos Wetland; and the National Audubon Society's plans for restoration and enhancement of Ballona Wetland). Much of the presumed value of brackish marsh habitats comes from studies of Upper Newport Bay (Zembal and Massey 1981a), where the State's largest population of light-footed clapper rails persists. Rails use both brackish and salt marsh habitats at Upper Newport Bay and at San Elijo Lagoon, and the nontidal brackish marshes are a likely refuge for the birds during high water. Thus, the proximity of several small brackish marshes along the periphery of saline marshes may improve conditions for rails. The cause-effect relationships need to be tested, not just for rails, but for the variety of brackish and saline marsh species. Furthermore, the reciprocal interactions, i.e., the use of saline marshes by brackish species, need to be investigated.

It may well be that fresh and brackish marshes function as a general refuge for animals when the estuary has high water. It has been assumed that the Dairy Mart Road Ponds, about 5 km upstream of Tijuana Estuary, are used by estuarine birds, because many species are seen in both localities. These ponds occur in areas where gravel mining has left large pits; the water source is both river flow and ground water. Black-crowned night herons (*Nycticorax nycticorax*; Figure 33), black-necked stilts (*Himantopus mexicanus*), American avocets (*Recurvirostra americana*; Figure 34) and snowy egrets (*Egretta thula*; see cover of this report) are conspicuous among these tree-lined ponds.

Boland's (1981) study of shorebirds in Tijuana Estuary provides supportive data for the concept that ponds provide alternative resting and feeding sites during high tides. He compared bird use in the intertidal flats with that of the river and the inundated salt pannes at the southern end of the estuary (Figure 3). Of the 21 shorebird species found at Tijuana Estuary, 10 used both the river and pool habitats for feeding (Table 6). Nearby, in the blocked channel (an area that was once tidal), a somewhat different group of birds, including black-necked stilt, phalaropes, and willets were commonly found feeding (Figure 35). Heavy use of these nontidal areas by waders, sandpipers, and plovers shows that estuarine shorebirds are not restricted to intertidal habitats.

On at least one occasion, brackish marsh species expanded into the estuary under nontidal conditions. During the 1984 closure, red-wing blackbirds moved into the lower salt marsh and set up territories in the cordgrass. Their effect on native salt marsh birds (e.g., Belding's Savannah sparrows and clapper rails) was not assessed, but it should be before recommendations are made to add brackish marshes along the periphery of
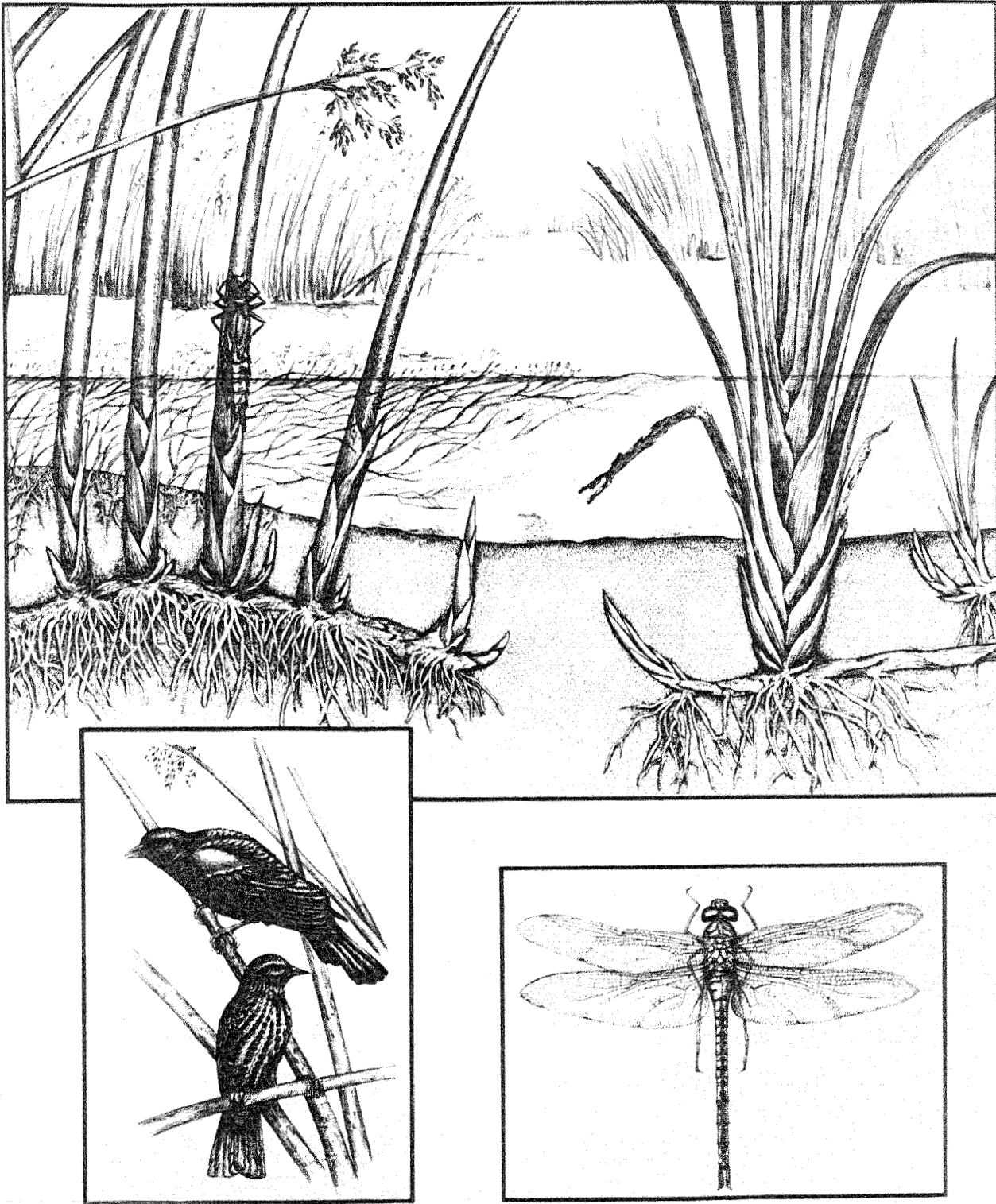
Figure 32. Brackish marsh habitats support large emergents, including bulrushes (*Scirpus americanus*) and cattails (*Typha domingensis*), as well as the submerged aquatic, ditch grass (*Ruppia maritima*). Dragonfly nymphs (on the bulrush stem) are common, as are adults, such as the green darner (*Anax junius*; Odonata: Aeschnidae). Red-wing blackbirds are characteristic residents of the emergent brackish marsh. McIntire collection, copyright 1986 by Zedler.

Tijuana Estuary salt marsh. Such experimental work will be possible with the creation of artificial fresh, brackish, and saline marshes at the Pacific Estuarine Research Laboratory (Chapter 6).
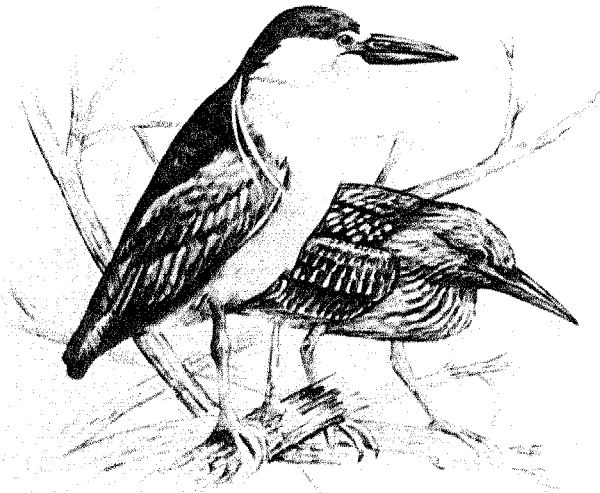
Figure 33. Black-crowned night herons. Juveniles (right) have streaked plumage. McIntire collection, copyright 1986 by Zedler.

Most of our understanding of how brackish marsh vegetation relates to saline conditions comes from studies at the San Diego River marsh (20 km north of Tijuana Estuary). There, 1980 floodflows were prolonged by reservoir discharge, and intertidal marsh soils were oligohaline (under 10 ppt) for 2-3 months. Cattails and several other brackish marsh species invaded and dominated the intertidal zone. As has been shown experimentally by Beare (1984), the adult cattails readily tolerate saline conditions. Some individuals in experimental treatments survived a year in 45 ppt water; aboveground parts died, but rhizomes were able to resprout when freshwater was resupplied. Thus, the limiting factors for invasion are seed germination, which declines to near-zero at 20 ppt, and the period of time required for the cattails to grow salt-tolerant rhizomes (estimated to be 2 to 3 months).

Once brackish species have invaded an intertidal area, it is likely that they will persist. With continually augmented streamflows, as would occur with upstream wastewater discharges, species with salt-tolerant, vegetatively reproducing adults might never die out. At San Diego River marsh, the cattail population that invaded in 1980 enjoyed a second expansion in 1983, when rainfall and streamflow continued late into spring. With drier conditions in 1984 and 1985, the population declined (Zedler and Beare, in press).

Figure 34. Black-necked stilts and American avocets (foreground) wade and feed in the open water of brackish habitats. McIntire collection, copyright 1986 by Zedler.

Table 6. Species that Boland (1981) saw feeding in the river and temporary pools at Tijuana Estuary. Data are frequency, i.e., the number of times the species was seen expressed as a percentage of the total number of visits to each habitat, and total numbers of birds censused (n = 10 visits to the river and 8 visits to pools).

Species	River	Pools
Least and western sandpipers	45[a]	88
Dowitcher	50	25
Willet	20	63
Greater yellowlegs	10	50
Black-necked stilt	80	63
American avocet	10	38
Semipalmated plover	10	25
Killdeer	90	100
Black-bellied plover	20	25
Total censused	226	1,019

[a]Averaged for the two species.

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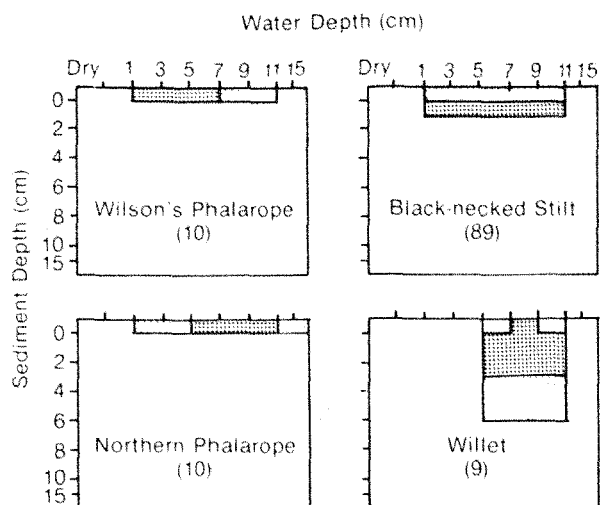
Figure 35. Comparison of feeding patterns for four species of birds that feed in the blocked channel of Tijuana Estuary. Foraging microhabitats (entire stippled area) were defined as the water depth where birds were observed feeding and the depth to which they probed the sediments; dense stippling indicates where species spent more than 80% of their time foraging; number in brackets is sample size (reprinted from Boland 1981 with author's permission).

3.6 ESTUARINE CHANNELS AND TIDAL CREEKS

The channel habitats are important for a variety of organisms including macroalgae, phytoplankton, invertebrates, fishes, and birds (Figure 36). The California least tern and other fish-eating species use deeper-water habitats, while shorebirds feed in the intertidal zone at low tide. Shorebird uses are discussed in the following section.

Channels are subjected to a wide range of environmental conditions. Tidal flushing is greatest at the mouth and decreases with distance from the mouth; this general gradient in turn influences water movement, salinity, temperature, nutrients, and dissolved gases. Finer sediments are removed by higher current velocities, so that substrates near the mouth have coarser sediments than in tidal creeks. Nutrients brought into the estuary by tidal flushing are more readily available to organisms near the mouth. Temperature, salinity, and dissolved oxygen are less variable in areas of deepest water than in tidal creeks. These environmental factors influence the species composition, distribution, and population dynamics of the channel organisms.

3.6.1 Algae

The obvious plants of intertidal and subtidal areas are the macroalgae. Vascular plants such as eelgrass (Zostera marina) are absent, perhaps because the area of shallow water is too small or too dynamic for rooted plants to become established. However, large populations of Enteromorpha sp. and/or sea lettuce (Ulva sp.; Figure 37) sometimes develop on the channel bottoms and later float to the water surface (Rudnicki 1986). Seasonal distribution patterns are highly variable, but their abundance is usually greatest in spring (Chapter 4).

Phytoplankton are also variable in species composition and density. Dinoflagellates (e.g., Gymnodinium spp.), diatoms, filamentous blue-green algae (cyanophytes), and unidentified unicells or "monads" are all present in the water column (Figure 37; Fong 1986). While most of these algae are typical planktonic species, the diatoms are all pennate forms with bilateral symmetry and longitudinal grooves that allow locomotion on substrates. Fong believes that most of these are resuspended from the sediments. The monads are so tiny (ca. 1-2 microns diameter) that identification is challenging; they appear to belong to the Cyanophyta (P. Fong, SDSU, pers. comm.). Many of the phytoplankton species also occur in nearshore habitats, where their densities are lower. During March-June blooms in the estuary, cell counts are higher than in marine waters by one to two orders of magnitude.

Both Rudnicki (1986) and Fong (1986) associate algal blooms with reduced tidal flushing. The air photo of March 1984 (Figure 13) shows high biomass of macroalgae in tidal creeks and along the shores of the abandoned sewage lagoons. Because the 1983 winter storm washed dune sands into the main estuarine channel, tidal flushing became sluggish and algal biomass accumulated. Likewise, algal growth was high during the nontidal period of 1984. Channel waters were green with phytoplankton during the summer (Chapter 4). During the 1985 monthly censuses of channel algae, Rudnicki and Fong found the highest biomass of both macroalgae and phytoplankton in small tidal creeks where current speeds were low.

3.6.2 Benthic Invertebrates

Studies of invertebrates at Tijuana Estuary have included resource inventories and short-term or species-specific investigations, but most were conducted before the catastrophic disturbances discussed in Chapter 2. Data collected from precatastrophic observations by a number of

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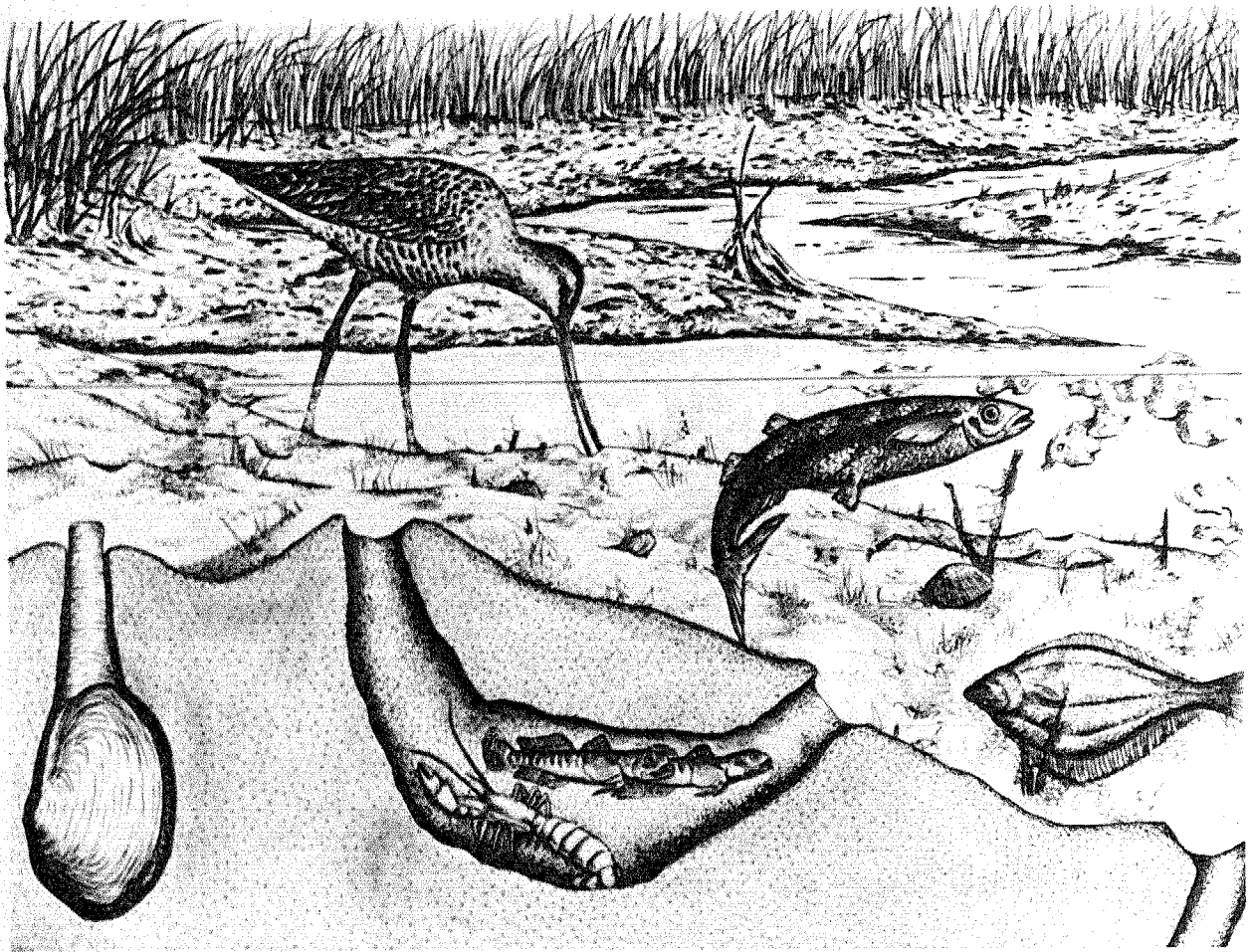
Figure 36. The channel and tidal creek habitats support an abundance of species including the marbled godwit, which probes the sediments for food, the topsmelt, which attaches its eggs to macroalgae, the diamond turbot, which feeds on the benthic organisms, and gaper clams (*Tresus nuttallii*), ghost shrimp, and commensal arrow gobies, which live within the sediments. McIntire collection, copyright 1986 by Zedler.

investigators (Bybee 1969; McIlwee 1970; Ford et al. 1971; Smith 1974; Peterson 1975; International Border Water Commission 1976; D. Dexter, SDSU, unpubl. data; and White and Wunderlich, unpubl.) are combined to depict the invertebrate community under more stable conditions (Table 7). More than 75 species of invertebrates, primarily benthic forms, were identified during this period.

Additional studies documented the effect of the 1980 flood (Rehse 1981) and the impoundment of 1984 (Griswold 1985). Griswold's observations and continuing monitoring by Dexter document recolonization in 1985 by invertebrate species that died during 1984's warm hypersaline conditions. In early 1986, however, most of the recolonists died out again under conditions of continual spills of raw sewage from Mexico. The present benthic

macrofaunal community is very different from that described in the 1970's.

Before 1980, the benthic community was dominated by bivalve molluscs, especially the purple clam (*Sanquinolaria nuttalli*), littleneck clam (*Protothaca staminea*), false mya (*Cryptomya californica*), California jackknife clam (*Tagelus californianus*), and bent-nose clam (*Macoma nasuta*). Polychaete worms, gastropod molluscs, and decapod crustaceans were also numerically important (Figure 38). Bivalve populations were sufficiently dense that hundreds of recreational clammers often took their limit on weekends (McIlwee 1970). In addition, ghost shrimp (*Callianassa californiensis*) were hydraulically harvested as bait (Bybee 1969).

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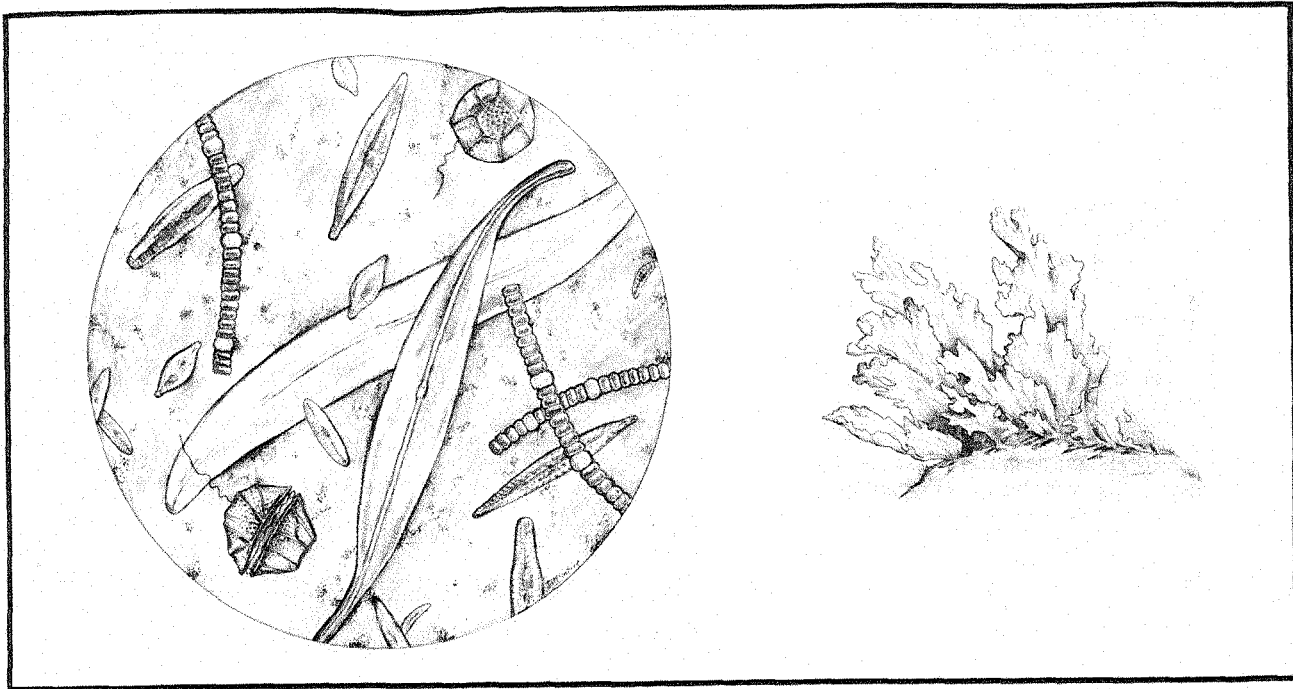
Figure 37. Channel producers include a phytoplankton community (on left) that includes blue-green algal filaments, dinoflagellates, such as *Gymnodinium*, and diatoms, such as the sigmoid *Pleurosigma* and *Gyrosigma*, and many species of *Navicula*. In addition, there is often an attached or floating mat of macroalgae (such as *Ulva*, shown on the right). McIntire collection, copyright 1986 by Zedler.

In general, the distributions of infauna are primarily influenced by sediment type. Most larval settlement is limited by substrate availability and adult distributions are influenced by grain size, pH, total organics, organic carbon and nitrogen, and dissolved oxygen. Filter feeders, such as the dominant bivalves, are associated with medium-sized grains because finer sediments contain too little organic material in suspension and because coarser sediments are too unstable. Finer sediments may also act to clog the filtering mechanisms. Deposit feeders, such as ghost shrimp and certain polychaetes, often occur on finer sediments, which have higher concentrations of organic carbon and nitrogen, but less dissolved oxygen and lower pH.

Hosmer (1977) found that distributions were correlated with sediment type for six species of bivalve molluscs that were common at Tijuana Estuary. Overall, there was a significant decrease in biomass of molluscs with smaller grain size, and the largest individuals were found in coarse, well-sorted sediments. Individual species exhibited a variety of patterns. The remaining nine species of bivalve molluscs found by Hosmer (1977) were not encountered frequently enough to characterize their distribution patterns.

Purple clams were present throughout a wide range of sediments. Higher biomass and densities were recorded in coarse sand, decreasing with finer sediments. This species was absent from sediments with high silt/clay contents. Littleneck clams occurred in very coarse to fine sediments with highest densities in finer sediments. Maximum biomass and density were found in 15%-20% silt/clay. False mya occurred in all sediment types from very coarse to very fine sand. Biomass and densities were bimodal, with highest values at around 35% silt/clay. California jackknife clams were collected in medium to fine sand. Biomass and density increased with a decrease in sediment size. Biomass was highest at 5%-10% silt/clay; density peaked at 20%-25% silt/clay; and size tended to decrease with higher silt/clay percentages. The bent-nose clam was found in sediments ranging from coarse sand to very fine sand. Biomass and density increased with a decrease in sediment size. Density and biomass were optimum at about 15% silt/clay. The white sand clam (*Macoma secta*) was found only in medium to fine sandy sediments and had the narrowest grain size distributional range. Both biomass and size of white sand clams were fairly constant with changes in grain size, although density was higher in medium sand.

Table 7. Invertebrates recorded from Tijuana Estuary before and after catastrophic flooding in 1980 and after closure to tidal flushing in 1984.

Organism	Pre-1980 (excluding Hosmer 1977)	Hosmer 1977	Rehse 1981	Griswold 1985	Dexter 1985
ECHINOID ECHINODERMS					
Dendraster excentricus	x			x	x
Molpadia avenicola				x	
SIPUNCULID WORMS					
Sipunculus nudus	x				
ECHIUROID WORMS					
Urechis caupo	x				
POLYCHAETE WORMS					
Axiothella rubrocincta	x				
Chaepopterus variopedatus	x				
Diopatra ornata	x				
Dipopatra spiendicissima	x				
Glycera dibranchiata	x			x	
Hapioscoloplos elongatus	x				
Nephtys spp.	x				
Nephtys caecoides	x				x
Nephtys californiensis	x				
Nephyts punctata	x			x	
Notomastus tenuis	x				
Ophelia limocina	x				x
Owenia fusiformis	x				
Magelona pitelkai	x				
Polydora spp.				x	x
Serpula vermicularis				x	
Glycera caitata					x
Amandia brevis					x
Prionospro spp.					x
Capitellidae					x
Goniadidae					x
Lumbrineridae					x
Magelonidae					x
Maldanidae					x
Orbiniidae					x
Phyllodocidae					x
Syllidae					x
BIVALVE MOLLUSCS					
Chione californiensis	x		x		x
Chione fluctifraga	x		x		
Chione undatella	x	x	x	x	x
Cryptomya californica	x	x	x		
Cooperella subdeaphana	x				
Diplodonta orbellus	x				
Donax californicus	x				x
Florimetis obesa	x	x			
Laevicardium substraitum	x	x		x	x
Leptopectin latiauratus	x		x		
Lucina nuttalli	x	x			
Macoma nasuta	x	x		x	x
Macoma secta	x	x			
Mactra californica	x	x			x
Mytilus edulis	x	x		x	x
Ostrea lurida	x			x	
Protothaca lacineata	x				
Protothaca stammea	x	x	x		x
Sanguinolaria nuttalli	x	x	x		
Saxidomus nuttalli	x	x			
Siliqua patula	x				

(continued)

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Table 7. *(Continued)*.

Organism	Pre-1980 (excluding Hosmer 1977)	Hosmer 1977	Rehse 1981	Griswold 1985	Dexter 1985
BIVALVE MOLLUSCS (Continued)					
Tagelus californianus	X	X	X		X
Tagelus subteres	X				
Tellina carpenteri	X	X			X
Tresus nuttalli	X	X			
Musculus senhousei	X				X
Spisula planulata				X	
Salen rosaceus					X
GASTROPOD MOLLUSCS					
Acteocina faculta	X				
Aplysia californica	X			X	X
Assiminea californica	X			X	X
Bulla gouldiana	X				X
Cerithidea californica	X			X	X
Crepidula fornicata	X				
Melampus olivaceus	X				
Nassarius fossatus	X				
Nassarius tegula	X				
Navanax inermis	X				X
Olivella batica	X				
Olivella biplicata	X				X
Polinices lewisii	X				
Crepidula onyx	X				
Collisella limatula				X	
Famincea vesicula				X	X
Serpulorbia scuamigeris				X	
Acteccina culcitella					X
DECAPOD CRUSTACEANS					
Callianassa californiensis	X			X	X
Callianassa gigas	X			X	
Cancer sp.	X				
Emerita analoga	X				
Hemigrapsus oregonensis	X			X	
Losorhynchus crispatus	X				
Pachygrapsus crassipes	X			X	
Pinnixa franciscana	X			X	
Portunas xantusi	X				
Scleroplax granulata	X				
Speocarcinus californiensis	X				
Uca crenulata	X			X	
Upogebia sp.	X				
Callianassa affinis				X	
Cancer antennarius				X	
Cancer productus				X	
Spirontocaris palpator				X	
Pagurus niritusculus				X	
Pagurus samuelis				X	
CIRRIPED CRUSTACEANS					
Balanus glandula				X	
Balanus amphitrite				X	
ISOPOD CRUSTACEANS					
Excirolana chiltoni	X				
AMPHIPOD CRUSTACEANS					
Eohaustorius washingtonianus	X				
Jassa falcata				X	
Ampithoe plumosa				X	

(continued)

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Table 7. *(Concluded)*

Organism	Pre-1980 (excluding Hosmer 1977)	Hosmer 1977	Rehse 1981	Griswold 1985	Dexter 1985
CNIDARIA (COELENTERATES)					
Pienilla kalliberi	x				
Corymorpha palma	x				
PLATYHELMINTHES					
Nemertia spp.					x
Stylochus sp.	x				x
Turbellaria spp.					x
HEMICHORDATA					
Saccoglossus sp.	x				
PHORONIDA					
Phoronis architecta	x				
BRACHIOPODA					
Glottidia albida				x	

In her studies of littleneck clams, Smith (1974) concluded that size and density increased with increasing tidal depth. She found average densities as high as 207/0.25 m² in the subtidal areas compared to 20/0.25 m² in the intertidal zone. She cited sediment grain size, temperature, salinity, duration of feeding time, and probability of predation as factors affecting survivorship of this species. Increased food availability and substrate stability are also associated with deeper water.

Niesen (1969) sampled areas near the mouth of Tijuana Estuary to characterize the sand dollar (*Dendraster excentricus*) population. Densities at that time ranged from 60-250/m² with a mean of 170/m² (n = 10). This species became locally extinct after storms and flooding in 1978 lowered water salinities. Its inability to reestablish appears to be related to recurring low salinities with more frequent river and wastewater flows entering the estuary in recent years.

The dominant crustacean in the estuary, the ghost shrimp, was studied by Homziak (1977). This species is of particular interest because it was once commercially harvested as fish bait. Hosmer (1977) investigated its competitive interactions with two sympatric burrowing shrimp of the same family: *Callianassa gigas* and a *Upogebia* species. His work suggested that the distribution and abundance of *C. californiensis* and *Upogebia* species are determined by specific substrates,

while *C. gigas* appears to be controlled by competitive interaction with the other two species, due to broad overlap in substrate and food exploitation.

Peterson (1975) took a more general approach to the study of the benthos at Tijuana Estuary and compared their interspecific relationships and community stability with those at Mugu Lagoon, California, 300 km to the north. Comparing the subtidal, sandy bottom habitats of the two areas, he found that the dominant macroinvertebrates each occupied a characteristic depth within the sediments. Sand dollars occupied the top few centimeters (Figure 38) and each had most of its test exposed to the water column. Littleneck clams were found within the top 6 cm. Ghost shrimp and its obligate commensal, false mya, occurred together at 0-55 cm. There was some overlap with the purple clam, which was found at 25-55 cm. The California jackknife clam burrowed up to 60 cm deep. Peterson attributed their vertical separation to competition for space, because there was little segregation in food utilization. All but one were suspension feeders; thus, they used the same food source, regardless of burial depth.

Tijuana Estuary and Mugu Lagoon had similar dominant species, but densities and relative abundances were very different (Table 8). The purple clam and California jackknife clam were much more abundant at Tijuana Estuary, which

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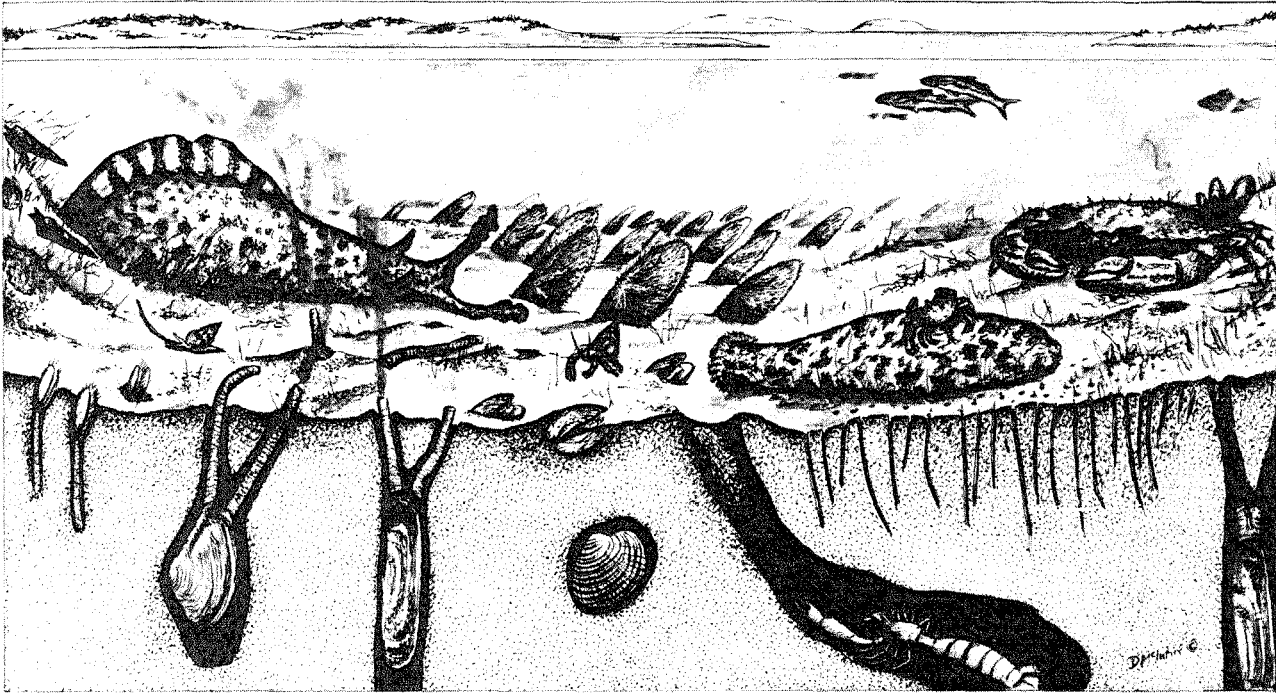
Figure 38. The channel benthic community includes a wide variety of invertebrates. Illustrated are mullet in the water column; surface benthic animals from left to right: the horn snail, sea hare (*Aplysia*), mud snails (*Nassarius*), sand dollars, hermit crabs (*Pagurus*), egg cockle (*Laevicardium*), sea cucumber (*Molpadia*) and its commensal pea crab (*Pinnixia barnharti*), and the crab (*Cancer productus*) with attached mussels (*Mytilus edulis*); and burrowing in the sediments from left to right: the mud-flat brachiopod (*Glottidia albida*), bent nose clam, Californa jackknife clam (*Tagelus californianus*), wavy chione (*Chione undatella*), ghost shrimp, and spionid worms. McIntire collection, copyright 1986 by Zedler.

Peterson (1975) thought was due to the rarity of other deep-burrowing competitors. Hydraulic harvesting of callianassid shrimp was common at Tijuana Estuary during the 1960's and 1970's; their removal, according to Peterson, allowed the clams to expand their populations with little effect on other dominant species. Manipulative field experiments supported his interpretation of the data.

During the winters of 1977-78, 1978-79, and 1979-80, San Diego County had unusually heavy rains, culminating in the flood of 1980 when approximately twice the normal precipitation and 28 times the mean annual streamflow were recorded. The influx of fresh water lowered channel salinity to zero ppt, and the increased streamflow significantly altered the sediment structure of the channel bottoms.

As a result of the flood, sediment grain size decreased at three of five sampling sites and increased at two (Rehse 1981). If sediment characteristics control species composition, then three predictions regarding silt/clay deposition would follow from Hosmer's (1977) study: (1) The purple clam should be most affected, because it was confined to coarser sediments; (2) the littleneck clam should be less affected because its highest density and biomass were at 15%-20% silt/clay; and (3) the false mya should be least affected, because their maximum biomass and densities were at 35% silt/clay.

In 1980, Hosmer resampled several areas that were included in his 1977 thesis work, and Rehse (1981) compared the two data sets on bivalves and callianassid shrimp. Flooding caused mass mortalities of many species. Absent from the 1980 collections were the yellow clam (*Florimentis obesa*), egg cockle (*Laevicardium substriatum*), bentnose clam, white sand clam (*Macoma secta*), California mactra (*Mactra californica*), Washington clam (*Saxidomus nuttalli*), Carpenter's tellen (*Tellina carpenteri*), and *Callianassa gigas*. The dominant bivalve before the 1978-80 period was the purple clam, while the dominant in 1980 was false mya.

Table 8. Average density (number/m²) and relative abundance (percent of total individuals) for each of the most numerous species of sandy bottom communities at Mugu Lagoon and Tijuana Estuary (modified from Peterson 1977).

Organism	Mugu Lagoon		Tijuana Estuary	
	Density	Rel. abund.	Density	Rel. abund.
Cryptomya californica false mya	269	47	2	1
Callianassa californiensis ghost shrimp	87	15	3	2
Protothaca staminea littleneck clam	58	10	35	19
Sanguinolaria nuttalli purple-hinged clam	46	8	75	42
Dendraster excentricus sand dollar	36	6	23	12
Tagelus californianus jackknife clam	9	2	14	8

Juvenile recruitment was high after the 1980 floods, particularly for ghost shrimp, whose density increased 72% while biomass decreased 95%. Significant decreases in mean size were also recorded for ghost shrimp, blue mud crab, and purple clam, indicating that mass mortality was followed by recruitment. However, the mean sizes of two species (false mya and littleneck clam) were not significantly less than in 1977, which suggested that both survived the stresses of reduced salinity and altered substrate.

These postflooding data bore out the prediction from Hosmer's (1977) work that the benthic macrofauna is strongly associated with sediment particle size. Other authors suggest that lowered salinities were also responsible for compositional changes in 1980 (Zedler et al. 1984b), after earlier flood events at Tijuana Estuary (Peterson 1975), and after flooding at Mugu Lagoon (Peterson 1975; Onuf, in press). Smith (1974) observed that the littleneck clam was not affected by low winter salinities; however, her study did not take place during a flood year.

While the benthic community was still recovering from the 1980 flood, Tijuana Estuary experienced other hydrologic changes. In 1983, reservoir discharges enhanced streamflow for most of the year, and estuarine salinities were below that of sea water in summer. Closure to tidal flushing in 1984 first impounded brackish water (ca. 15 ppt) during winter and then saline to hypersaline water through summer and fall. The extremes of salinity and stagnant water affected the channel and tidal creek invertebrate communities. Unusual species were noted in the estuary for the first time.

Swimming crabs (*Portunus* sp.) were so abundant in 1984 that some people collected bucketfuls for food (Jorgensen, pers. comm.). Casual sampling of the benthos during closure produced mainly polychaete worms (Spionidae, Figure 39), amphipods (Corophidae), and water boatmen (*Trichocorixia*; K. Dyke, SDSU, pers. comm.). The polychaetes and amphipods dominated these collections, constituting 97% of the specimens taken from both the algae-covered tidal flats and sandy intertidal areas. Mean densities as high as 16,500 animals/m² were encountered (Dexter, unpubl. data).

After the estuary had been restored to tidal flushing, Griswold (1985) conducted a qualitative benthic invertebrate survey of several habitat types (Table 7). Eight species of bivalves were present in 1985, although none occurred in high densities. Eight had also been recorded in 1980, but only two species (jackknife clams and wavy chione) were common to both inventories. A single specimen of wavy chione had been collected by Rehse. In addition, Griswold collected several species that were not previously recorded from the estuary (Table 7). A small population of sand dollars (*Dendraster excentricus*) was detected on a sandy area of the main north channel in 1985. The largest individuals recorded were 13 mm in diameter. This species had not been recorded in the estuary since the 1978 flood (Dexter, pers. comm.).

Certainly, the compositional changes of the past several years have been complicated. The ability of various species of estuarine invertebrates to withstand physiological stress induced by sudden
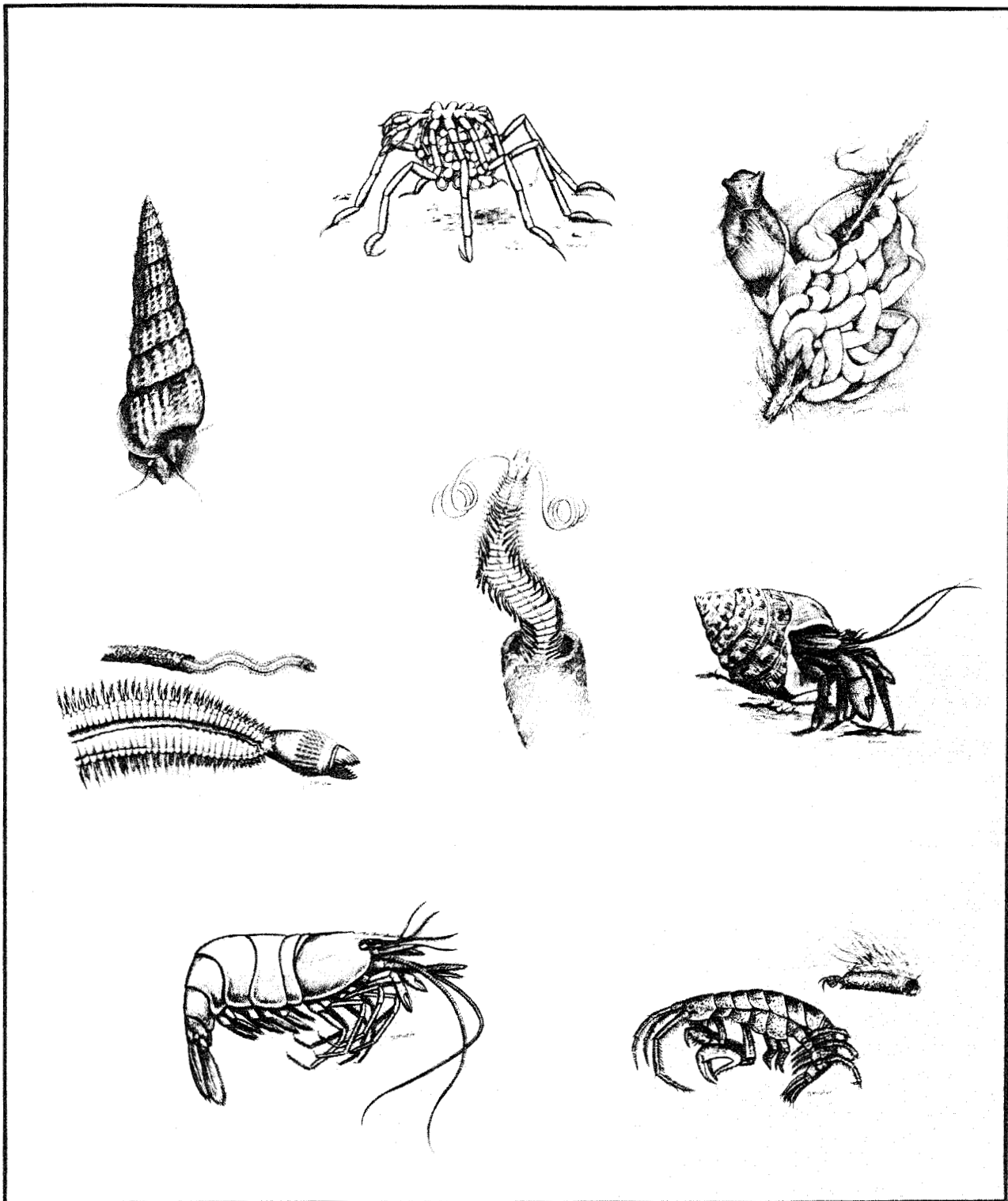
Figure 39. Invertebrates of the channels and tidal creeks include, in the top row, California horn snail, sea spider (*Ammothella biunguiculata* var. *californica*, male with eggs), white bubble snail (*Haminoea vesicula*); in the middle row, fire worm (*Nephtys caecoides*), spionid worm (*Polydora* sp.), hairy hermit crab (*Pagurus hirsutiusculus*; and on the bottom row, broken back shrimp (*Spirontocaris palpator*), and amphipods (e.g., *Jassa falcata*). McIntire collection, copyright 1986 by Zedler.

changes in environment has not been fully examined. The short-term tolerance of selected species to reduced salinity is being tested (D. Kyle, SDSU, pers. comm.), and it appears that adults of several species can survive widely ranging conditions for at least 4 weeks. Whether or not those same species could reproduce under the same conditions or survive several months of altered salinity is not yet known. The ability of invertebrates to recover from extreme conditions is largely determined by their life history characteristics, but chance also plays a role. Species with large numbers of larvae present at the time when estuarine habitats are accessible and suitable for settling will have the highest probability for recruitment. The qualitative data for 1985 indicate that recruitment from ocean waters can occur rapidly, once conditions become favorable,

and that a variety of species can become established within one year. A benthic monitoring program will begin in 1986 to track future shifts in or stabilization of benthic community structure.

3.6.3 Fishes — Adults and Juveniles

The distribution and abundance of the fishes that use the channel habitats of Tijuana Estuary have also been affected by the variable tidal regimes and climatic catastrophes. These disturbances affected the fishes directly by physiological stress and indirectly by elimination of food items.

Before the 1978 flood, 29 species of fish were found in Tijuana Estuary (Table 9). The community

Table 9. Fishes and rays recorded from the Tijuana Estuary (Zedler et al. 1983b).

	Source of data						
	Ford et al. 1971[a] Sites			IBWC 1976	White and Wunderlich	Nordby 1982	
					Unpubl.	Larvae	Eggs
Organism	1	2	3				
ATHERINIDAE (Silversides):							
Atherinops affinis - topsmelt	1	324	119	x[b]	A[c]	x[d]	x
BATRACHOIDIDAE (Toadfishes):							
Porichthys myriaster - specklefin midshipman				x	U		
BLENNIDAE (Combtooth blennies):							
Hypsoblennius gentilis - bay blenny	6	0	< 1	x	C	x[d]	
BOTHIDAE (Lefteye flounders):							
Citharichthys spp. - sanddabs							x
Paralichthys californicus - California halibut	8	0	7	x	A	x	x
CLUPEIDAE (Herrings):							
Sardinops sagax caeruleus - Pacific sardine						x	x
COTTIDAE (Sculpins):							
Artedius harringtoni - scalyhead sculpin						x	
Leptocottus armatus - staghorn sculpin	11	12	14	x	A	x	
CYNOGLOSSIDAE (Tonguefishes):							
Symphurus atricauda - California tonguefish				x	U		x
CYPRINODONTIDAE (Killifishes):							
Fundulus parvipinnis - California killifish	29	692	3	x	A	x	
DASYATIDIDAE (Stingrays):							
Urolopus halleri - round stingray				x	U		
EMBIOTOCIDAE (Surfperches):							
Amphistichus argenteus - barred surfperch	32	25	30	x	U		
Cymatogaster aggregata - shiner perch				x	U		
Hyperprosopon argenteum - walleye surfperch				x	U		

(continued)

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Table 9. (Concluded).

	Ford et al. 1971[a] Sites			IBWC 1976	White and Wunderlich Unpubl.	Nordby 1982 Larvae	Nordby 1982 Eggs
Organism	1	2	3				
ENGRAULIDAE (Anchovies):							
Anchoa compressa - deepbody anchovy					C		
Anchoa delicatissima - slough anchovy	0	4	<1	x	C		x
Engraulis mordax - northern anchovy						x	x
GOBIIDAE (Gobies):							
Clevelandia ios - arrow goby	245	1,896	15	x	C	x[d]	
Gillichthys mirabilis - longjaw mudsucker				x	C	x	
Ilypnus gilberti - cheekspot goby	534	0	32	x	C	x[d]	
Quietula y-cauda - shadow goby	29	0	0	x	C	x[d]	
KYPHOSIDAE (Sea chubs):							
Girella nigricans - opaleye	31	44	<1	x	C	x	
LABRIDAE (Wrasses):							
Semicossyphus pulcher - California sheephead							x
MUGILIDAE (Mullets):							
Mugil cephalus - striped mullet				x	A		
MYLIOBATIDAE (Bat rays):							
Myliobatus californicus - bat ray				x	R		
OPHIDIIDAE (Cusk-eels):							
Otophidium scrippsi - basketweave cusk-eel							x
PLEURONECTIDAE (Righteye flounders):							
Hypsopsetta guttulata - diamond turbot	47	0	16	x	A	x	x
Pleuronichthys coenosus - C-O turbot							x
Pleuronichthys ritteri - spotted turbot				x	A	x	x
Pleuronichthys verticalis - hornyhead turbot						x	x
RHINOBATIDAE (Guitarfishes):							
Rhinobatus productus - shovelnose guitarfish				x	R		
SCIAENIDAE (Croakers):							
Genyonemus lineatus - white croaker				x	U	x	x[d]
Menticirrhus undulatus - California corbina				x	U	x	x[d]
Seriphus politus - queenfish						x	x[d]
SCOMBRIDAE (Mackerels):							
Scomber japonicus - Pacific mackerel						x	x
SERRANIDAE (Sea basses):							
Paralabrax clathratus - kelp bass				x	U		
Paralabrax maculatofasciatus - spotted sandbass				x	C		
Paralabrax nebulifer - barred sandbass	5	0	<1	x	C		
SPHYRAENIDAE (Barracudas):							
Sphyraena argentea - California barracuda						x	x
SYNGNATHIDAE (Pipefishes and Seahorses):							
Syngnathus leptorhynchus - bay pipefish				x	U	x	

[a]numbers = individuals/500m^2

[b]x = species present

[c]A = abundant, C = common, U = uncommon, R = rare

[d]The larvae or eggs of these species could not be identified to the species level. It is likely that the species are represented, however.

was dominated by goby species, California killifish (*Fundulus parvipinnis*), and topsmelt (*Atherinops affinis*), striped mullet (*Mugil cephalus*), and longjaw mudsucker (*Gillichthys mirabilis*; Figure 40), all of which are considered resident species. Commercial/recreational species that use the estuary include California halibut (*Paralichthys californicus*), surfperches, anchovies, pleuronectids, croakers, and sea bass, although none of these occur in high numbers relative to so-called residents.

Nordby (SDSU, unpubl. data) sampled three sites for adult and juvenile fishes from August to November 1979, and from mid-February through March 1980, using a 1/4-inch-mesh seine. Sampling was interrupted from late November to mid-February due to flooding, and the sampling effort was abandoned after mid-March because of flood-induced changes. The catch from five sampling dates was dominated by topsmelt and included eight other species. During late January and early February 1980 and again in mid-February through March, major flooding in the estuary lowered salinities to zero. Samples collected after the 1980 flood had fewer species, with topsmelt and mullet most abundant. These data support the findings of other investigators in
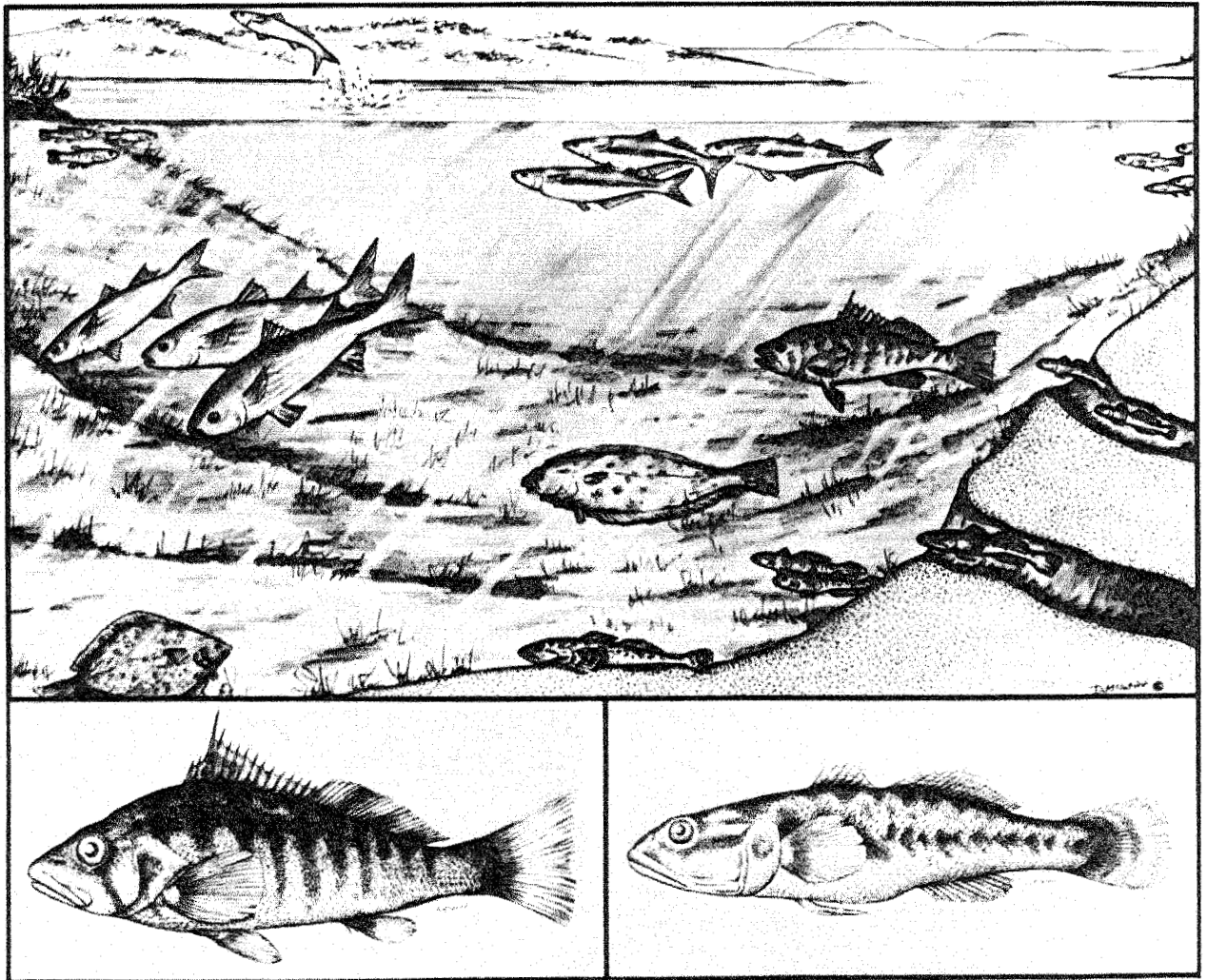
Figure 40. The fish community includes killifish (upper left and upper right, in shallow water), mullet (above water and left center), topsmelt (center, near surface), barred sandbass (right, in water column), diamond turbot (lower left, on substrate), California halibut (center, on substrate), staghorn skulpin (center foreground, on bottom), cheekspot goby, longjaw mudsucker (in lower burrow) and arrow gobies (in upper burrow). Enlarged below are the longjaw mudsucker and barred sandbass. McIntire collection, copyright 1986 by Zedler.

similar habitats, which indicate that species diversity decreased after periods of reduced salinity (Allen 1980; Onuf and Quammen 1983).

The effects on fishes of the 1984 closure to tidal flushing were examined in the fall of 1984 (C. Donohoe, SDSU, unpubl. data). At this time the mouth had been closed for approximately 6 months. Water levels were lower than normal, salinities were as high as 60 ppt, and many areas of former mudflat were sunbaked and cracked. Fish were collected by means of a 1/4-inch-mesh bag seine at seven locations. Of the 575 individuals caught, 74% were topsmelt, 22% were California killifish, and 4% were longjaw mudsucker. All of the species collected during mouth closure have wide salinity tolerances (Zedler et al. 1984b). It is likely that gobies and mullet were undersampled by this sampling technique. Many gobies can take refuge in burrows or pass through a 1/4-inch-mesh seine, while mullet can escape around or over most seines. However, since both Nordby and Donohoe used the same sampling gear, it is clear that diversity of fishes was lower in 1984 than in the 1970's.

The most abundant species collected in 1979-80 and in 1984 was topsmelt. A comparison of the length-frequency distribution of this species showed significantly smaller size during 1984 (Figure 41). The decrease may have resulted from size-selective mortality due to increased salinity and temperature, with the larger, older individuals being eliminated. Alternatively, suboptimal conditions may have stunted the older fish. In 1981, when the estuary had good tidal flushing, Nordby (1982) found that peak topsmelt spawning occurred from April through June. The 1984 closure occurred in April and continued through October, so it is likely that the 1984 topsmelt population did not reproduce during impoundment. If they did, there was probably low survival of larvae under warm, hypersaline conditions.

3.6.4 Ichthyoplankton

Estuaries are often considered essential spawning and nursery grounds for many fish species. Determining the value of estuarine channels to these functions requires comparisons with shallow coastal waters. Nordby (1982)
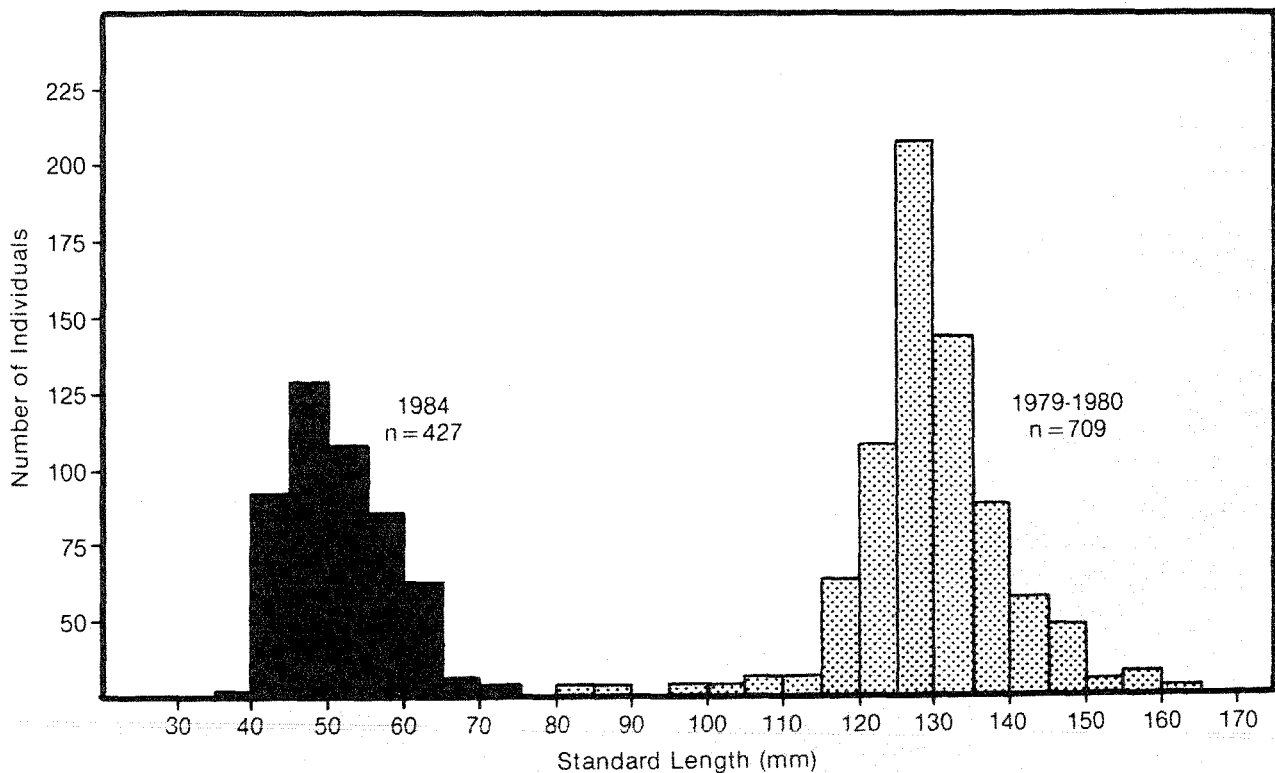
Figure 41. Length-frequency distributions for topsmelt collected in Tijuana Estuary in fall and winter, 1979-1980 (Nordby, unpubl. data), and fall 1984 (C. Donohoe, SDSU, unpubl. data).

compared the ichthyoplankton communities of the estuarine channels within Tijuana Estuary with those in adjacent nearshore waters. In addition, comparisons were made between large, main estuarine channels and tidal creeks.

A total of 28 taxa of fish larvae representing 19 families and more than 27 genera (some taxa included multiple genera) were collected during the study period while 18 taxa and one unknown variety of fish eggs from 13 families and including more than 18 genera were collected (Table 9). There were distinct differences in the ichthyoplankton assemblages collected from each habitat. Estuarine larvae demonstrated patterns of spatial distribution, related to channel morphometry and other channel organisms, that indicated spawning habitat preferences.

Tidal creek larval collections were dominated by longjaw mudsucker (*Gillichthys mirablis*) and Atherinidae, presumably topsmelt. The longjaw mudsucker is known to prey upon and inhabit the burrows of the yellow shorecrab (MacDonald 1975). High densities of these larvae were collected where crab burrows were abundant. Atherinid larvae and eggs were associated with macroalgal mats, primarily *Enteromorpha* species, that grow in the low tidal-velocity creeks. Topsmelt attach their eggs to the blades of algae, and the juveniles and adults feed on the abundant plant material (Allen 1980; Nordby 1982).

A complex of three indistinguishable goby larvae, comprised of arrow goby (*Clevelandia ios*), shadow goby (*Quietila y-cauda*) and cheekspot goby (*Ilypnus gilberti*), dominated main channel larval collections (61%) while longjaw mudsucker made up 29% of the total. The goby-complex larvae were most dense at the sampling station closest to the mouth of the estuary, apparently due to substrate preference. The substrate at this site was mud/sand rather than the mud and clay/shell substrates of the other main channel sampling stations. The arrow goby was the most abundant postlarval goby collected; this species has been reported to live commensally with ghost shrimp (MacDonald 1975). Ghost shrimp burrows were common in mud/sand substrate. Thus, it appears that the distribution of goby-complex larvae is related to substrate and interaction with another channel organism.

Because of their position relative to the mouth of the estuary, larvae of the goby complex were tidally transported to the nearshore habitat where they made up 57% of the total. These species spawn where tidal velocity is low and sediments are fine (Brothers 1975); thus, it is doubtful that spawning occurred in the nearshore habitat. Conversely, eggs from nearshore-spawning species, especially Sciaenidae and Pacific sardine

(*Sardinops sagax caeruleus*), were imported to the estuary during flooding tides. These two species made up 69% and 12% of main channel eggs and 70% and 11% of nearshore eggs, respectively. However, very few larvae from nearshore species were collected within the main channels, suggesting that most imported eggs are not retained until hatching. The nearshore larval dominants, queenfish (*Seriphus politus*), white croaker (*Genyonemus lineatus*) and northern anchovy (*Engraulis mordax*), were rarely collected within the estuary.

Tidal flushing appears to be a determining factor in the distribution of ichthyoplankton in Tijuana Estuary. The presence of postlarval Sciaenidae within the estuary suggests that some nearshore-spawned eggs can hatch or develop there. The transportation of goby species to the nearshore environment is probably fatal. Brothers (1975) measured 98% mortality for spawned cohorts of arrow goby at a similar wetland habitat in Mission Bay (25 km north of Tijuana Estuary) and determined that tidal translocation was the major source of mortality for this species.

The Gobiidae larvae that dominate Tijuana Estuary are common to other enclosed bays and estuaries of southern California. While not of commercial importance except as baitfish, these low-trophic-level species are important ecologically in that they make the primary productivity of the estuarine system available to higher order consumers. For example, arrow gobies have been shown to be important food items for California halibut as well as other sport fishes (MacDonald 1975).

3.6.5 Birds

The channels of Tijuana Estuary are important foraging and resting areas for a variety of bird life such as great blue herons, which prey on channel fishes (Figure 42). The estuary is a part of the Pacific Flyway, which is used by millions of waterfowl and shorebirds during winter migration. Shorebirds forage primarily for invertebrates in the sand and mud sediments and in the water column; diving birds prey on fishes; wading birds use both fishes and invertebrates for food; dabbling ducks feed on vegetation; and plovers feed on surface insects. Three Federally listed endangered birds and one California endangered bird use channel organisms for prey. These include the California least tern, the California brown pelican (*Pelecanus occidentalis californicus*), the light-footed clapper rail, and Belding's Savannah sparrow. Other bird species that feed on fishes in the channels are the belted kingfisher (*Megaceryle alcyon*), osprey (*Pandion haliaetus*), and double-crested cormorant (*Phalacrocorax auritus*). Another Federally listed
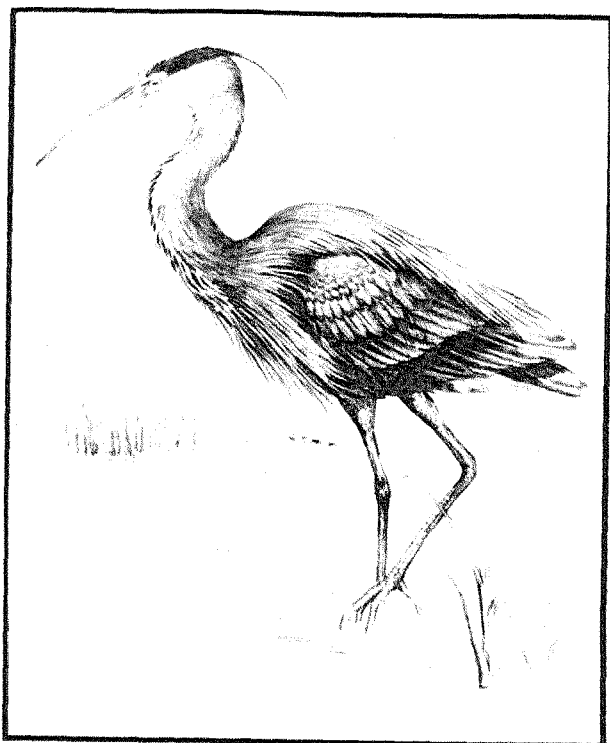
Figure 42. The great blue heron. McIntire collection, copyright 1986 by Zedler.

endangered bird, the peregrine falcon (*Falco peregrinus anatum*), has been reported from the estuary.

In all, 298 bird species have been recorded in Tijuana Estuary and river valley (White and Wunderlich, unpubl.). Of these, 69 are found primarily within the estuarine habitat, 144 occur mainly in adjacent upland and riparian habitat, and 85 species are found in both habitats. In 1973-74, a census of the northern section of Tijuana Estuary revealed that the following 15 birds were most abundant: willet, marbled godwit, western sandpiper (*Calidris mauri*), least sandpiper (*Calidris minutilla*), dowitcher (*Limnodromus* spp.), Belding's Savannah sparrow, house finch (*Carpodacus mexicanus*), white-winged scoter (*Melanitta fusca*), elegant tern (*Sterna elegans*), Northern pintail (*Anas acuta*), ring-billed gull (*Larus delawarensis*), black-bellied plover (*Pluvialus squatarola*), Forster's tern (*Sterna forsteri*) and long-billed curlew (White and Wunderlich, unpubl.). With the exception of the house finch and possibly the ring-billed gull, all of these species forage in estuarine channels.

Several water-associated birds that are rare in California are often seen at Tijuana Estuary. These include the little blue heron (*Florida caerulea*), tricolored heron (*Hydranassa tricolor*) and black skimmer (*Rynchops nigra*). The black skimmer recently began to nest at the salt ponds of south San Diego Bay; that population is the only breeding one in the western United States (White, pers. comm.). Its use of Tijuana Estuary as a foraging area shows that birds residing in one wetland may rely upon several others for survival. The best wetlands for birds may be those where a variety of wetland habitats are available nearby.

Channels are important foraging habitats for a variety of birds from other habitats. Belding's Savannah sparrows rely on tidal creek and channel edge habitats for feeding. Clapper rail foraging behavior has been discussed in Section 3.3. Feeding studies of California least terns (Minsky 1974; Atwood and Minsky 1983) document feeding in nearshore waters, as well as estuarine channels and bay habitats. Preferred fishes include northern anchovy, topsmelt, and jacksmelt (*Atherinops californiensis*). Breeding adults catch and feed these small fish (4-9 cm long) to the chicks. The young begin to fly at about 20 days of age and the fledglings develop foraging skills in calm, protected waters. "Even estuarine and freshwater localities that are distant from active nesting sites . . . may be heavily used by least terns during post-fledgling dispersal; loss or disturbance of such areas may reduce the survivorship of dependent young" (Atwood and Minsky 1983).

3.7 INTERTIDAL FLATS

The conspicuous species of the sandflats and mudflats are the shorebirds that feed and rest there during low tide (Figure 43). Most of their invertebrate food species were discussed in Section 3.6.2. Many of the prey animals are distributed from the subtidal channels to the lower limit of the salt marsh.

Four invertebrate species that are characteristic of exposed flats are the California horn snail, the yellow shore crab, the fiddler crab and the lined shore crab (Figure 43). There are no quantitative data on any of these at Tijuana Estuary. We know only that the horn snails can be extremely abundant (hundreds to thousands per square meter), and that both horn snails and crabs are important foods for the clapper rail (Jorgensen 1975). It is likely that all these species were negatively affected by estuarine closure in 1984. Large numbers of empty horn snail shells were collected from the mudflat adjacent to the inland lagoons in 1984; only an occasional live individual was found. Lined shore crabs were found dead and floating in the hypersaline water during 1984.

Our discussion emphasizes the shorebirds that were studied extensively in 1979-80. Boland
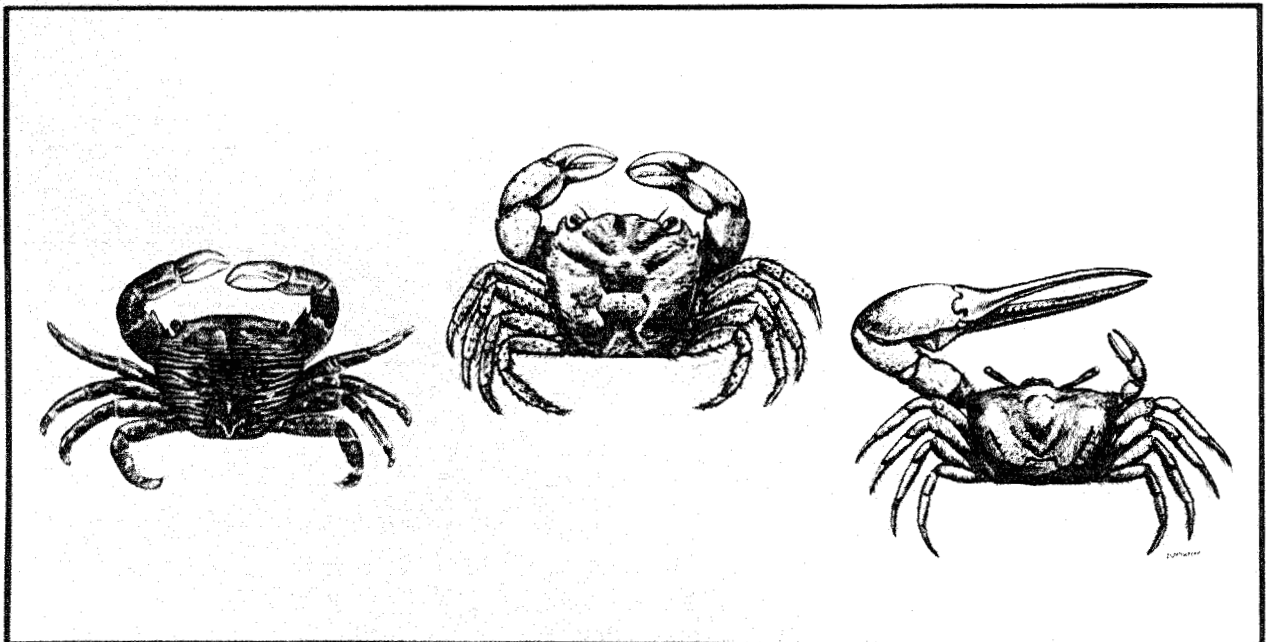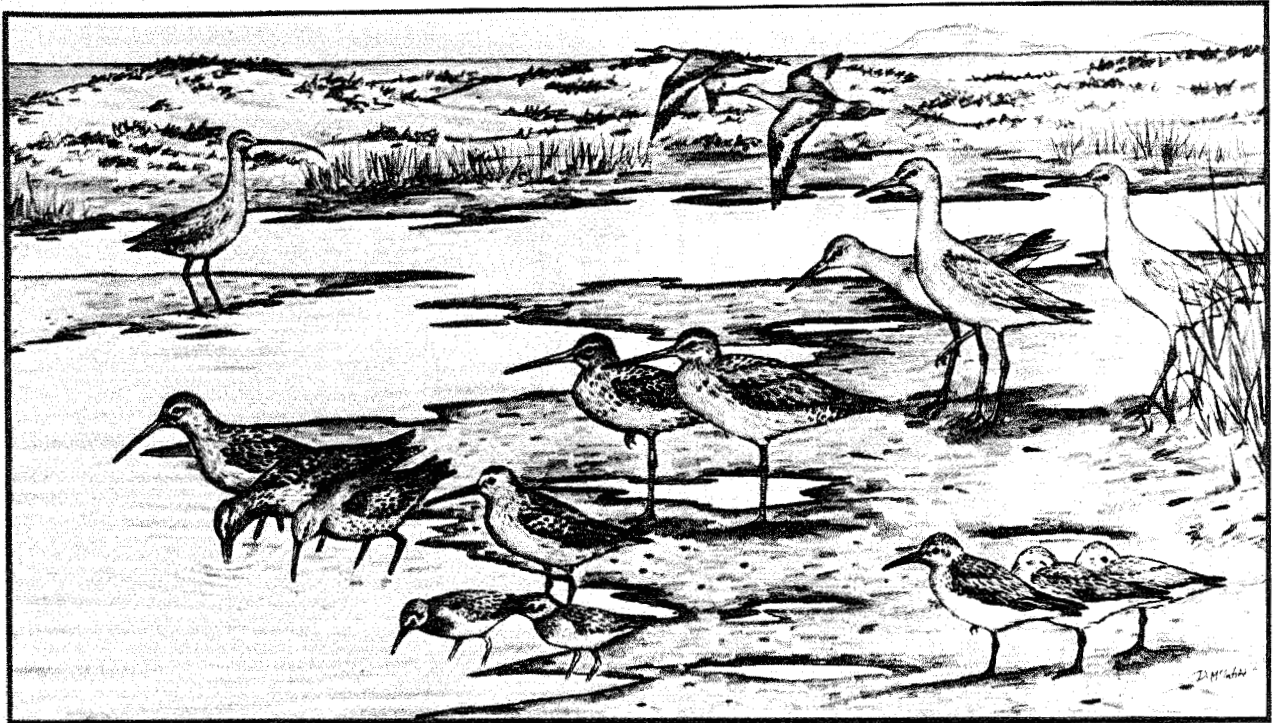
Figure 43. Birds of the intertidal flats include the long-billed curlew (upper left) and willets (five larger birds on right; wing bars visible on the two in flight). In the foreground of the mudflat are two least sandpipers (the smallest shorebirds) and three western sandpipers (lower right). Long-billed dowitchers are shown in the center of the mudflat (two on the left and two in the middle), with two dunlins (black patch on shoulder) just behind the least sandpipers. All are drawn in their winter plumage, as usually seen at Tijuana Estuary. The macroinvertebrates of this habitat include lined shore crabs, yellow shore crabs, and abundant fiddler crabs (below, from left to right). McIntire collection, copyright 1986 by Zedler.

Table 10. The shorebird species sampled by Boland (1981) and abbreviations of their common names. Nomenclature from AOU (1983).

Species	Code
SANDPIPERS	
Least sandpiper, *Calidris minutilla*	LS
Western Sandpiper, *C. mauri*	WS
Sanderling, *C. alba*	S
Dunlin, *C. alpina*	DUN
Red knot, *C. canutus*	RK
Ruddy turnstone, *Arenaria interpres*	RT
Short-billed dowitcher, *Limnodromus griseus**	DOW
Long-billed dowitcher, *L. scolopaceus**	DOW
Willet, *Catoptrophorus semipalmatus*	WIL
Whimbrel, *Numenius phaeopus*	WH
Marbled godwit, *Limosa fedoa*	MG
Long-billed curlew, *N. americanus*	LBC
WADERS	
Wilson's phalarope, *Phalaropus tricolor*	WP
Northern phalarope, *P. lobatus*	NP
Greater yellowlegs, *Tringa melanoleuca*	GYL
Black-necked stilt, *Himantopus mexicanus*	BNS
American avocet, *Recurvirostra americana*	AA
PLOVERS	
Snowy plover, *Charadrius alexandrinus*	SP
Semipalmated plover, *C. semipalmatus*	SPP
Killdeer, *C. vociferus*	K
Black-bellied plover, *Pluvialus squatarola*	BBP

*The short-billed dowitcher and long-billed dowitcher are difficult to distinguish in the field and were combined by Boland.

Figure 44. Field sites used in Boland's (1981) study of shorebirds.

(1981) focused on habitat utilization and feeding strategies. He recorded 21 species (scientific names provided in Table 10) and observed feeding behavior in five tidal habitats (Figure 44): steep wave-swept beach, sandflat, mudflat, mudbanks, and salt marsh. Data on abundance for all five habitats are included here for comparison, while feeding strategies on the beach are discussed in Section 3.8. The estuarine channels were by far the most heavily used foraging habitat in 1979-80 (Table 11).

The shorebird community is highly seasonal in its occurrence, with highest densities found in winter. The times of arrival and departure of different species did not coincide during Boland's study. Differences were great enough that he was able to separate early from late fall-arriving species and species that wintered at Tijuana Estuary from those that migrated further south (Table 12). Only three shorebirds (snowy plover, killdeer, and black-necked stilt) used Tijuana Estuary for breeding.

Boland found that many more species and individuals fed on sandflats and mudflats than mudbanks, beach, or salt marsh areas (Table 13). Willets and western sandpipers dominated the data set, and both were found primarily on the sandflat. Dowitchers, which were the most abundant species in December-January, were common on both sandflats and mudflats.

The species that fed in the same habitats appeared to partition their activities among different sediment depths and water depths (Figure 45). Waders, such as the greater yellowlegs, fed on items in the water column and on the sediment surface. Long-billed sandpipers (e.g., marbled godwit) probed deep into the sediment, often wading deeply into the water. Short-billed sandpipers like the western sandpiper probed less deep and remained near the edge of the water; while plovers (e.g., semipalmated plover) fed on the surface of moist-to-dry sediments.

Boland concluded that the length of leg and bill determined the feeding strategy of each species,

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and that the community was composed of species that differed in leg and bill lengths (Figure 46). Such different morphologies should reduce competitive interactions by reducing overlap in where the birds feed. However, as Boland pointed out, tides constantly change the depth of water so that longer and shorter legged birds that take foods from the same spots do so at different times. Thus, they cannot avoid competition where food supplies are limiting. Boland (Universiy of California, Los Angeles, pers. comm.) has begun to test these ideas through gut analyses of eight shorebird species and quantitative analyses of invertebrate food availability at Morro Bay, California (central California).

While there were no studies that quantified the effect of estuary mouth closure on shorebirds, Jorgensen (pers. comm.) estimates that shorebird abundance was reduced 70% during this period, an effect attributed to the absence of tidal submergence and exposure of bottom sediments. Since the sandy shore habitat was not affected by the obstruction of the estuary mouth, some species may have shifted to this habitat for feeding or may have migrated to other intertidal flats in the region. The return of shorebirds to Tijuana Estuary has been much more rapid than that of the former dominant bivalves, and a diverse community utilized the mudflat and sandflat habitats during the fall 1985 migration. The potential for recovery

Table 11. Principal foraging habitats for the shorebirds at Tijuana Estuary, as identified by Boland (1981).

Shore	Shore & Channels	Channels	Marsh & Channels	Shore, Marsh, & Channels

Sanderling
Whimbrel
	Ruddy turnstone
	Marbled godwit
	Snowy plover
	Black bellied
	  plover
		Least sandpiper
		Western sandpiper
		Dunlin
		Red knot
		Dowitcher
		Wilson's phalarope
		Northern phalarope
		Greater yellowlegs
		Black-necked stgilt
		American avocet
		Semipalmated plover
		Killdeer
			Long-billed
			  curlew
				Willet

Table 12. Seasonal occurrences of shorebirds at Tijuana Estuary, as determined by Boland (1981).

Early arriving migrants	Early arriving & wintering	Late arriving & wintering	Breeding & wintering	Breeding migrant

Ruddy turnstone
Whimbrel
Wilson's phalarope
Northern phalarope
Semipalmated
  plover
	Least sandpiper
	Western sandpiper
	Sanderling
	Red knot
	Dowitcher
	Willet
	Marbled godwit
	Long-billed curlew
	Greater yellowlegs
	Black-bellied plover
		Dunlin
		American
		  avocet
			Snowy plover
			Killdeer
				Black-necked
				  stilt

Table 13. Seasonal abundances and habitat utilization of shorebirds at Tijuana Estuary: mean number of individuals in five tidal habitats; numbers are scaled to 500-m segments of shoreline; species abbreviations are in Table 10 (from Boland 1981).

Species	July-August						October						December-January					
	Beach	Sand-flat	Mud-flat	Mud-bank	Salt marsh	Total	Beach	Sand-flat	Mud-flat	Mud-bank	Salt marsh	Total	Beach	Sand-flat	Mud-flat	Mud-bank	Salt marsh	Total
LS	0	16	3	1	0	20	0	45	17	1	0	63	0	7	1	0	0	7
WS	0	103	2	0	0	105	0	113	62	0	0	175	0	192	20	0	0	211
S	13	<1	0	0	0	14	11	<1	0	0	0	12	9	1	0	0	0	10
DUN	0	0	0	0	0	0	0	12	9	<1	0	21	0	56	16	0	0	72
RK	0	8	<1	0	0	9	0	3	<1	0	0	3	0	37	1	0	0	38
RT	2	1	2	<1	0	6	1	1	1	1	0	4	<1	<1	<1	0	0	1
DOW	0	12	46	<1	0	58	0	159	46	2	0	207	0	113	135	3	1	252
WIL	36	108	11	5	2	161	13	118	26	8	10	175	4	132	14	4	60	213
WH	6	6	0	<1	0	12	0	0	0	0	0	0	0	0	0	0	0	0
MG	4	45	10	3	0	62	2	47	24	6	0	78	1	46	18	8	5	76
LBC	0	2	2	3	1	8	0	1	1	3	3	8	0	2	2	2	1	7
WP	0	<1	0	0	0	<1	0	0	0	0	0	0	0	0	0	0	0	0
NP	0	0	<1	0	0	<1	0	0	0	<1	0	<1	0	0	0	0	0	0
GYL	0	2	2	0	0	3	0	2	2	<1	0	4	0	2	1	<1	0	4
BNS	0	<1	<1	0	0	1	0	<1	<1	0	0	1	0	<1	<1	0	0	<1
AA	0	<1	<1	0	0	<1	0	1	1	0	0	2	0	127	<1	0	0	127
SPP	0	2	1	0	0	3	0	1	1	0	0	1	0	0	0	0	0	0
SP	4	4	<1	0	0	8	1	4	0	0	0	5	1	4	<1	0	0	5
K	0	0	1	0	0	1	0	2	3	<1	0	5	<1	<1	<1	<1	0	1
BBP	2	18	3	0	0	24	1	26	4	1	<1	33	<1	23	1	2	0	27
Total Indiv.	67	329	83	12	3	494	29	535	196	23	13	796	15	742	209	19	66	1050
Total Species	7	18	16	8	2	19	6	17	15	11	3	18	7	16	15	7	4	16

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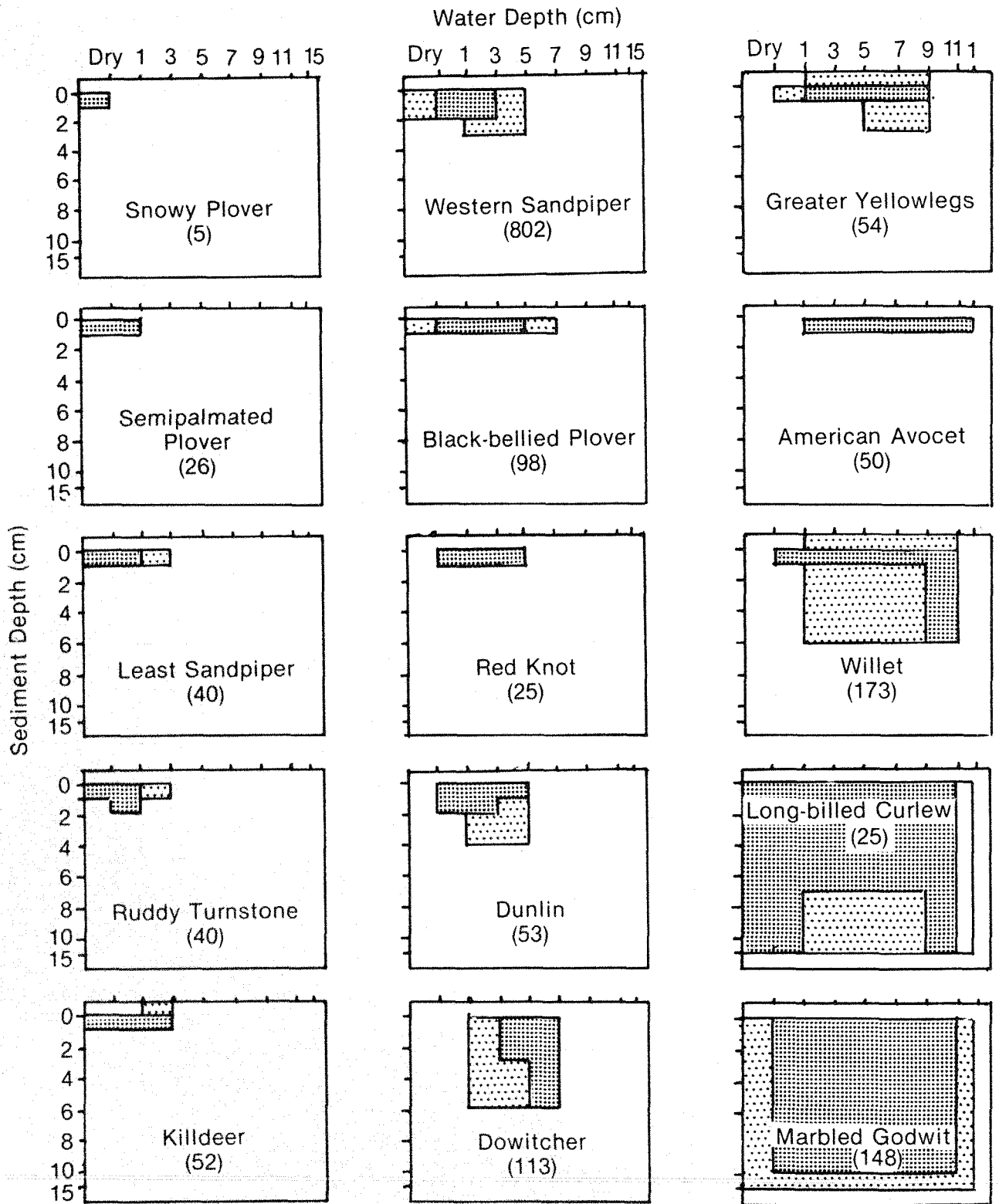
Figure 45. Foraging microhabitats (entire stippled area) of shorebirds for sandflats and mudflats. Areas where birds foraged were defined by water depth and depth to which birds probed the sediments; dense stippling indicates where species spent more than 80% of their time foraging; sample sizes are in brackets. Reprinted from Boland (1981) with permission.
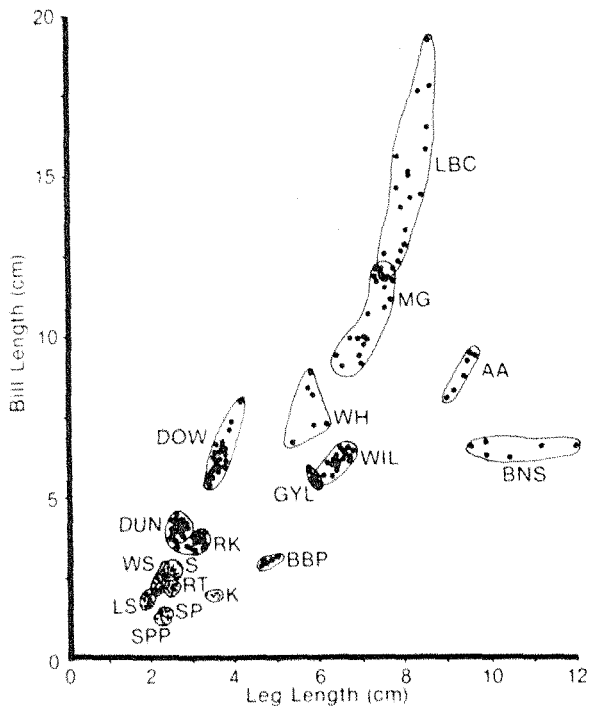
Figure 46. Relationships between leg (tarsus) length and bill (culmen) length for 18 shorebird species. Species abbreviations are in Table 10. Reprinted from Boland (1981) with permission.

appears to be high for migratory species; if suitable habitat is available, birds will use it. The regional impact on birds of temporary habitat losses may never be known.

3.8 DUNES AND BEACH

The shoreline is a dynamic habitat, subject to a variety of environmental influences such as wind and wave action, salt spray, high temperature, and moisture stress. A number of plants and animals have adapted to these factors and many are found only on dunes. Because of this and because most of the dune habitat in southern California has been destroyed (Powell 1981), dune species are particularly vulnerable to extinction on a local scale. Thus, this small portion of the estuary is of high value to wildlife.

Dunes that are not stabilized by vegetation can be blown or washed away. The original dune vegetation at Tijuana Estuary has been disturbed by construction and recreation activities that resulted in the denudation of the system. In the winter of 1983, storms washed the dunes into the main channel of the estuary. The reduction of the tidal prism eventually resulted in closure of the estuary mouth in 1984.

Before housing development in the late 1940's and early 1950's, the vegetation of the Tijuana Estuary dune system was similar to that of the Silver Strand, approximately 3 km to the north (Table 14). Plant species such as dune primrose (*Camissonia cheiranthifolia*), sand verbena (*Abronia maritima*), and dune ragweed (*Ambrosia chamissonis*) were present (Figure 47). The dunes were stable and did not change position significantly. Following human impacts, some native species, most notably the shrub lemonadeberry (*Rhus integrifolia*), were eliminated, while several exotics, such as hottentot-fig (*Carpobrotus edulis*), sea rocket (*Cakile maritima*), and *Atriplex* species have invaded. These exotics often have adverse effects on native organisms. The hottentot-fig displaces native dune plants (Williams and Williams 1984) and provides little food or habitat for native insects (Nagano, pers. comm.). The relationship of sea rocket to native dune plants is under investigation (L. Wood, SDSU, in prog.). Management decisions regarding revegetation of denuded areas must be based on the relative merits of dune stabilization by exotic species versus maintenance of the native flora and fauna (Chapter 6).

Insects are important components of the dune habitat. Several threatened species and one candidate for listing as an endangered species are found at the Tijuana Estuary dunes (Nagano 1982). The globose dune beetle (*Coelus globosus*; Figure 47), inhabits foredunes and sand hummocks. It burrows beneath the surface of the sand and is most common under native dune vegetation; it is absent from areas covered by hottentot-fig. This beetle is a candidate for Federal listing and is threatened with trampling by humans, vehicles, and horses.

Tiger beetles are threatened by loss of habitat at Tijuana Estuary and elsewhere. The sandy beach tiger beetle (*C. hirticollis gravida*) and the sand dune tiger beetle (*C. latesignata latesignata*; Figure 47) are found on the dunes (Nagano 1982; McIntire 1985). Both species lay their eggs in the sand, and the larvae construct vertical burrows approximately the same diameter as the head, from which they trap food in a manner similar to that described in Section 3.4. These beetles are found in only two or three other localities in southern California. Another beetle, *Notoxus monodon*, feeds on detritus beneath dune vegetation (Figure 47). This species has glossy white hairs on its body, presumably to protect it from the sun. The larvae inhabit burrows beneath dune plants (McIntire, pers. comm.).

It is evident from the above discussion that the insects of the dunes are closely associated with the dune vegetation, particularly native species. In contrast, the birds that use the dunes prefer the

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Table 14. Early information on dune vegetation at Silver Strand, the beach that extends north from Tijuana Estuary (from Purer 1936b). Species present in 1936 and their common names are listed. Taxonomy follows Munz (1974) and (USDA 1982).

Species present	Common name	Distributional notes
Ambrosia maritima	ragweed	"one of the most conspicuous plants...forms extensive mats along the dunes as well as inland...where the sand is unstable"
Abronia umbellata	sand verbena	"grows in more stabilized place in the sand strand...forming extensive mats"
Ambrosia chamissonis	dune ragweed	"holds a conspicuous and important place...in unstabilized areas"
Atriplex leucophylla	salt bush	"forms hummocks of sand...associated with *Abronia* and *Ambrosia*"
Cakile edentula	sea rocket	"finds itself at home...close to the ocean"[a]
Camissonia cheiranthifolia ssp. *suffruticosa*	dune primrose	"fluorishes on the [plain] of the strand"
Carpobrotus aequilaterale	seafig	"a conspicuous feature of the landscape"
Gasoul nodiflorum		"quite well distributed"
G. crystallinum	ice plant	"forms large mats"
Rhus integrifolia	lemonadeberry	"growing extensively on the strand...in many places...growth is considerably stunted...to a mere few inches"
Rhus laurina	laurel sumac	"growing to some 10 feet in height"[b]

[a]This species has been entirely replaced by *C. maritima*, which was absent in 1936.
[b]Noted as present at Silver Strand Beach State Park, but not necessarily on the dune.

open sand areas. Two rare species nest on the dunes of Tijuana Estuary, and a variety of other species feed on the sandy shores adjacent to the dunes.

The Federally endangered California least tern (Figure 48) nests in depressions in the sand along the dunes. Their eggs and chicks are vulnerable to a number of terrestrial and avian predators, as well as accidental or intentional disturbances by humans. If the first clutch fails, adult least terns may attempt to nest again. The least tern is a colonial nesting species that prefers sandy dunes with low amounts of dune vegetation and debris (less than 3%; Minsky et al. 1983). Females lay an average of two eggs in a small depression or scrape in the substrate. Young are fed exclusively on fish by both parents. Young least terns fledge at 3 weeks, and they gradually learn to feed on their own in inland lakes and estuaries.

The number of nesting pairs at Tijuana Estuary fluctuates widely from year to year, as at other nest sites that are unprotected from predation and human disturbance. Adult terns breeding for the first time do not show a clear preference for their natal colonies but tend to return to a site once they have bred (Massey and Atwood 1984). The estimates of nesting pairs have ranged from 21 to 66 in the past 4 years (Table 15). Factors such as winter mortality have not been examined but could help to explain annual variations. The 1984 closure of Tijuana Estuary to tidal flushing may have adversely affected recruitment. In 1984, about 50 pairs nested but no fledglings were observed. The stagnant channel water and corresponding reduction in fish and invertebrate populations may have contributed to nesting failure (L. Copper, ornithologist, pers. comm.).

Also nesting on the dunes is the relatively rare snowy plover (Figure 48). This bird is not a colonial nester but often associates with colonies of California least terns (White, pers. comm.). Snowy plovers lay an average of three eggs. Chicks leave the nest within 24 hours of hatching and immediately follow the parents to foraging areas along the sandy shoreline and mudflats. Snowy plovers feed mainly upon invertebrates along the water's edge on the sandy shoreline. While less well studied than the least tern colonies, the snowy plover breeding population at Tijuana Estuary is observed annually during least tern censusing (Copper, pers. comm.).
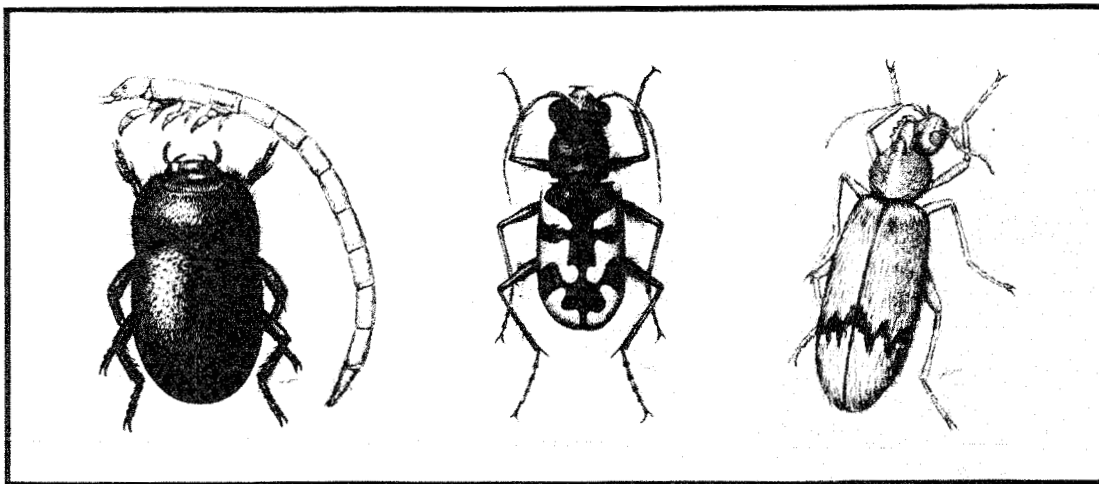
Figure 47. The native dune vegetation includes salt grass on the back dune (left), dune ragweed (left foreground), sand verbena (right foreground), and dune primrose. Insects that burrow beneath the plants include the globose dune beetle, the sand dune tiger beetle, and flower beetles (*Notoxus*). McIntire collection, copyright 1986 by Zedler.
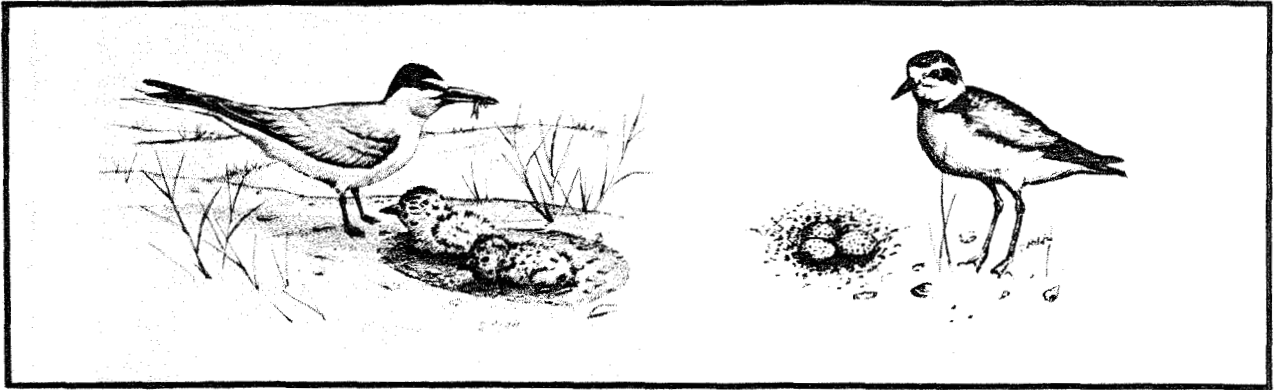
Figure 48. Birds that nest on the sand dunes are the California least tern and the snowy plover. McIntire collection, copyright 1986 by Zedler.

Table 15. California least tern nesting data, 1982-1985 (from Least Tern Recovery Team, unpubl.).

| Year | Tijuana Estuary | | California |
	Nesting Pairs	Fledglings	Nesting Pairs
1982	21-30	17	1015-1245
1983	60-65	50+	1196-1321
1984	66	12-20	931-1002
1985	32	18-20	1100-1112

Boland (1981) found that six species of shorebirds were abundant in his beach study site. These included sanderling, willet, marbled godwit, whimbrel, snowy plover, and black-bellied plover. Additional species that were not present on his beach site but are commonly observed feeding in the intertidal beach areas include the least sandpiper, western sandpiper, and dowitcher. Boland characterized the partitioning of beach habitats on the basis of the depth of sediment that the prey organisms occupy and the depth of water in which the birds would forage. The results (Figure 49) describe feeding strategies of the six abundant species on his beach site. The beach was most heavily used during July-August and least during December-January.

Belding's Savannah sparrows often forage on the dunes, especially when an abundance of kelp has washed ashore. The decaying kelp harbors large numbers of insects, especially flies. At Tijuana Estuary, several sparrows nest in small patches of pickleweed and saltgrass that are surrounded by dunes and dune vegetation (White, pers. comm.).

The dunes and beach habitats are dynamic, and recent storm damage has altered the native communities. In order to open the estuary to tidal flushing, the sand that had blown and washed into the estuarine channels was dredged and replaced on the dunes in December 1984. A revegetation program designed to stabilize the dunes and prevent recurrence of mouth closure has been initiated (Jorgensen, pers. comm.; B. Fink, SDSU, in prog.). This program will examine the response of three native species, primrose, sand verbena, and dune ragweed, transplanted to the foredune, dune ridge, and backdune. A complementary study on interactions between native (sand verbena) and non-native (sea rocket, Cakile maritima) species is also in progress (Wood, in prog.)
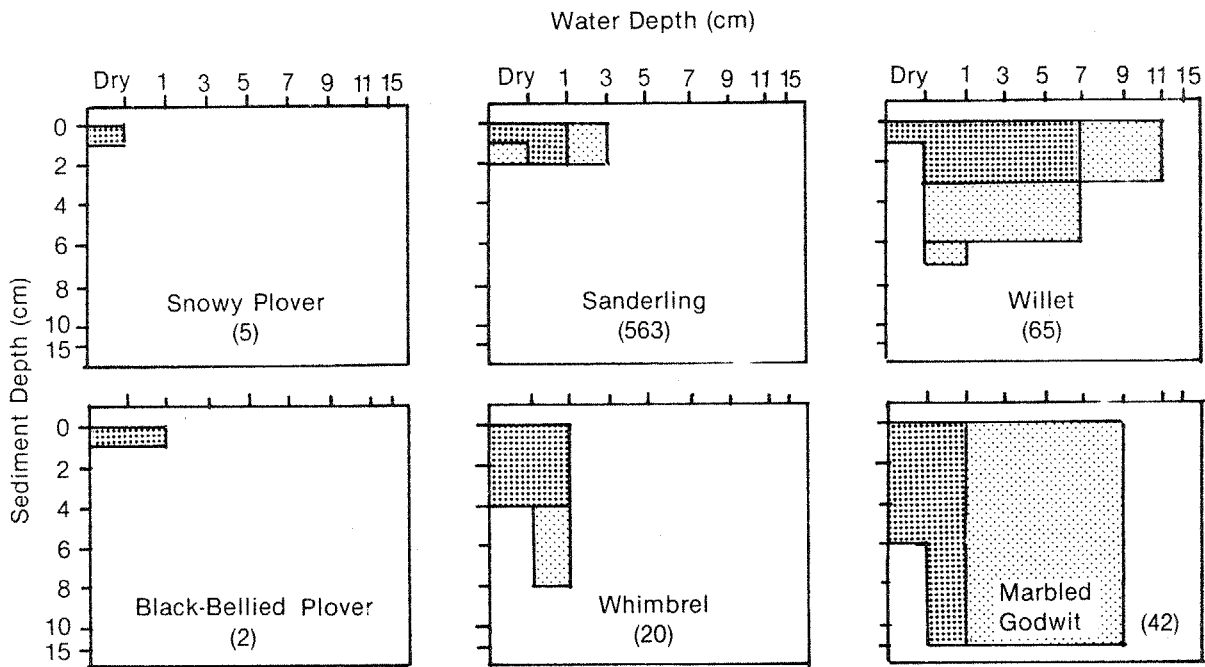
Figure 49. Feeding activities of six species of shorebirds on the beach were quantified by Boland (1981). Data are explained in the legend for Figure 45 (reprinted with the author's permission).

CHAPTER 4

ECOSYSTEM FUNCTIONING

Studies of energy flow and nutrient cycling at Tijuana Estuary began with the salt marsh in 1976, when researchers began to test the "East Coast dogma" about coastal wetlands. Research on the extensive coastal plain marshes in Georgia and elsewhere had indicated extremely high rates of vascular plant productivity, which in turn subsidized coastal food chains. The early work in southern California indicated that salt marshes were indeed different, with rates of primary productivity lower for vascular plants and higher for epibenthic algae underneath the open canopy (Sections 4.2-4.3). No functional models of the ecosystem were developed, because the system simply was not stable long enough for energy flow rates to be characterized. Later work focused on short-term growth rates in response to variations in specific environmental factors. For example, studies of the algal growth in channels were initiated in 1984, when problems of sewage spills and threats of year-round wastewater discharges indicated the need to understand what triggers nuisance algal blooms. Our ability to characterize ecosystem functioning has thus been limited by variability. On the other hand, our understanding of species composition (Chapter 5) has been aided by witnessing responses to the same environmental fluctuations.

4.1 PRIMARY PRODUCTIVITY OF CHANNEL ALGAE

The research of Rudnicki (1986) and Fong (1986) has characterized temporal patterns of algal abundance in five habitats at Tijuana Estuary, and manipulative experiments have shown how algae respond to different salinities and nutrient inputs. Throughout this section, the observations on macroalgae are based on Rudnicki's work, and information on phytoplankton is based on Fong's research. The term macroalgae generally refers to *Enteromorpha* and/or *Ulva*, although these genera are not always easy to distinguish. As used here, phytoplankton includes all microscopic algae

suspended in the water column, whether derived from the channel sediments or always planktonic (free-floating).

Chlorophyll concentrations and cell counts, rather than changes in productivity rates, have been used to measure responses to nutrient influxes. Maximum concentrations of chlorophyll in the plankton occurred during the 1984 nontidal episode, when Fong documented a bloom of unicellular blue-greens (Table 16). On the other hand, maximum populations of macroalgae may have occurred during the winters of 1983 and 1984 when tidal flushing was sluggish and nutrient concentrations were high due to sewage spills. However, our only evidence of this is the March 1984 air photo, which shows substantial macroalgal growth along the shores of the inland lagoons and within the northern tidal creeks. After tidal flushing was reinstated, neither algal type developed blooms of nuisance proportions.

Rudnicki and Fong's joint monitoring program began in 1985 and provided monthly data on the seasonal dynamics of channel algae (Figure 50). Three tidal creeks, the dredged channel, and the inland lagoons were sampled for phytoplankton, by collecting water samples to measure chlorophyll concentration and count cells. The same sites were sampled simultaneously for macroalgae by determining their cover and maximum biomass. Macroalgae germinate and develop on the sediments, under shallow water. At some later stage, the algae may be dislodged, float to the surface, and be moved about by wind and water currents. As a result, cover can be highly variable in both space and time, and areas of similar cover can have very different biomass. The field survey was devised to identify conditions that led to maximum biomass (called blooms); thus, areas with the greatest volume of algae were sampled at each monitoring station.

Of the five habitats sampled, phytoplankton were most dense in the tidal creek that had the lowest tidal circulation. Seasonal peaks in chlorophyll and cell counts occurred in spring when weather was warm and tidal action minimal. Together, the 1984 observations of blooms during closure and the 1985 field study suggested that phytoplankton accumulate when water currents are reduced and when nutrients are plentiful.

Macroalgal growth patterns were more variable. During 1985, the cover of floating macroalgae never reached nuisance levels, i.e., the water column did not become anoxic and there were no fish kills. Maximum standing crops averaged only 15 g/m² (n = 12), with a range from 0-185. Highest values tended to occur in the inland lagoon. This does not necessarily mean that productivity was highest there, because macroalgae are moved by the prevailing westerly winds. Rudnicki determined that several factors act together to increase macroalgal biomass in estuarine channels. Algal establishment coincided with daytime low tides, which occur primarily in winter. Germination mainly occurred along the shallow edge of creeks and channels where current speeds and light levels were suitable. Following establishment, growth was stimulated by nutrient inputs from rain and runoff and by afternoon exposure. When the cold tidal water receded, algae became warmer and received more light. However, macroalgae biomass did not necessarily accumulate in all areas of high productivity. Maximum volumes of macroalgae developed under two conditions, where circulation was reduced and where prevailing winds moved the floating mats. Neither *Enteromorpha* nor phytoplankton reached peak densities in well-flushed channels. Any current strong enough to scour the macroalgae would certainly limit the accumulation of phytoplankton as well.

The conditions that stimulate macroalgal growth were further researched by Mary Kentula (Oregon State University, in prep.) in the salt marsh of Mission Bay (25 km north of Tijuana Estuary). In winter, she collected *Enteromorpha*-dominated algal mats from soils beneath cordgrass and measured their light-saturation points. Under a broad range of temperatures (17-33° C), the mats became light-saturated at 400-600 μEinsteins/m²/s. By comparison, photosynthesis of the summer algal mats (dominated by blue-green algae and by mixtures of blue-greens and diatoms)

Table 16. Water quality at Tijuana Estuary during nontidal and tidal conditions (summary data from Fong 1986 and Rudnicki 1986).

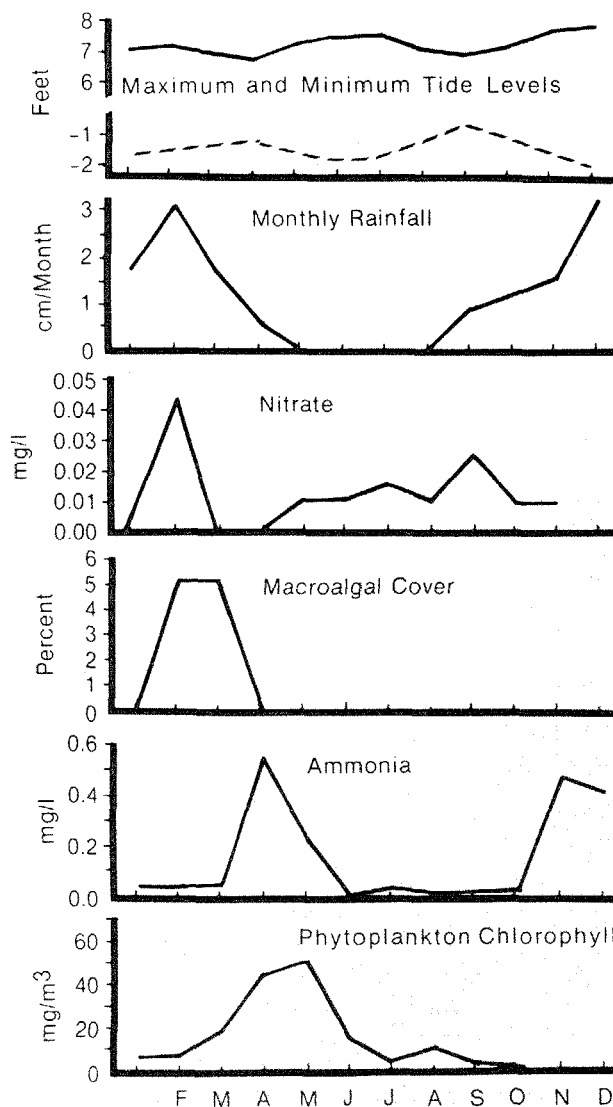| Data	Nontidal	Tidal
Temperature °C	14	18
Salinity ppt	13	34
Dissolved oxygen ppm	4.4	7.7
% cover of macroalgae	0	5
Chlorophyll a mg/m³	147	8
Phytoplankton cells/ml	2,000,000	15,000
Extinction coefficient	31	2.5
Total Kjehldahl nitrogen ppm	4.4	1.0
Ammonium ppm	0.05	0.02
Nitrate ppm	0.007	0.010
Total phosphorus ppm	1.7	0.1
Phosphate ppm	0.88	0.02

Figure 50. Seasonal dynamics in channels and creeks sampled monthly during 1985. Data for nutrient concentrations and algal abundance are presented according to the timing of maximum values. Phytoplankton data are from tidal creek 1; all data are from Fong (1986) and Rudnicki (1986).

were not light-saturated until exposed to 900 μEinsteins/m^2/s. Comparing the two types of algal mats under high light and temperature, the summer community was 30% more productive than *Enteromorpha*. As space and nutrients become limiting in spring and early summer, blue-green algal mats would have the competitive advantage. Furthermore, Rudnicki found that *Enteromorpha* deteriorated rapidly in warm, drying field conditions, as there is no resistance to desiccation. Winter conditions thus favor growth of this green alga over the species that dominate in summer.

Rudnicki (1986) and Fong (1986) tested the role of environmental conditions in stimulating algal blooms by exposing known mixtures of phytoplankton and macroalgae to three salinities (10, 20, and 34 ppt) and three levels of fertilization (Milorganite, a dried sewage-sludge product, was added in high, low, and zero levels). They devised a floating rack with 27 15-liter microcosms anchored in one of the estuary's tidal creeks; they then followed algal growth weekly for a month. Separate experiments were set up: (1) in winter 1985 using *Enteromorpha* sp. and the monad-dominated plankton, (2) in spring 1985 with *Enteromorpha* and a dinoflagellate-dominated plankton community; and (3) in fall 1985 with phytoplankton only, because macroalgae were rare in the estuarine channels.

In these experiments (Figure 51), phytoplankton responded rapidly to nutrient addition, with biomass increasing substantially after 1-2 weeks. Macroalgae took somewhat longer to reach maximum biomass. Blooms of *Enteromorpha* developed in the third week. It is possible that interactions between these two groups of producers occurred, if competition for nutrients or light developed. Such interactions were not tested, but the phytoplankton blooms in the high nutrient treatments of the summer experiment, which lacked macroalgae, were consistently larger than the winter and spring experiments, which had both *Enteromorpha* and phytoplankton.

Salinity affected the growth of both phytoplankton and macroalgae. Lowered salinity delayed phytoplankton blooms, and the species composition of the bloom differed in low-salinity treatments. Blue-greens dominated at 10 ppt, just as they had dominated the stagnant channels in April-June 1984 when brackish water (12-15 ppt) was impounded. *Enteromorpha* grew best at 33 ppt. It survived 10 ppt best where nutrient concentrations were high.

The recent changes in channel algae at Tijuana Estuary are well explained by the experimental results (Table 17). Nutrient additions maximize biomass of both primary producer components, but current speeds and temperature have differential effects. Thus, in years of good tidal flushing and fewer sewage spills (i.e., through the 1970's), neither type of algae was likely to develop bloom conditions because of continual dilution and export. With more frequent and larger sewage spills, blooms became possible. When currents became sluggish following the 1983 winter storm, macroalgae were able to accumulate in the nutrient-rich, quiet waters of the estuary, but phytoplankton were still prevented from developing high densities. Then, with no tidal flushing in 1984, phytoplankton densities reached nuisance proportions, while warm water, hypersalinity (60 ppt), and possibly competition for nutrients and light limitation at the channel bottom, reduced establishment and growth of *Enteromorpha*. Further refinement of this conceptual model of algal dynamics is in progress, with experiments varying salinity, nitrogen, and phosphorus concentrations planned for 1986.

4.2 PRODUCTIVITY OF EPIBENTHIC ALGAL MATS

Epibenthic algal mats are characteristic of the salt marsh benthos, although the community is frequently supplemented by species entrained from the channels. For example, *Enteromorpha* extends into the lower salt marsh in winter and spring. Likewise, some salt marsh algae extend into the channels. Filamentous blue-green algae develop patches in the tidal creeks during summer. Thus, there is an overlap in species composition. The distinction between the two communities is convenient, because the salt marsh algae comprise a matrix or mat of filaments and associated unicells that is usually bound to the substrate, while the algae found floating in the channels are considered the channel algae.

Dense algal mats are often found beneath the canopy of salt marsh vegetation. Biweekly field measurements in 1977 suggested that their annual productivity could match or exceed that of the vascular plants (Table 18). The highest productivity rates were measured in the most open canopies of frequently inundated areas during the warm season. The lowest rates were measured in winter in areas where moisture was limiting. In 1977, the lowest productivity occurred in April when there was little rainfall and neap tides did not inundate the higher marsh. A hypothesis was developed (Zedler 1980, 1982b) that the saline soils reduced vascular plant biomass, thereby increasing sunlight availability and algal productivity on the soil surface.

Kentula (in prep.) tested the model of algal-vascular plant interactions at Mission Bay Marsh during 1984, when Tijuana Estuary was nontidal and too dry for soil algae to grow. Her focus was on the cordgrass-dominated lower marsh; she
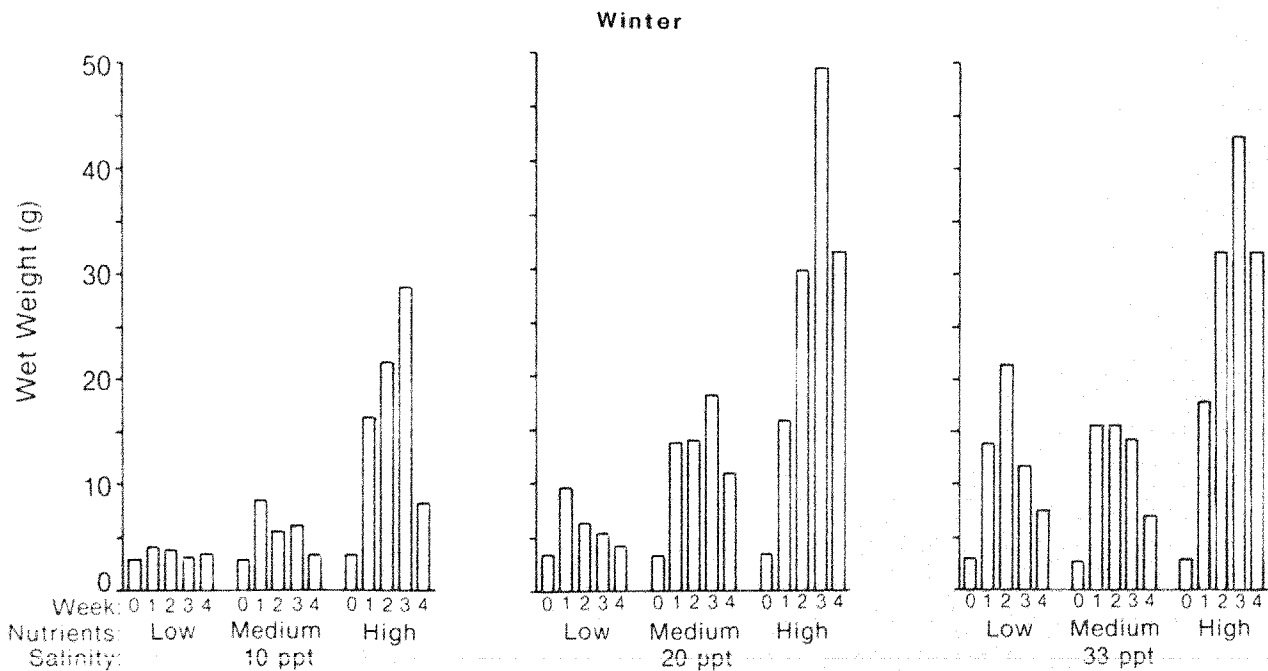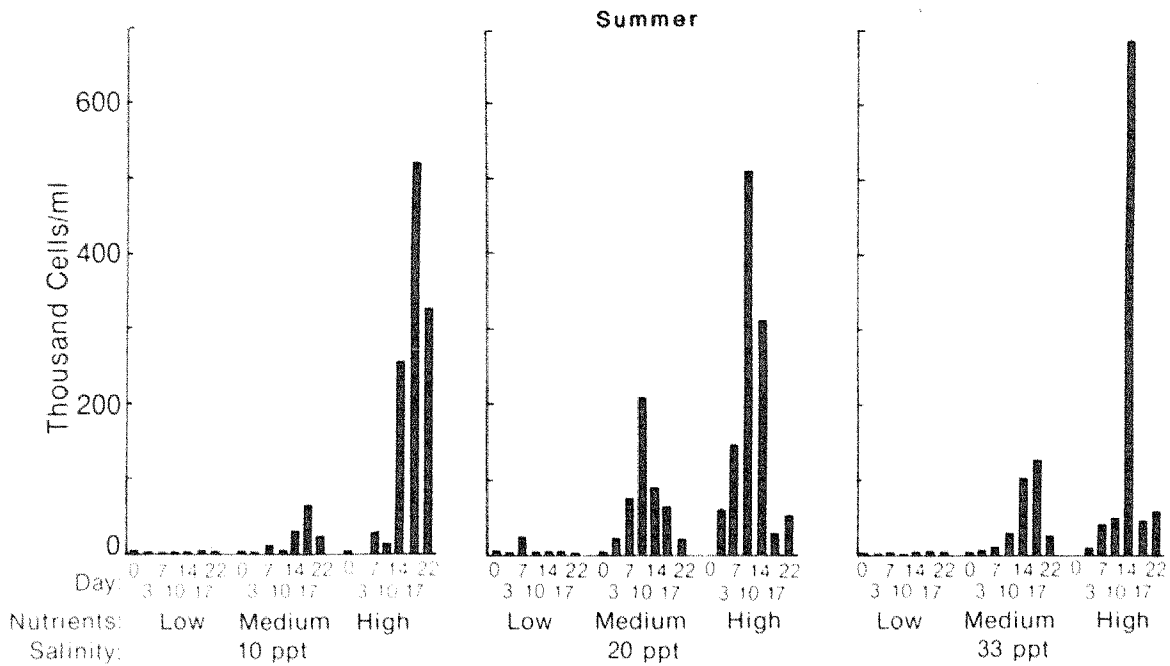
Figure 51. Results of manipulative experiments that varied water salinity and nutrient concentrations (using Milorganite additions) in microcosms at Tijuana Estuary. The phytoplankton response in the summer experiment is shown as increased cell density; the macroalgal response in the winter experiment is shown as increased biomass. Reprinted with permission from Rudnicki (1986) and Fong (1986).

Table 17. Conceptual model of channel algal dynamics, based on the work of Rudnicki (1986) and Fong (1986).

Environmental condition	Phytoplankton response	Macroalgal response
Marine tides dominate	Initial low biomass	Initial low biomass
Nutrient addition	Increase	Increase
Warm temperatures	Increase Dinoflagellates bloom	Decrease
Salinity reduction	Bluegreen monads bloom at 10 ppt	General decrease unless high nutrient conc.
Sluggish currents	Dilution and export	Biomass accumulates bloom develops
No currents	Blooms develop	Water temperature rises and limits macroalgal bloom
Optimal environmental conditions	High nutrients No tidal flushing Warm temperatures Any salinity	High nutrients Reduced currents Cool temperatures Saline water

Table 18. Productivity of benthic algal mats and comparison with vascular plants (from Zedler 1980).

Algal productivity estimates	Under cordgrass	Under *Jaumea*	Under saltwort	Under shore grass
Gross primary productivity (1977) (mean hourly, mg O_2/m^2/hr)	348	425	236	319
c.v.[c]	42%	33%	54%	51%
(mean daily, g O_2/m^2/day)	2.8	3.5	1.9	2.6
(annual, g O_2/m^2/yr)	1038	1285	695	951
Gross primary productivity (1978) (mg O_2/m^2/hr)	250	279	122	164
c.v.[c]	42%	38%	34%	90%
Net primary productivity				
Vascular plants (g C/m^2/yr)	340	243[b]		164
Algae[a] (g C/m^2/yr)	276	341	185	253
Ratio of algae:vascular plants	0.8	1.4	0.8	1.0

[a]Net primary productivity estimate = 0.85 Gross pri. prod.; PQ = 1.2.
[b]Middle marsh datum.
[c]coefficient of variation.

manipulated light levels in field experiments (10%, 25%, 50%, and 100% of incident light). After 2 or more weeks of exposure to the light conditions, replicate cores of algae were taken to the laboratory, and treatment effects were assessed with measures of chlorophyll concentration and photosynthetic light-response curves. Her experiments were repeated in winter and spring, when *Enteromorpha* dominated the algal mats, and in summer, when blue-green algae were abundant. The composition of the algal mat communities was similar to those at Tijuana Estuary during periods of good tidal flushing.

Kentula's results (unpubl.) suggest that the hypothesis of Zedler (1980, 1982b) is too simple. Winter algal communities failed to increase productivity in proportion to increased light availability. Algal mats quickly became light-saturated (at 500-600 μEinsteins/m^2/s for temperatures ranging from 15° C to 33° C). Chlorophyll concentrations were significantly higher for algae grown in full sunlight, but rates of photosynthesis per unit chlorophyll were not much greater for this winter community. Only the summer community responded as expected. The rates of photosynthesis for mats of blue-green algae and diatoms increased substantially with increased light (saturation at 900 μEinsteins/m^2/s for temperatures of 20° C to 33° C). Under conditions of high light, summer algal mats are thus limited by the shade of salt marsh vegetation. With light saturation and ambient temperatures, the summer algal mats are twice as productive as the winter community. The revised hypothesis is that canopy shade is a major limiting factor for the summer community of epibenthic algae, which dominates the annual productivity. The relatively open vegetation canopies thus allow algae to contribute substantially to salt marsh productivity.

The *Enteromorpha*-dominated algal mats declined in summer, and increasing light availability appeared to limit the duration of the winter community indirectly. Kentula noted that green algae began to decline in late spring, but they did so more rapidly in open areas than under the cordgrass canopy. Higher temperatures and desiccation were likely causes. This suggestion is consistent with Rudnicki's (1986) finding that *Enteromorpha* declines in warm water and helps explain the predominance of epibenthic green algae only in winter at the Tijuana Estuary salt marsh (Zedler 1982a). In marshes at both Mission Bay and Tijuana Estuary, mats with blue-green algae and diatoms were dominant in summer.

4.3 VASCULAR PLANT PRODUCTIVITY AND BIOMASS

Salt marshes are often said to have the highest productivity of any natural plant community, rivaling energy-subsidized agriculture in tons of carbon fixed per unit area per year. This generalization originated from studies in Georgia, where smooth cordgrass (*Spartina alterniflora*) dominates the intertidal zone. There, the widespread occurrence of cordgrass, the high rainfall and long growing season, the abundance of nutrients, and good tidal flushing are all reasons for productivity rates in excess of 3-5 kg/m^2/yr (Odum 1971; Pomeroy and Wiegert 1981; Chalmers 1982). But in Tijuana Estuary, as in many other Pacific Coast estuaries, cordgrass has restricted dominance and summer droughts lead to hypersaline soils. Furthermore, Seneca and Blum (1984) recently demonstrated that the Pacific cordgrass (*S. foliosa*) has lower photosynthetic potential than its eastern counterpart, at least when grown and measured in the laboratory. Substantial doubt that high productivity would be found in southern California salt marshes led Winfield (1980) and Onuf (in press; Onuf et al. 1978) to assess plant productivity in detail.

Winfield's work at Tijuana Estuary supported the hypothesis that the marshes of the region are less productive of vascular plant material than those in Georgia and elsewhere along the Atlantic and Gulf of Mexico Coasts. His use of the harvest method and Smalley's (1959) calculation, which sums biomass peaks of individual species, suggested that annual rates were well below 1 kg/m^2/yr net above-ground dry weight (Table 19). Winfield measured very low carbon content, however, indicating that ash (i.e., salts and metals) contributed much to the oven-dry weights. The carbon content of 11 plant species ranged from 19%-35% of dry weight (Winfield 1980), compared to 45% for smooth cordgrass (McIntire and Dunstan 1976). After correcting the dry-weight data to grams of carbon fixed, Winfield obtained an average marsh productivity of 239 g C/m^2/yr, which was much less than the average given for Georgia (454 g C/m^2/yr) by Turner (1976).

However, Onuf's (in press) work at Mugu Lagoon established clearly that harvest methods significantly underestimate productivity of pickleweed, sea lavender, and other southern California salt marsh species. Much greater production was estimated by tagging and remeasuring growth of individual plants. In the case of pickleweed, estimates from monthly harvests totaled half those measured by the tagging method, because so much plant material was broken off and exported between harvests. Succulents are very important in the Tijuana Estuary marsh; thus, it is likely that Winfield's 1976 and 1977 data underestimated vascular plant productivity.

Two considerations discouraged us from repeating the vascular plant productivity studies. First, Onuf's experience convinced us that the work

Table 19. Net aboveground productivity and net carbon productivity (estimated from plant carbon data of 5/31/78) of salt marsh vascular plants (data are per m²/yr from Winfield 1980).

	Grams dry wt		Grams carbon	
Species	1976	1977	1976	1977
Batis maritima saltwort	40	80	8	16
Frankenia grandifolia alkali heath	13	3	4	1
Jaumea carnosa	85	126	23	34
Limonium californicum sea lavender	0	<1	0	0
Monanthochloe littoralis shore grass	21	102	8	36
Salicornia bigelovii annual pickleweed	52	145	10	28
S. subterminalis perennial glasswort	9	14	3	4
S. virginica pickleweed	110	128	25	30
Spartina foliosa cordgrass	307	224	98	72
Suaeda esteroa sea-blite	17	53	4	11
Triglochin concinnum arrow grass	0	15	0	4
Total	689	904	191	239

was enormously labor intensive, that funding agencies were unlikely to support further efforts, and that journals were unwilling to publish the detailed demographic analyses required to track branch production, loss, and replacement. Secondly, large changes in biomass followed the 1980 flood and indicated that short-term intensive studies were inappropriate for temporally variable marshes. An alternative approach was called for, namely, longer monitoring of end-of-season biomass. Comparisons of productivity numbers with eastern marshes were no longer profitable— we had discovered a much greater difference. Tijuana Estuary, and probably all southern California marshes (cf. data for Los Peñasquitos Lagoon in Zedler et al. 1980), were found to be extremely variable from year to year. Understanding how and why individual marshes differ in time became a more promising research goal (Chapter 5).

Biomass data for the vascular plants provide straightforward characterizations of the Tijuana Estuary salt marsh, and the remaining discussion summarizes differences among species, seasons, and years. Winfield's (1980) sampling scheme began with 46 randomly sampled stations within a

0.8 ha area of the marsh. More stations were added for the August sample (n = 56), then cut to 25 stations in 1977. At each station, plants were clipped to ground level within 0.25-m² circular quadrats.

Frequent sampling (Table 20) showed that there were differences in the timing of peak standing crop for each species. Pickleweed reached its maximum in August, while cordgrass peaked in July and again in September following fruit production. The standing crop for all species combined was at its minimum in March and maximum in August of 1976 and 1977 (Figure 52). Whole-marsh sampling was repeated in August of 1978, but efforts in later years were restricted to the lower marsh (Table 21).

In both 1976 and 1977, standing crops doubled between March and August, but even in March, substantial live biomass was present (Figure 52). The criterion for "live" biomass was any stem with green material attached to it. Much of the live winter biomass consisted of fibrous shore grass, second-year cordgrass, and woody pickleweed stems. Despite large mortality between August and March, the standing dead biomass remained relatively constant. Thus, dead stems and leaves were rapidly incorporated into litter, exported, or decomposed.

Species-specific differences in standing crop are easiest to see in the 1977 harvest data, for which the number of sampling stations was constant. The annual pickleweed (*Salicornia bigelovii*) had the largest temporal increase (13.4-fold), while shore grass had the least (1.4-fold). Year-to-year differences in August biomass were also large. Variability, then, is the rule; it is high from species to species, season to season, and year to year. Onuf (in press) reached the same conclusion in his analysis of pickleweed biomass at Mugu Lagoon.

4.4 NUTRIENT INTERACTIONS

Our understanding of the nutrient cycles at Tijuana Estuary is limited. Most of the work has focused on nitrogen, because nitrogen has long been accepted as the major limiting factor in coastal ecosystems. Smith (1984) recently challenged that dogma and claimed that phosphorus is likely to limit estuarine systems, even though small-scale experiments might indicate that nitrogen controls plankton growth. Howarth and Cole (1985) support the theory of nitrogen limitation and provide a convincing argument that anaerobic conditions favor nitrogen limitation.

Winfield (1980 and Section 4.4) studied nitrogen dynamics in detail and determined that

Table 20. Standing crop (g dry wt/m²) of major salt marsh vascular plants for March (minimum biomass) 1976, 1977 and August (biomass peak) in 1976, 1977, and 1978 (from Winfield 1980).

Species	3/76	8/76	3/77	8/77	8/78
Batis maritima saltwort	15	55	55	121	82
Jaumea carnosa	a	218	66	181	195
Monanthochloe littoralis shore grass	a	170	159	218	143
Salicornia bigelovii annual pickleweed	<1	35	9	125	85
S. virginica pickleweed	31	124	55	179	173
Spartina foliosa cordgrass	55	211	130	280	256
Total standing crop	426	858	514	1153	954

[a]*Jaumea* and shore grass were not separated in the March 1976 sample.
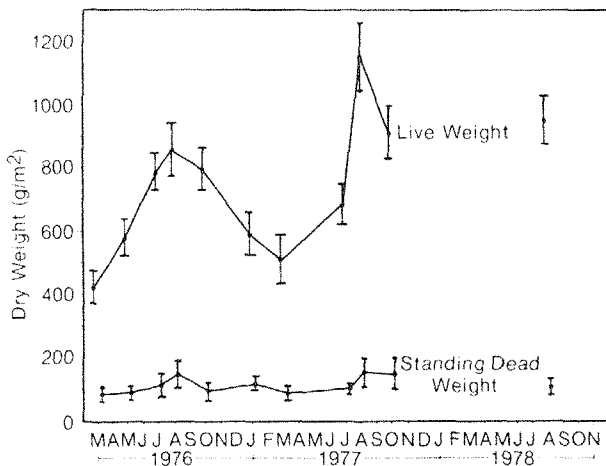
Figure 52. Live biomass and dead standing crop for salt marsh vascular plants. Vertical bars are ±1 standard error, n = 25. Reprinted with permission from Winfield (1980).

Table 21. August biomass in the cordgrass marsh areas only (from Zedler et al. 1980 and Zedler 1982b). s.e. = standard error

Year	g/m²	s.e.
1976	914	38
1977	1099	63
1978	1032	38
1980	1400	113

there is a net flux of inorganic nitrogen from the tide waters to the marsh. His estimate of the amount of nitrogen imported by the marsh (2.2 g N/m²/yr) was far less than the total required for above-ground plant growth (only 28%), and even a smaller portion of the nitrogen required for vascular-plant and algal productivity combined (6%). While these calculations do not rule out phosphorus or other nutrients as limiting, they do show a nitrogen deficit.

Data from the San Diego Regional Water Quality Control Board (G. Peters, WQCB, pers. comm.) show high ratios of phorphorus to nitrogen, so that phosphorus is less likely to limit whole-system productivity than nitrogen. Field sampling of soil nitrogen (Covin 1984) and channel nitrogen concentrations (Winfield 1980; Rudnicki 1986; Fong 1986) indicate that inorganic nitrogen is often present in very low quantities. Nitrogen fixation rates have not been measured.

In most of the experimental work carried out at Tijuana Estuary, nitrogen additions have stimulated vascular plant growth (Covin 1984). In 1983, frequent sewage spills from Mexico turned our attention to the more practical problems of how wastewater affects estuarine organisms, and nutrient-algae interactions were investigated in manipulative experiments using Milorganite (commercially available dried sewage sludge). The work of Rudnicki (1986) and Fong (1986; Section 4.1) focused on channel macroalgae and phytoplankton, while that of Beare and Beezley (unpubl. data) dealt with salt marsh vegetation. The latter study compared urea and Milorganite additions.

4.4.1 Nitrogen Fluxes in 1977-1978

Winfield (1980) set out to determine (1) the net direction of inorganic nitrogen movement of selected tidal cycles, (2) the relative importance of ammonium, nitrate and nitrite in channel waters, and (3) the seasonal patterns in inorganic nitrogen flux. His field data included both flood and nonflood years, so that comparisons became possible and our ability to extrapolate to longer periods of time was improved.

Concentrations of inorganic nitrogen were sampled monthly in two tidal creeks during the flood and ebb cycles of spring tides. Water samples were analyzed for ammonium, nitrate, and nitrite, using methods outlined in Strickland and Parsons (1972). One of the tidal creeks drained an area dominated by mixed cordgrass and pickleweed, and the other drained an area dominated by succulents. The two stations did not differ in nitrogen dynamics, despite their difference in vascular plant dominance. Therefore, they were averaged to calculate nitrogen fluxes.

Ammonium was usually the dominant form of nitrogen. Only after the January-February 1978 flooding of Tijuana River did nitrate concentrations exceed those of ammonium. Ammonium (as atomic N) ranged from 0 to 16.8 μg N/l (monthly means), with higher concentrations in winter and spring, and higher concentrations in flood, rather than ebb tides (Figure 53). A net import was calculated for the study period. Concentrations of nitrate, averaged monthly, ranged from 0.2-3.6 μg N/l, except for the March 1978 postflood sample (25 μg N/l). Nitrite was lower, at 0.7-1.4 μg N/l, and was usually highly correlated with nitrate concentrations. Calculations for the study period indicated that both nitrate and nitrite were exported in small amounts. Overall, however, there was a net import of inorganic nitrogen (2.2 g N/m²/yr; Figure 54).

Streamflows did not appear to be important to the nitrogen cycle except during flood years. The shift from dominance of dissolved inorganic nitrogen by ammonium to dominance by nitrate is a good indictor of riverine influence. Sewage inputs, on the other hand, are dominated by ammonium (Covin 1984). The preponderance of ammonium in 1977-78 channel waters and also in 1985 data of Rudnicki (1986) and Fong (1986) indicate long-term nitrogen subsidies from urban and agricultural wastewater.

Fluxes of organic nitrogen have not been measured but can be assumed from Winfield's data, which show a net export of dissolved organic carbon (Section 4.5.3). It is likely that the inorganic nitrogen that is imported with the incoming tide is fixed into organic matter and
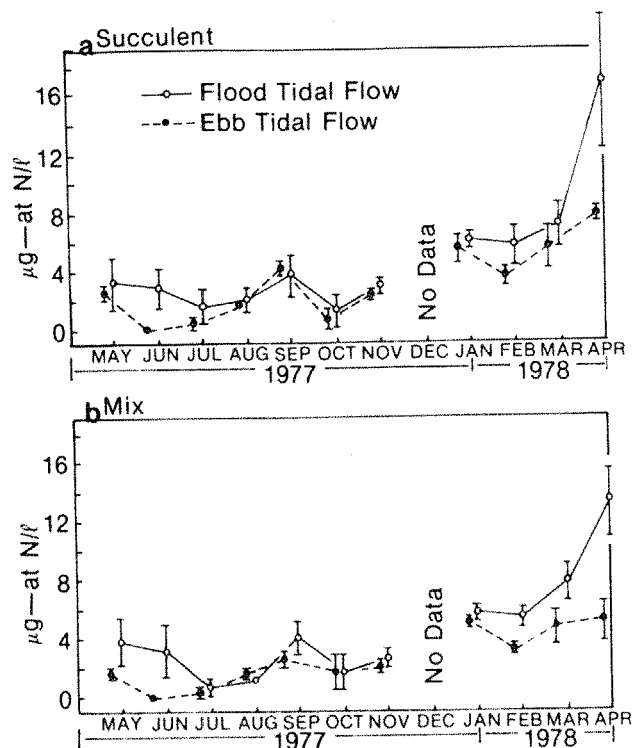
Figure 53. Concentrations of ammonium nitrogen in flood and ebb tidal waters for (a) the succulent-dominated study site and (b) the mixed cordgrass-succulent study site of Winfield (1980). Vertical bar is ± 1 standard deviation. Reprinted with permission from Winfield (1980).

released to channel waters as particulate and/or dissolved organic nitrogen. Thus, imported nutrients could enter the marine food chain as amino acids and detrital particles become available to consumers. During sewage spills, concentrations of organic nitrogen are much higher, and both water quality and estuarine organisms are severely damaged.

4.4.2 Nitrogen Additions to Salt Marsh Vegetation

We have long been aware of spatial and temporal variability in marsh plant growth, especially for cordgrass. While soil salinity reductions that accompany flooding (Chapter 5 and Zedler 1983b) have been shown to be important in controlling growth, flooding does not explain all of the growth dynamics. Furthermore, freshwater influence is not independent of nutrient influxes, as the previous section shows. When the Tijuana River flows, there are many changes in total water chemistry.

a Succulent

b Mix
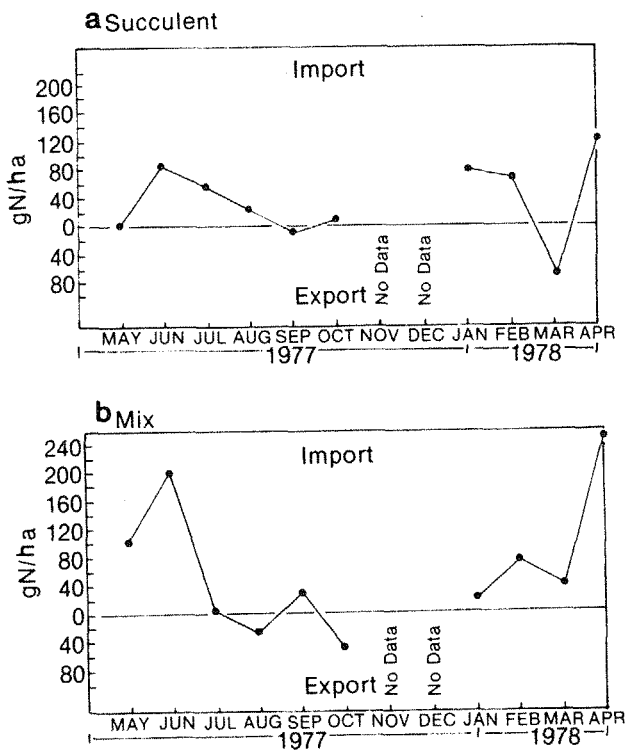
Figure 54. **Net flux of total inorganic nitrogen dissolved in the tidal waters for (a) the succulent-dominated study site and (b) the mixed cordgrass-succulent study site of Winfield (1980). Reprinted with permission from Winfield (1980).**

Before Covin's (1984) study at Tijuana Estuary, the influence of nitrogen on salt marsh vegetation was in question. D. Turner (SDSU; unpubl. data) had fertilized pickleweed-dominated vegetation at San Diego River Marsh and found large increases in vascular plant productivity. However, when Nordby added the same concentrations of urea to cordgrass transplants at Tijuana Estuary, he failed to see a growth response (Nordby et al. 1980). The latter experiment took place during 1980, when major floodwater may have enriched the marsh soils with nitrogen or stimulated local nitrogen recycling. These conflicting results stimulated Covin to develop a detailed investigation of nitrogen-plant interactions.

Covin's first step was a broad survey of soil nitrogen in 1981, using 67 of the 102 lower marsh monitoring stations at Tijuana Estuary (Chapter 5). Soil nitrogen proved to be variable within stations, among stations, and among transects. There was only a hint that cordgrass growth was related to soil nitrogen concentrations; the transect with

highest soil nitrogen had the highest total stem length (a biomass estimate) of cordgrass.

Reasoning that nutrient uptake by cordgrass might be enhanced by nitrogen concentrations or reduced by competitive uptake on the part of pickleweed, Covin set up two-way experiments with both nitrogen (± urea) and presence of competitors (± pickleweed) as variables. In addition, he repeated the ± urea experiment in an area of pure cordgrass. The field experiments were carried out in 1983 near transects TJE-28 and TJE-30 (Chapter 5). Urea was broadcast onto the marsh soils biweekly through the growing season in + urea plots. Biomass was measured in August 1983 and significant treatment effects were found. Urea stimulated only the growth of pickleweed; competitor removal stimulated only the growth of cordgrass (Table 22). Pickleweed was the superior competitor for nitrogen uptake; its biomass increased significantly with urea additions, with no significant effect from the presence of cordgrass.

Nitrogen added to pure stands of cordgrass was readily taken up by the plants — so thoroughly that soil nitrogen concentration did not increase. Instead, the nitrogen went directly into the leaves, and could be measured only as increased nitrogen concentrations in plant tissues. Insects seemed able to locate plants with enhanced tissue nitrogen, and it appeared that local outbreaks did serious damage to cordgrass. Thus, the net effect of urea fertilization on pure stands of cordgrass may be beneficial, by stimulating growth, or detrimental by causing insect damage. This cause-effect relationship is under further study by Covin (in prog.) at the Pacific Estuarine Research Laboratory.

The experimental results (Table 22) were complex, and they led to a new model of nitrogen-marsh dynamics (Covin 1984; Covin and Zedler, unpubl. ms.): Nitrogen is certainly limiting to vascular plant growth. Additions will stimulate cordgrass in pure stands, but herbivores may gain the ultimate benefit from the increased nutritional quality of the plants. In mixed stands, additions stimulate pickleweed, which then outcompetes cordgrass.

Some interesting questions remain: Why didn't nutrient additions stimulate herbivory on pickleweed? Was it chance that precluded an outbreak in the fertilized plots? Perhaps, but a 1984 experiment performed by Beare and Beezley (unpubl. data) suggests otherwise. Plots with urea added had less herbivory than plots fertilized with Milorganite. In replicate plots of pure pickleweed, urea was added biweekly along with fresh water to cylinders of 0.33 m² area that penetrated 10 cm of soil and protruded 30 cm aboveground. Milorganite was added in low, medium, and high concentrations to additional cylinders, with the high treatment

Table 22. Standing crop of cordgrass and pickleweed in August 1983 in replicate (n = 2) plots with and without urea additions and with and without competitors removed. All data are aboveground biomass in g/m² (from Covin 1984).

Cordgrass	With pickleweed	Without pickleweed
With urea	625	1,282
Without urea	577	898

Pickleweed	With cordgrass	Without cordgrass
With urea	1,525	1,484
Without urea	1,038	1,316

adding an amount of nitrogen equal to that in the urea treatment. Other cylinders received fresh water only. Each treatment was replicated four times. Plant growth increased with nutrients added in high concentrations, but results were complicated by insect attack.

Beetle herbivory became pronounced in August, and the lengths of chew marks were summed for stems sampled from each treatment. Insect damage in plots fertilized with Milorganite averaged 40 mm/branch, while those with urea averaged 4 mm/branch. The growth response to the two fertilizers was similar, but the insect response was not. Likewise, Covin did not find insect damage on urea-fertilized pickleweed, although he did on cordgrass (see above). There may be a differential insect response to different plant species fertilized by the same nitrogen source.

However, these results actually suggest more questions than they answer. Because the work was initiated in a year of unusual hydrological conditions (no tidal flushing for most of the year, no rainfall in winter of 1984), because field breakdown rates of Milorganite are unknown, and because fertilizers were applied in water solution, it is not clear how broadly the findings can be generalized. Finally, if some plant species become more palatable upon urea fertilization than others, what mechanism is involved? Is it a difference in cordgrass vs. pickleweed herbivores, or a difference in the grass vs. succulent plant chemistry? Clearly, there are multiple routes of research to be pursued in understanding how nitrogen and other nutrients influence salt marsh functioning.

4.5 ENERGY FLOW

For many years, salt marshes have been viewed as food producers that subsidize coastal bays and nearshore waters (Odum 1971). Haines (1979) and Nixon (1980) have challenged that dogma for Atlantic Coast marshes, as has Winfield (1980) for Tijuana Estuary. As a result, investigators have concluded that coastal marshes display a high degree of individuality. Their ability to fix carbon at remarkable rates remains unchallenged, but the ecological fate of that carbon is highly variable. Systems with large river flows are likely to transport large fractions of their net primary production during spring runoff; systems with broad tidal amplitude may be highly susceptible to exporting organic matter year round; marshes experiencing rapid sea-level rise may accumulate plant matter in the sediments; small semienclosed wetlands may use the energy of photosynthesis and recycle large portions of their fixed carbon. The high productivity, then, is either exported (usually as detritus), accumulated (as peat) or released in respiration (energy lost as heat; carbon recycled as carbon dioxide).

Studies at Tijuana Estuary add another complication — that of tremendous temporal variability in the processes that determine the fate of organic carbon. This section reviews research that has evaluated detrital production (Winfield 1980), feeding and growth rates of estuarine animals (Williams 1981; Boland 1981), carbon fluxes (Winfield 1980), and variations in the system's ability to "filter" materials from incoming waters (Zedler and Onuf 1984).

4.5.1 Detrital Production

As live plant material dies and is transformed into small particles, detritus is "produced." It is much more than a mechanical process, because fungal and bacterial decomposers are integrally involved in the transformation. As they help to break down the fixed carbon, they simultaneously enrich the particles with organic nitrogen gleaned from tidal waters. Two lines of evidence indicate that detritus production is far from constant at Tijuana Estuary. The first is Winfield's (1980) work on litter dynamics (dead organic matter beneath the marsh canopy); the second is his direct measurements using litter bags.

The seasonal changes in litter (Figure 55) were highly variable. Litter accumulated through May in 1976 but decreased through November in 1977. August values were high in 1976 (about 200 g/m²) and low in 1977-78 (100-130 g/m²). The processes responsible for litter removal are likewise variable, and tracing the fate of plant losses is a complex problem. Casual observations indicate that the coincidence of high tides and strong winds results in major transport of litter from the low marsh to the high tide line. Large wrack deposits are occasionally obvious, but there are many months when debris lines are hard to locate.
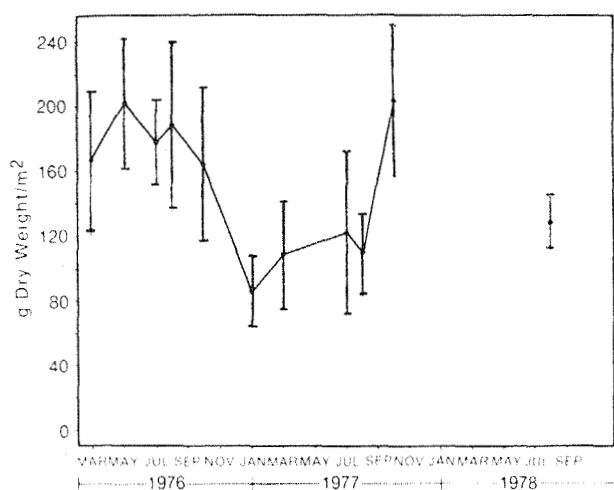
Figure 55. Seasonal dynamics of litter in the salt marsh of Tijuana Estuary. Vertical bars are ±1 standard error, n = 25. Reprinted with permission from Winfield (1980).

Table 23. Decomposition rates of selected plant material (from Winfield 1980).

Material	Location[a]	%/mo.	%/yr
LIVE:			
Cordgrass shoots	ecotone	7.1	85
Cordgrass leaves	ecotone	9.1	100
Whole shore grass	upper marsh	3.1	37
Whole Jaumea	ecotone	9.1	100
Pickleweed shoots	ecotone	9.1	100
Annual pickleweed	ecotone	9.1	100
DEAD:			
Cordgrass shoots	creek	11.1	100
Cordgrass shoots	ecotone	4.0	48
Cordgrass leaves	creek	33.3	100
Cordgrass leaves	ecotone	8.3	100
Annual pickleweed	creek	20.0	100
Annual pickleweed	midmarsh	4.2	50

[a]Ecotone = upper extent of cordgrass zone.

Data on decomposition rates (Table 23) show large differences between: species, leaves and stems, live and dead fractions, and locations of litter bags in the marsh. While litter bags were deployed in the marsh only during one year, other data indicate year-to-year differences in the availability of plant parts for various marsh species (Section 4.3). Furthermore, some of the succulent plants are highly susceptible to breakage (e.g., saltwort, Batis maritima), while the grasses are not. Leaves of saltwort are readily detached and floated away at the end of the growing season, as are their fleshy fruits. Coupling the differences in plant production and mortality through time with differences in disappearance rates of species and plant parts shows high temporal variation in detritus production.

4.5.2 Feeding and Growth Rates

Plant material produced by the salt marsh is used both directly (herbivory) and after fractionation to detrital particles (detritivory). We are almost entirely ignorant of the first process at Tijuana Estuary. But the abundance of insects found on various salt marsh plants insures that it is an important energy flow pathway (e.g., outbreaks of Diptera on cordgrass documented by Covin 1984; Coleopteran damage on pickleweed documented by Beare and Beezley, both discussed in Section 4.4). Other evidence that herbivores consume large fractions of live plants comes from wetland restoration studies, wherein new cordgrass transplants were usually grazed to the nubbins by ground squirrels and rabbits (Zedler 1984a). It became necessary to cage transplants in order to

insure their survival; yet mature stands of cordgrass were relatively unharmed. While the cause of differential grazing can only be hypothesized (e.g., changing nutritional quality following transplantation?), the fact remains that live cordgrass can be highly palatable to marsh consumers.

Additional evidence for in situ consumption of estuarine productivity comes from studies of invertebrate growth rates. Williams (1981) examined growth rates of mussels (Mytilus edulis) at Tijuana Estuary for comparison with laboratory-reared individuals fed diets of cordgrass and pickleweed detritus. In the laboratory, mussels lost weight when fed freshly made detritus but grew slightly when fed aged detritus. The highest growth rates were found with mussels grown in the dredged channel at Tijuana Estuary. Williams (1981) concluded that bacteria and phytoplankton are more important in the funneling of estuarine productivity to benthic consumers than detritus from vascular plants. It remains to be demonstrated how much the bacteria or phytoplankton use dissolved organic carbon that has been fixed by, and later leached from, marsh vegetation.

4.5.3 Carbon Fluxes

At the same time that Winfield (1980) studied nitrogen fluxes in tidal creeks, he sampled organic carbon to determine the net flux of different components: dissolved organic carbon (DOC) and particulate organic carbon (POC). Because POC is the sum of three major components, live phytoplanton, other live plankton, and dead particles, Winfield identified these analytically. Live biomass was determined from measurements of ATP (total live) and the algal portion was

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calculated from chlorophyll a measurements, so that other plankton could be estimated by subtraction from totals. Dead biomass was calculated by subtracting the live fraction from total POC. The difficult but precise analyses were necessary to quantify tidal water composition. Over 1,850 samples were processed for carbon analysis in the 2-year study (Winfield 1980).

Most studies of carbon flux ignore the DOC component. Yet at Tijuana Estuary, this was the major form of carbon export (Figure 56). Concentrations of DOC in ebb tide water often exceeded concentrations in flood tide water (Figure 57). Furthermore, concentrations of C in the dissolved form averaged much higher than in the particulate form (Figure 58). DOC ranged from 1 to 11 mg C/l, while POC ranged from 0.4 to 1.8 mg C/l of creek water. Thus, the ultimate removal of organic materials produced in the marsh results from processes such as leaching of DOC from both live and dead plants and animals and excretion of organic molecules by plants and animals.

Detrital carbon dominated the particulate component in tidal waters, sometimes making up 98% of the POC, and never less than 36% (Winfield

1980). Live organisms made up the majority of the particulate matter only in June 1977 and April 1978. Both times the live POC was largely algae, as indicated by chlorophyll concentrations. In contrast with DOC results, the POC data suggested that the salt marsh entrains particulate materials, although this is the net result of frequent import and occasional export.

What fraction of marsh productivity is exported to tidal creeks? Based on his 10-month study period, Winfield (1980) estimated an annual export of 40 g C/m²/yr as DOC for the area dominated by succulents and 110 g C/m²/yr for the area of mixed cordgrass and succulents. A net import of particulate carbon was determined for POC, with annual estimates at 5-6 g C/m²/yr for the areas included in his two sampling stations. At most, then, there was a net removal of 105 g C/m²/yr, which is well below the net amount produced by vascular plants (approximately 220 g C/m²/yr; Section 4.3) and epibenthic algae (185-340 g C/m²/yr). Additional fluxes of debris probably occurred on the water surface and as wind-borne materials; neither was measured because of enormous difficulties in sampling. Because temporal variability in all of these processes is
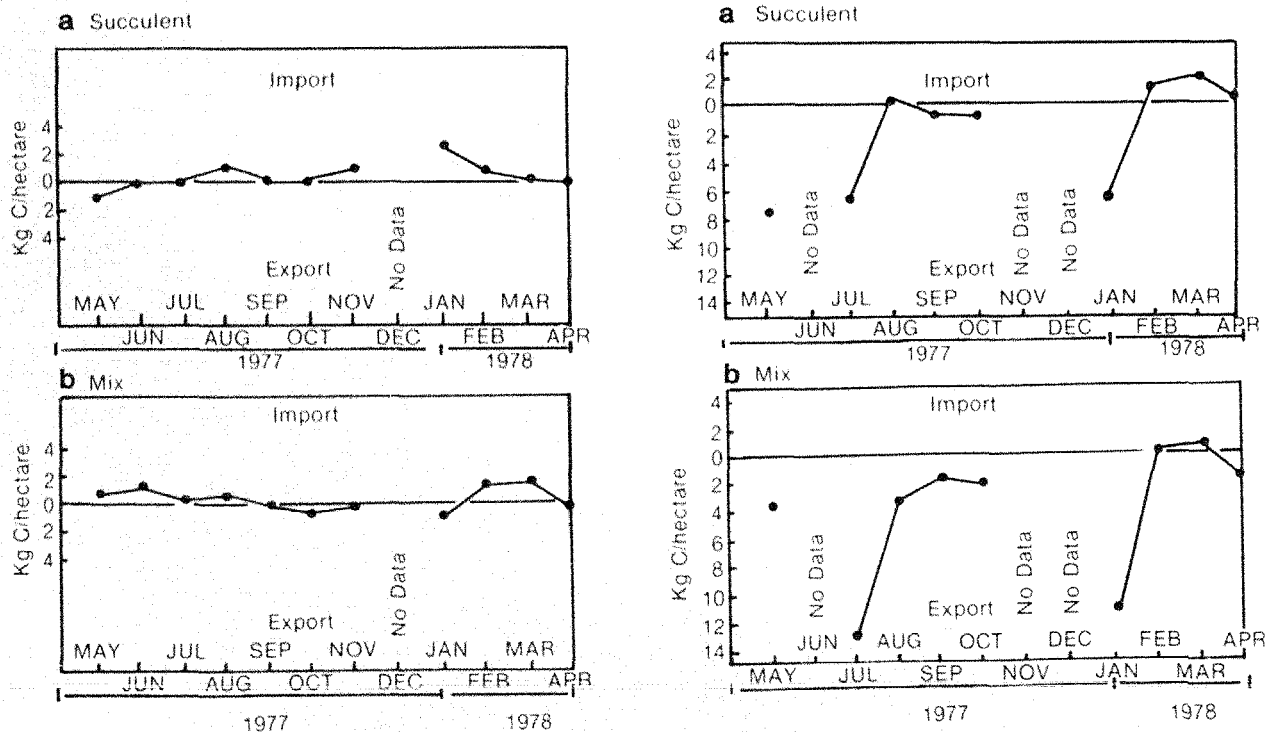

Figure 56. Net flux of particulate (left) and dissolved (right) organic carbon in tidal waters of (a) the succulent-dominated and (b) mixed cordgrass-succulent study sites of Winfield (1980). Reprinted with permission from Winfield (1980).

a Succulent

b Mix
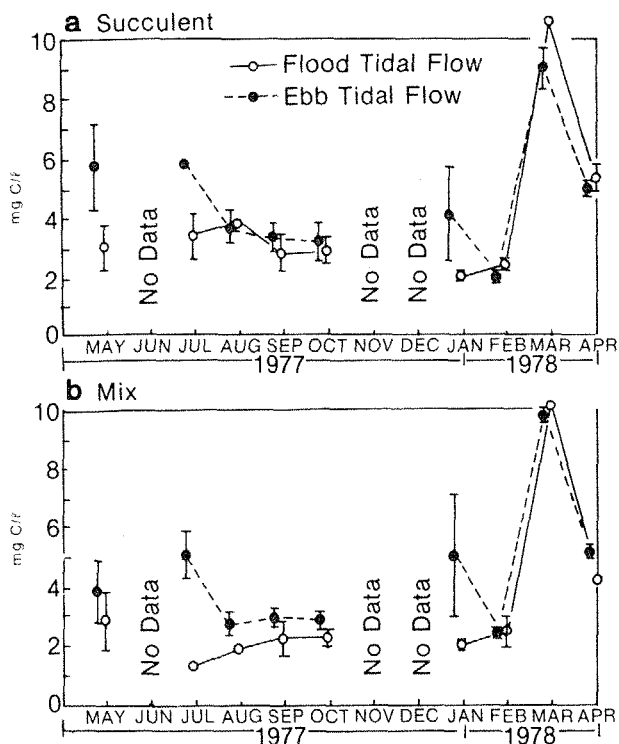
Figure 57. **Mean concentrations of dissolved organic carbon for flood and ebb tidal waters of (a) the succulent-dominated and (b) cordgrass-succulent study sites of Winfield (1980). Reprinted with permission from Winfield (1980).**

high, it is unwise to set a percentage for materials lost from the marsh to adjacent tidal creeks. Suffice it to say that, from these early data, most of the marsh plant production appears to be used within the marsh.

4.5.4 Temporal Variability in Filtering Functions

There is little information on year-to-year differences in nutrient uptake rates, sediment accretion, and peat formation. Limited studies of peat accumulation (Scott 1976; Mudie and Byrne 1980) show that marsh elevations have increased through geologic time, and comparisons of elevations before and after flooding (Zedler 1983b) document short-term accretion. Not much can be said about the processes that reverse these "filtering" functions, either. No measurements have been made of erosion, other than what is obvious from aerial photos (Chapter 2). Overall, Tijuana Estuary is accumulating sediments within the channels and losing area due to shoreline retreat, but the processes appear to be more catastrophic than chronic.

A conceptual model was developed by Zedler and Onuf (1984) to describe estuarine filtering during the wet and dry seasons of nonflood years and during flood years (Figure 59). Nonflood years are the most commonly occurring condition. During these times, the estuary is believed to be a sink for nutrients and sediments coming from both the watershed and the ocean. It is also a sink for salts that are brought in by tides and accumulated through evaporation.

We have no data on nutrient inputs during natural flood events at Tijuana Estuary, and can only speculate that nutrient influxes and accumulation rates are greater during flood than nonflood years. All studies of filtering functions during flooding came after hydrological modifications had changed both the availability of sediments for transport and the rates and timing of streamflows. Onuf's comparisons of flood effects at Mugu Lagoon before and after 1970 indicate that sedimentation was much less during floods that preceded watershed development. The combined floods of 1978 and 1980 filled in the central bay of Mugu Lagoon and decreased low-tide volume by 40% (Onuf, in press).

Disturbances within the watershed of Tijuana Estuary have destabilized slopes and made available large volumes of sediment, just as in the watershed of Mugu Lagoon. Unlike Mugu Lagoon, Tijuana Estuary is somewhat protected from sediment deposition by dams that regulate 78% of the watershed. Still, agricultural and urban developments below Rodriguez Dam disturb soils that can be mobilized by flooding. Aerial photos of the 1980 flood show major sediment plumes flowing out of the mouth of Tijuana Estuary. Only a small portion of the sediment was deposited within the wetland.

Because the bulk of the filtering process occurs as sedimentation during catastrophic events, it is not clear how important the vascular plants are in controlling the processes of accretion and erosion. In coastal systems worldwide, there are attempts to stabilize shorelines by maintaining good cover of beach grasses and cordgrass. At Tijuana Estuary, the importance of beach vegetation in reducing sediment mobilization is clear, but the role of cordgrass is not. Cordgrass does not occur in the path of the river; thus, it cannot reduce erosion along the river banks. Some areas of pickleweed in the estuary and even some woody vegetation upstream were scoured out by the 1980 flood. Cordgrass may be effective in increasing sedimentation within the salt marsh. Whether this is beneficial or detrimental to maintenance of wetland habitats depends on the combined rates of accretion and sea level rise.
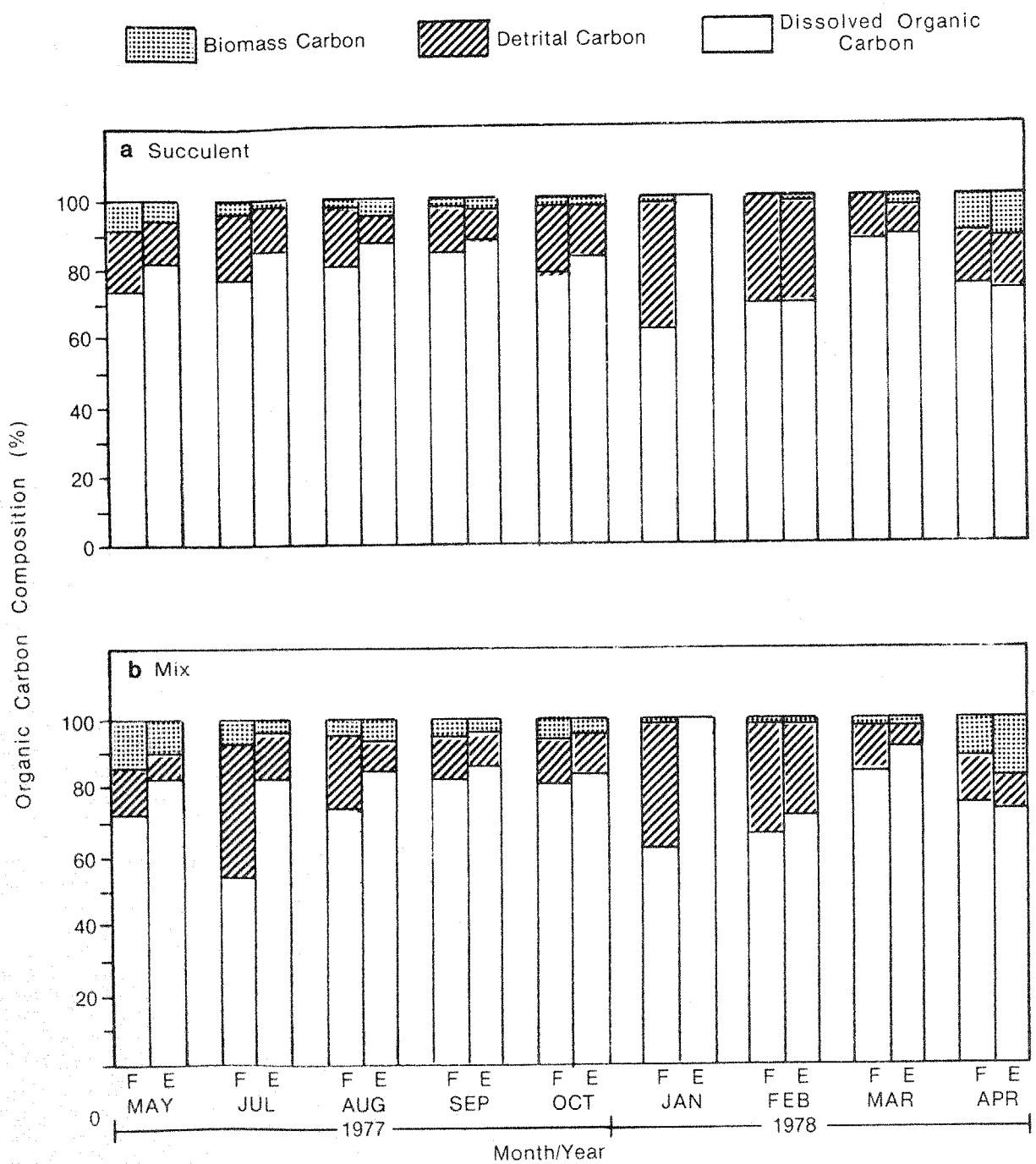
Figure 58. Percent composition of total organic carbon in flood and ebb tidal waters in   (a) the succulent-dominated and (b) the cordgrass-succulent study sites of Winfield (1980).   F = flood tidal flow; E = ebb tidal flow. Reprinted with permission from Winfield (1980).

WET SEASON: Plants take up nutrients; animals consume POC. Sediments are deposited in channels.

Tide
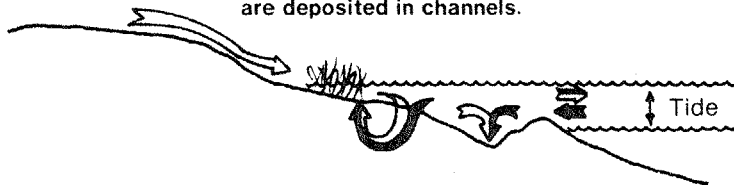
DRY SEASON: No input from the watershed; organisms filter food from water; salts accumulate in intertidal soils.
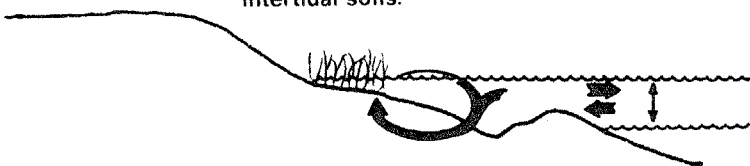
FLOOD EVENT: Biological filters may break down; physical phenomena predominate.

Sediment, Salt

Watershed

Marsh

Channel

Ocean
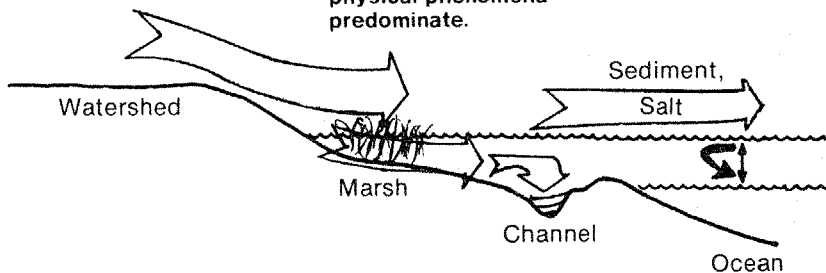
Figure 59. Conceptual model of filtering functions during nonflood years and during catastrophic flooding; white arrows indicate fresh water; black arrows indicate sea water (from Zedler and Onuf 1984, with permission from Academic Press).

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CHAPTER 5

THE ROLE OF DISTURBANCES IN MODIFYING SALT MARSH COMMUNITY STRUCTURE AND FUNCTION

Recent changes in species distributions and growth rates have been documented in detail for the salt marsh of Tijuana Estuary. A general understanding of what controls invasion and extinction of species at the ecosystem scale has developed, as well as ability to predict expansions and declines at the population scale. Catastrophic events, though destructive in many ways, have proved to be scientifically valuable. Their effects have been documented through an extensive monitoring program that began as a survey of cordgrass habitats in 1979 and has continued to date. This chapter provides extensive evidence of the estuary's temporal variability and indicates why no single description of productivity or biomass can fully characterize the salt marsh ecosystem.

5.1 MONITORING PROGRAM

The lower salt marsh has been sampled consistently at approximately 100 stations along eight transects (Figure 60). The exact number of stations has varied slightly with our ability to relocate station markers and the expansion of the distribution of cordgrass. The transects were set up to characterize the cordgrass community; thus they extended from upper distributional limits toward channels. In all cases, transects were named for the nearest Army Corps of Engineers benchmark (e.g., TJE-31).

In 1984, the monitoring program was expanded to include upper marsh habitats. An additional 115 stations were set up to extend from the upper distributional limit of cordgrass inland. After surveying their elevations, we found that many of the sampling stations set up to characterize upper marsh distribution were within the range of elevations included in the lower marsh transects (Table 24). They are actually cordgrass and noncordgrass transects. This emphasizes that the distribution of cordgrass is not entirely predictable from elevation. Other factors, including competition by succulent species, limit the occurrence of

cordgrass, and the monitoring program has helped to elucidate these and other distributional patterns.

Measurements taken at the monitoring stations are as follows: Elevations are periodically measured relative to Army Corps of Engineers benchmarks. Each April, soil salinity is measured in samples near all stations. In the lower marsh, interstitial soil water is collected by expressing soil water (from 0 to 10 cm depth) through filter paper onto a salinity refractometer. In the upper marsh, the drier soil samples (0-10 cm depth) are collected and taken to the laboratory, where uniform soil pastes are made and measured with a conductivity meter (Richards 1954). In September, soil salinity sampling is repeated and vegetation is measured. Cordgrass is assessed by measuring heights of stems within 0.25-m^2 circular quadrats (or 25% of that area if densities are too high for complete measurements). Flowering stems are noted; live and dead stems are counted. The percent cover of each of the other species present is estimated within cover classes (<1%, 1%-5%, 6%-25%, 26%-50%, 51%-75%, 76%-100%).

5.2 PHYSICAL CHANGES FOLLOWING ECOSYSTEM-WIDE DISTURBANCES

5.2.1 Soil Salinity Changes

Interstitial soil salinities, which have been measured annually in April and September, indicate that the lower marsh is usually hypersaline (i.e., more saline than sea water; Figure 61). The following data stand out:

a. Reductions in soil salinity (to 15 ppt) occurred in April 1980, after the "100-year" flood. Because the flooding occurred primarily in January and February, the April measurement may not represent minimum soil salinity. Evaporation was no doubt high throughout the spring (Section 2.2), and tidal waters influenced the marsh throughout 1980; thus the period of brackish soils was short-lived.

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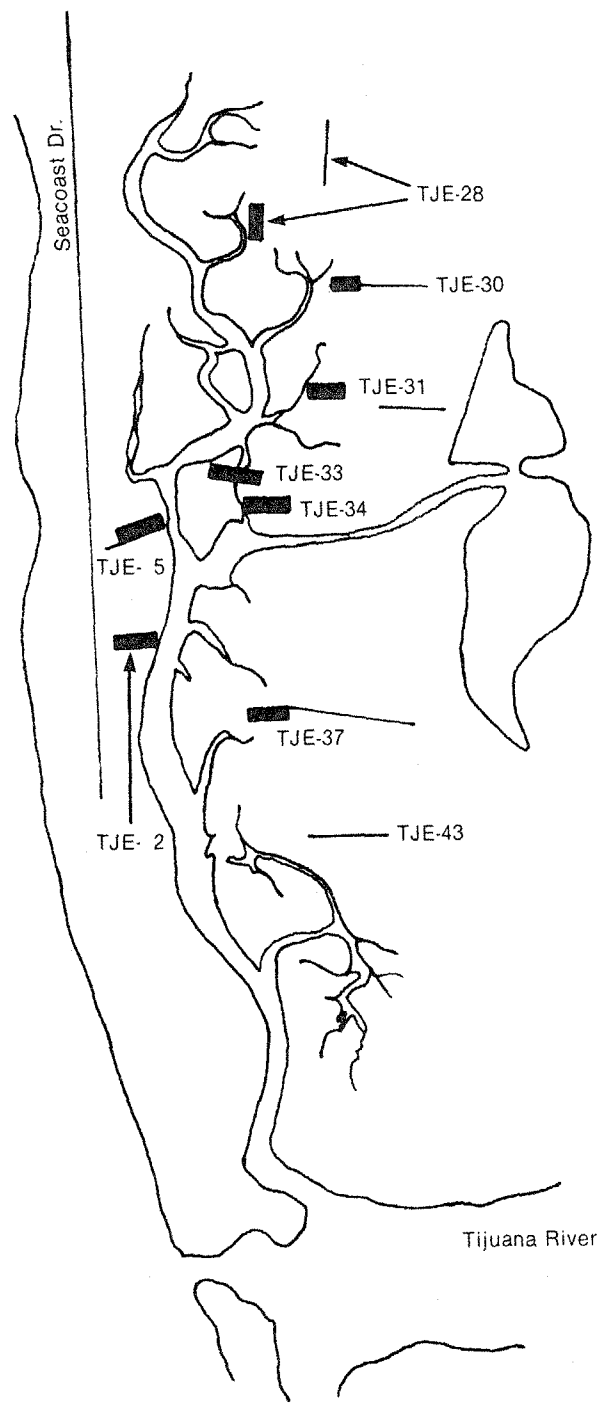
transects dominated by cordgrass ("lower marsh") n =102 stations monitored since 1979.

transects dominated by succulents ("upper marsh") 115 stations established in 1984.

Figure 60. Map of lower and upper marsh monitoring transects at Tijuana Estuary.

b. Soil salinity was again low (30 ppt) in April 1983, when a long winter distributed rainfall well into spring. It is likely that the average for April overestimated salinities later in the growing season, because of major influxes of fresh water from Rodriguez Dam throughout the growing season (IBWC 1983) that dropped channel water salinities to zero in August (Zedler et al. 1984a).

c. The September 1984 data point is the most unusual. An average soil salinity of 104 ppt in September 1984 resulted from estuarine closure in April 1984 followed by evaporation throughout the hot, dry summer. Again, this is an underestimate of salinity, because several readings exceeded the 0-150 ppt refractometer scale. Soil moisture at the end of summer was extremely low; channels were dried and cracked. The water table was 30 cm below the surface on May 31, 1984, and more than 75 cm below the surface on October 9, 1984.

5.2.2 Sedimentation in the Salt Marsh

Elevations increased an average of 5 cm after the 1980 flood (Table 25). Most of the accretion in the marsh was due to sediment deposition. In addition, large rafts of wood and plastic floated downstream and accumulated in the lower marsh. Later, during the 1983 winter, the estuary mouth closed briefly and a large volume of sea water was impounded for several days. Sea levels were much higher during the January 1983 storm than during previous tidal maxima (Figure 5; Cayan and Flick 1985). Debris that had accumulated in 1980 was floated inland, pushed by the prevailing west winds. Large rafts of wood and plastic can still be found along the high ground to the east of the salt marsh.

Table 24. Elevation (cm above MSL) of quadrats included in the 1984 monitoring program. Lower marsh transects are designated cordgrass; upper marsh transects are called noncordgrass.

Elevation	Cordgrass	Noncordgrass
51-60	5	1
61-70	36	7
71-80	42	35
81-90	2	24
91-100	11	12
101-110	5	6
111-120		11
121-130		4
131-140		5
141-150		6
151-160		2
161-170		1
171-180		1
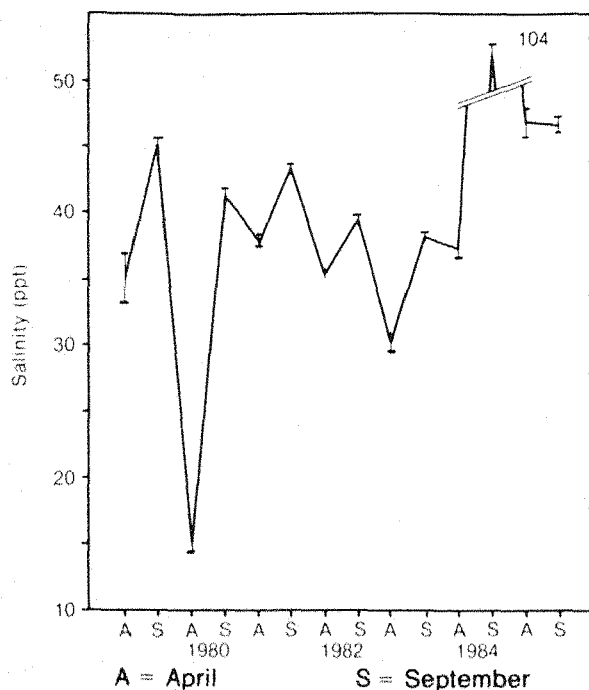
Figure 61. Changes in interstitial soil salinity in the cordgrass-dominated monitoring stations (n = 102). Vertical bars are ±1 standard error.

Table 25. Changes in elevation in the lower marsh before flooding (1979), after flooding (1980), and after sea storms (1984).

Transect	Average elevation (cm)		
	1979	1980	1984
TJE-2	66	71	99
TJE-5	no data	97	96
TJE-28	56	64	62
TJE-30	66	73	71
TJE-31	70	74	74
TJE-33	67	70	68
TJE-34	72	82	73
TJE-37	67	67	67
Average	67	72	74

Additional changes in elevation no doubt occurred with drying and shrinkage of the clay-dominated soils. Resurvey of the marsh elevations in August 1984 (Table 25) documented elevations similar to pre-1980 levels for all but transect TJE-2. There, an increase of 28 cm appears to have been caused by sand and mud deposited during the same winter storm that moved much of the coastal dune into the estuarine channels. Transect TJE-2 is closest to the area of maximum channel sedimentation; these before/after data document local sedimentation rates during that extreme event.

5.3 EFFECTS OF ECOSYSTEM-WIDE DISTURBANCE ON SALT MARSH STRUCTURE

For southern California, rare events are very important to overall wetland structure and functioning (Zedler and Onuf 1984). This section focuses on the role of extreme conditions in controlling the most basic structural feature of a plant community: its species composition. The presence of a species is determined first by its ability to establish and second by its ability to persist. It is hypothesized that germination and establishment are limited to the "low salinity gap" that follows winter rainfall, and that expansion and persistence are limited by the environmental stresses of hypersaline drought and/or excessive inundation.

At Tijuana Estuary, the salt marsh monitoring program begun in 1979 was again shown to be of value when we were able to document increased growth, vegetative expansion, and seedling establishment of cordgrass (Zedler 1983b) following the 1980 flood. Associated field research projects that were suggested by the monitoring program have in turn identified causes of observed vegetation changes.

5.3.1 Cordgrass Marsh Vegetation Changes

Cordgrass and its associated succulents have undergone tremendous variations in growth and distribution in recent years. The changes are neither cyclic nor predictable from past understandings of salt marsh ecology. The vegetation dynamics appear to be related to both salinity and elevation changes that have occurred between 1979 and 1985.

From 1979 to 1983, the distribution of cordgrass expanded (Figure 62). Debris deposited by the 1980 flood eliminated some patches of cordgrass through smothering, but there was a general progression landward. Then, during the 1984 drought, there was substantial mortality of cordgrass, which was severe at the lowest elevations. Each tidal creek was lined with a band of dead cordgrass. The widespread pattern of mortality was unprecedented in our data base, and there is every reason to conclude that it was caused by drought and hypersalinity. The finding that mortality rates were greater near the tidal creeks than within the marsh is consistent with mortality patterns seen in controlled watering experiments (see below).

Pickleweed (*Salicornia virginica*) was the second most abundant species in the lower marsh,
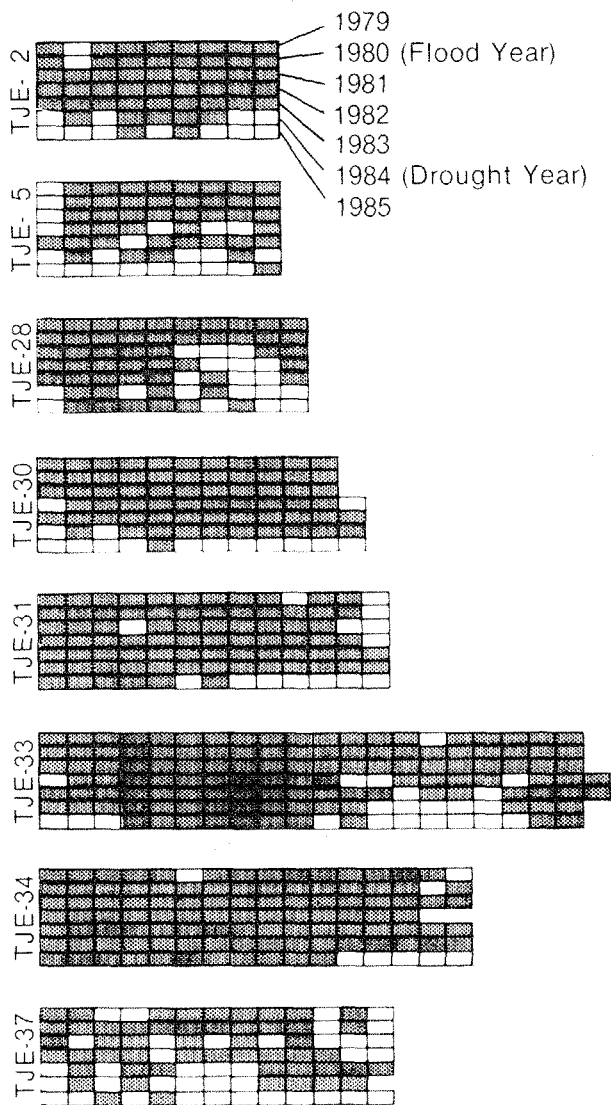
Figure 62. A graphical summary of cordgrass distribution changes along eight transects that extend from channels (on the left) inland (see Figure 60). Sampling stations (0.25 m² circular quadrats) were at 5-m intervals; each is represented by a rectangular box; darkened boxes indicate presence; open boxes indicate absence. Through time, holes in the distribution have developed and persisted. The frequency of cordgrass changed as follows: 1979 = 89%, 1980 = 94%, 1981 = 86%, 1982 = 83%, 1983 = 89%, 1984 = 72%, 1985 = 38%.

and its pattern of change was nearly the opposite of the cordgrass. Because of the highly branched, trailing form of pickleweed, we assess its abundance by estimating cover in standard classes, rather than attempting to count stems. This is a crude measure, so that only large changes in cover can be identified. In 1980,

pickleweed was significantly lower in cover than in 1979 (Table 26). By 1983, it had increased again and in 1984, through a major drought, it reached its maximum cover, with 33 quadrats having 75%-100% cover of pickleweed. This species changed little in its spatial distribution until 1985 (Figure 63); instead it changed in growth, a finding that is consistent with earlier suggestions that pickleweed is a highly tolerant species capable of survival in a wide variety of salinity and moisture conditions (Zedler 1982b). Expansion in 1985 occurred in many areas that were previously occupied by cordgrass.

5.3.2 Succulent-Dominated Marsh Responses to Drought

The 1984 expansion of the monitoring program to include 115 quadrats beyond the cordgrass habitat provided an opportunity to compare 1974 and 1984 data sets in detail and to document species that were eliminated by the 1984 drought. The upper marsh was sampled for the first time in 1974 using 357 quadrats (cf. Zedler 1977 for detailed community description). Additional information was obtained in 58 stations used for productivity measurement in 1976 (Winfield 1980) and 9 quadrats along one transect used for a study of annual pickleweed (Salicornia bigelovii) in 1975 (Zedler 1975). While less extensive, these interim censuses help to determine when compositional changes occurred. Throughout our work at Tijuana Estuary, we have assessed species composition with the same cover classes and 0.25 m² circular quadrats, so that data are readily comparable.

Some of the compositional differences between 1974 and 1984 may be due to sampling in different locations. The 1974 data set included three transects, located at TJE-36, 40, and 43. In addition, the 1984 data set included a larger proportion of samples from cordgrass-dominated areas. [The higher frequency of cordgrass in 1984 is a consequence of having more quadrats within its distribution, rather than a real increase in the marsh.] For these reasons, the 10-year comparison should ascribe significance only to large changes in occurrence or cover. If drought is affecting the salt marsh, it should have its greatest impact on shallow-rooted species, especially annuals. Species known to have broad ecological tolerance as adults (e.g., the perennial pickleweed and alkali heath, Frankenia grandifolia) should show little decline in response to drought.

Most notable in the 10-year comparison are the absences of annual pickleweed (Salicornia bigelovii) and sea-blite (Suaeda esteroa, formerly called S. californica) in the 1984 data. Annual pickleweed was a dominant component of the marsh in 1974 (64% frequency), as well as during the 1976 productivity study (Chapter 4) and the 1975 population study of annual pickleweed, when

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Table 26. Change in pickleweed canopy cover in cordgrass transects from 1979 to 1985 (no data in 1982). The Kolmogorov-Smirnov two-sample test was used to compare cumulative distributions for consecutive years. The 1981-83 comparison was not significant; all others were different at the 10% level ($p < 0.1$).

Cover class	Number of quadrats per cover class					
	1979	1980	1981	1983	1984	1985
0%	32	23	24	26	23	12
<1%	0	7	4	6	2	2
1-5%	5	14	3	12	1	4
6-25%	15	11	14	19	8	6
26-50%	14	4	13	9	17	5
51-75%	12	42	15	16	17	10
76-100%	22	0	23	15	33	62
Mean cover[a]	50%	38%	50%	38%	61%	71%
Total number of occurrences	68	78	72	77	78	89

[a]Mean cover was calculated from cover class midpoints using quadrats where pickleweed occurred (0's omitted).

densities of over 4,000/m² were documented. In spring 1984, the species was observed in seedling stage, although densities were not particularly great. However, no seedlings were seen in the monitored quadrats, either in the upper or lower marsh (n = 215 quadrats). A tiny patch was located near TJE-28, so it has not been completely lost at Tijuana Estuary; also, annual pickleweed is still abundant at the tidally flushed marsh in Mission Bay, San Diego. The sea-blite is a short-lived perennial that occurred in 37% of the 1974 quadrats and none of the upper marsh quadrats of 1984. We found one occurrence in 1984, so it has not disappeared altogether. Sea-blite was present in the 1976 productivity study and has been commonly seen up until this year. The large change in frequency documents a significant decline, and we attribute it to the nontidal drought condition of the marsh.

Pickleweed was the dominant species throughout the marsh in both 1974 and 1984 (Table 27), which supports the hypothesis that adults of species with a broader ecological tolerance would be less susceptible to drought. In 1984, alkali heath was rare in the cordgrass transects, but not at the higher elevations. Between 80 and 110 cm MSL, alkali heath was over 80%-90% frequent in 1974 (Zedler 1977), and it persisted with frequencies of 60%-85% during the 1984 drought. Compared to the near extinctions of annual pickleweed and sea-blite, the longer-lived species were much less affected by the prolonged dry period.

The fact that sea-blite is a short-lived plant without a well-developed root system (Purer 1942) may explain its susceptibility to drought. Likewise, rooting depth and root development limit survival of young seedlings. Mature, long-lived perennials may be able to track a declining water table by extending their roots further into the substrate. Both the perennial pickleweed and alkali heath are frequent and high in biomass at Los Peñasquitos Lagoon, where tidal flushing has been intermittent over the past several decades (Purer 1942; Bradshaw 1968; Carpelan 1969; Zedler et al. 1980). The tolerance of mature perennials to extreme environmental conditions exceeds that of species that rely on seed germination and establishment for persistence.

Both annual pickleweed and sea-blite are good invaders. In 1985, both species appeared in abundance on newly dredged habitat at Sweetwater Marsh (San Diego Bay), where the California Transportation Department has a major marsh restoration project. However, recovery of both species has been slow at Tijuana Estuary. First, the seed bank was depleted, because many seeds germinated in 1984 and died before reaching maturity. Second, the predrought abundance of annual pickleweed was related to an open canopy of saltwort (Batis maritima; Zedler 1977). Since the drought, the canopy of saltwort has closed (total cover averaged 40% for all elevations of occurrence in 1984). Like the perennial pickleweed, saltwort appears to have increased its biomass during estuary closure.
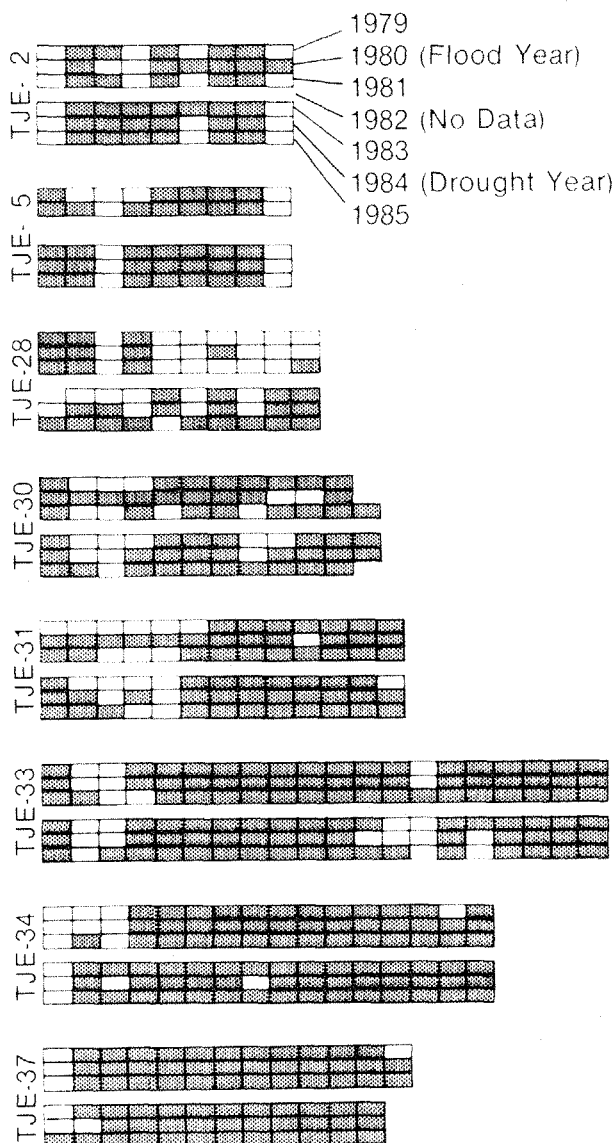
Figure 63. Changes in pickleweed distribution along eight transects (see Figure 60; data are explained in Figure 62). See Table 26 for changes in frequency and percent cover.

These hypotheses of reduced seed bank and competitive effects of pickleweed are being tested experimentally.

It is likely that expansion and shrinkage of species distributions is the norm for the region's highly dynamic wetlands. The estuary's history of variable rainfall and streamflow, fluctuating sea levels, and alternating conditions of good and sluggish tidal flow, all suggest that the abundance and distributional limits of marsh species should

also vary. However, the combination of severe environmental stresses, such as drought combined with estuary closure, is probably rare. Thus, local extinction is not viewed as a common event for this estuary. Species richness in the region's wetlands is high for systems with good tidal flushing and low for systems that frequently close to tides (Zedler 1982b); the near loss of annual pickleweed and sea-blite was no doubt due to a combination of events.

Whether or not either species will recover depends in part on management of the estuary. The dredging that preceded reopening of the estuary mouth in December 1984 appears to have increased tidal flushing beyond what it was in 1983. If tidal flushing is greatly improved after pickleweed has become dominant, this may well be detrimental to recovery of short-lived species. Without tidal action, soils dry in summer, and perennial pickleweed grows very well (78% cover in 1984). With sluggish tides, drainage of the intertidal marsh is incomplete, soils remain saturated for long periods of time, and perennial pickleweed is at a disadvantage. These were the conditions of 1983, when pickleweed cover was at a low of 38% (Table 26). With maximal tidal flow, the marsh is periodically well-drained, and pickleweed cover may remain high (as in 1985). If these conditions persist, competitive dominance by perennial pickleweed is expected to preclude reestablishment of annual pickleweed and sea-blite and to reduce the ability of cordgrass to recover. This hypothesis is being tested with manipulative experiments at Tijuana Estuary.

5.3.3 Summary of Compositional Changes

The species characteristic of southern California coastal wetlands do not conform to the classical separation of halophytes and glycophytes on the basis of tolerance to 0.5 ppt salinities (Waisel 1972). There is a spectrum of tolerances, and establishment is determined by the degree and duration of freshwater influence: the low-salinity gap. Salinity determines germination, and duration of the required salinity and soil moisture conditions determines seedling survival. This is consistent with the regeneration niche concept of Grubb (1977), who hypothesized that multiple characteristics of both species and environment influence establishment. Once established, salt marsh plant populations may persist or go extinct, depending on environmental conditions that may differ greatly from those controlling establishment.

A conceptual model was developed to summarize how low-salinity gaps control invasions and extreme stresses control extinctions (Figure 64). Conditions at both Tijuana Estuary and San Diego River were used in comparison with changes following wetter and drier conditions (Zedler and Beare, in press).

Table 27. Occurrence (in circular 0.25m² quadrats) of the most frequent species of the Tijuana Estuary salt marsh, 1974 and 1984.

| Species | 1974[a] | | 1984[b] | |
	Total occurrences	Frequency (%)	Total occurrences[c]	Frequency (%)
Salicornia virginica pickleweed	247	69	83 + 78 = 161	75
S. bigelovii annual pickleweed	229	64	0 + 0 = 0	0[d]
Jaumea carnosa	195	55	40 + 11 = 51	24
Batis maritima saltwort	183	51	55 + 27 = 82	38
Frankenia grandifolia alkali heath	175	49	53 + 4 = 5	26
Monanthochloe littoralis shore grass	146	41	35 + 0 = 35	16
Suaeda esteroa sea-blite	131	37	0 + 1 = 1	<1[d]
Salicornia subterminalis perennial glasswort	64	18	21 + 0 = 21	10
Spartina foliosa cordgrass	56	16	17 + 84 = 101	46
Distichlis spicata salt grass	48	13	7 + 1 = 8	4
Limonium californicum sea lavender	34	10	8 + 0 = 8	4
Triglochin concinnum arrow grass	32	9	35 + 0 = 35	16
Cressa truxillensis alkali weed	24	7	6 + 0 = 6	3
Cuscuta salina dodder	23	6	8 + 0 = 8	4

[a]Data from 357 quadrats along 3 transects; elevation range was 30-130 cm above MSL (Zedler 1977).
[b]Data from 216 quadrats; elevation range was 50-180 cm MSL.
[c]Occurrences in noncordgrass transects + cordgrass transects = total.
[d]Species that were nearly eliminated in 1984.

a. With typical winter rainfall, brief salinity reduction stimulates seed germination and allows seedling establishment. Fresh-to-brackish marsh species cannot invade during the narrow low-salinity gap. The full complement of salt marsh species persists in the absence of extreme environmental stresses.

b. Extreme flooding reduces salinities substantially; cordgrass and other halophytic species can become established from seed. However, because the low-salinity gap is brief, seedling establishment is limited to the normal complement of salt marsh species. Short-term flooding does not appear to cause plant mortality.

c. If the low-salinity gap is artificially prolonged, a variety of fresh and brackish marsh species can germinate and become established. If they grow to rhizome stage within the gap, they may persist after hypersaline conditions return. Species that cannot tolerate prolonged inundation (i.e., species with little aerenchyma) will undergo heavy mortality or go extinct. Impoundment can eliminate salt marsh species, such as pickleweed (*Salicornia virginica*). Summer inundation events may be even more damaging than winter. In the Netherlands, experimental studies of several halophytes indicated that warm temperatures reduce inundation tolerance (Groenendijk 1984); this is reasonable, since respiration rates would increase and growth would decline.

d. Without winter rainfall, seeds of only a few species may germinate, but seedling establishment can be limited by drought and hypersalinity, especially when an estuary closes to tidal flushing. During dry years, most vegetatively-reproducing
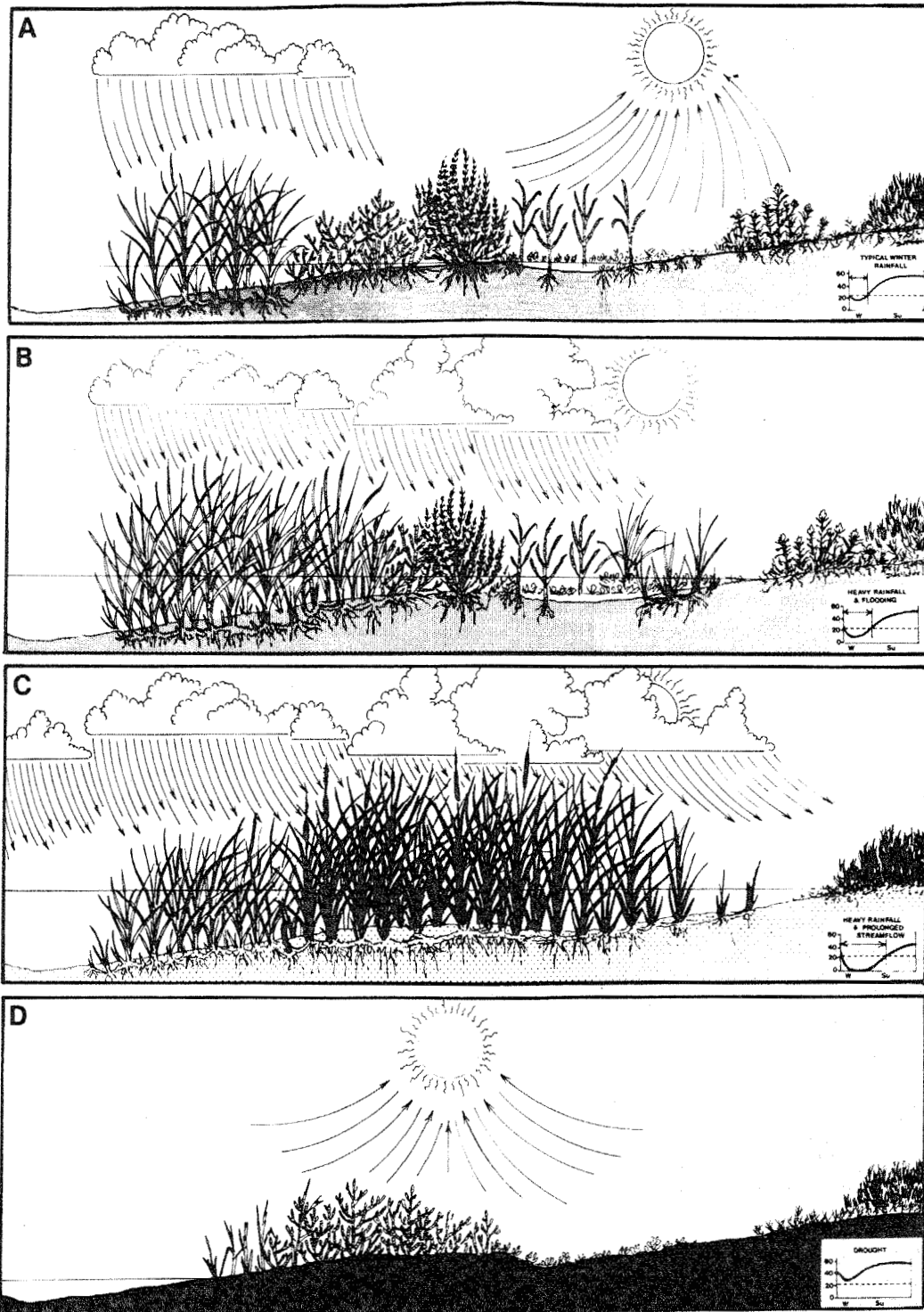
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Figure 64. Conceptual model of species compositional changes with different environmental conditions (see text). The nature of the low-salinity gap (lower right of each panel) determines what can establish and expand in distribution (drawn by McIntire; reprinted from Zedler and Beare, in press, with permission from Academic Press).

perennials can survive long periods of hypersalinity. Even though cordgrass had high mortality, its population did not go extinct at Tijuana Estuary. Short-lived species that rely on seedling recruitment undergo local extinction; only longer-lived perennials persist. Low-marsh species that have less tolerance for the stresses of hypersalinity and drought will experience mortality.

Conditions that limit cordgrass (hypersaline drought) differ from those that limit pickleweed (inundation). Pickleweed usually outcompetes cordgrass (Zedler 1983b; Covin 1984), which helps to explain their reciprocal responses to recent environmental conditions. With prolonged flooding, pickleweed loses its competitive advantage. The diverse plant communities found in this region may well result from the highly variable environment, because no one species has optimal environmental conditions or the competitive advantage indefinitely.

Extreme events have altered wetland structure dramatically in southern California. At the same time, they have helped to reveal cause-effect relationships. The wetland vegetation is resilient as a whole, but individual species undergo dynamic change. The causes of these vegetation dynamics are summarized in a model of community composition: invasion and expansion of species are controlled by the annual "low-salinity gap," which varies both in duration and degree of salinity reduction. Population declines and local extinctions are caused by drought, hypersalinity, and prolonged inundation, to which species have differential tolerance.

5.4 EFFECTS OF ECOSYSTEM-WIDE DISTURBANCES ON SALT MARSH FUNCTION

The monitoring of vegetation at Tijuana Estuary has tracked the responses of cordgrass through periods of major flooding (1980), prolonged freshwater discharge (1983), and drought (1984). Total stem length (tsl) data provide an overview of cordgrass responses to these events (Figure 65). The correlation between cordgrass tsl and dry weight is significant ($r = 0.85$, $n = 104$, $p < 0.001$). Thus, tsl in September provides a good, nondestructive estimate of end-of-season live aboveground biomass.

There was a significant increase in tsl in 1980 and a rapid decline in 1981. This growth response has been interpreted as an effect of reduced soil salinity that resulted from catastrophic flooding (Zedler 1983b). At the time, it was thought to indicate a maximum growth response for the site, because floodwater volumes were enormously high (the 1980 water year had 28 times the average streamflow of previous years). On the average, plants grew over 10 cm taller in 1980 than the

previous year (Figure 66). In addition, plants reached maximum heights that were 20 cm greater than in 1979 (Figure 67). The tallest plants exceed 100 cm.

The second major growth response occurred in 1983. In contrast with the 1980 response of increased height, the 1983 response was largely one of increased density (Figure 68). Height also increased, as maximum heights averaged 90 cm (Figure 67), but it did not show up as an increase in mean height (Figure 66) because production of new, short individuals dominated the vegetation response. The high tsl in September 1983 followed freshwater influence that was of lower volume than the 1980 floodflows but of longer duration.

Finally, in September 1984, we found extremely low tsl due to poor growth and heavy mortality of cordgrass following drought conditions. The effect of drought became even more apparent in 1985, when the lowest tsl was documented. Both density
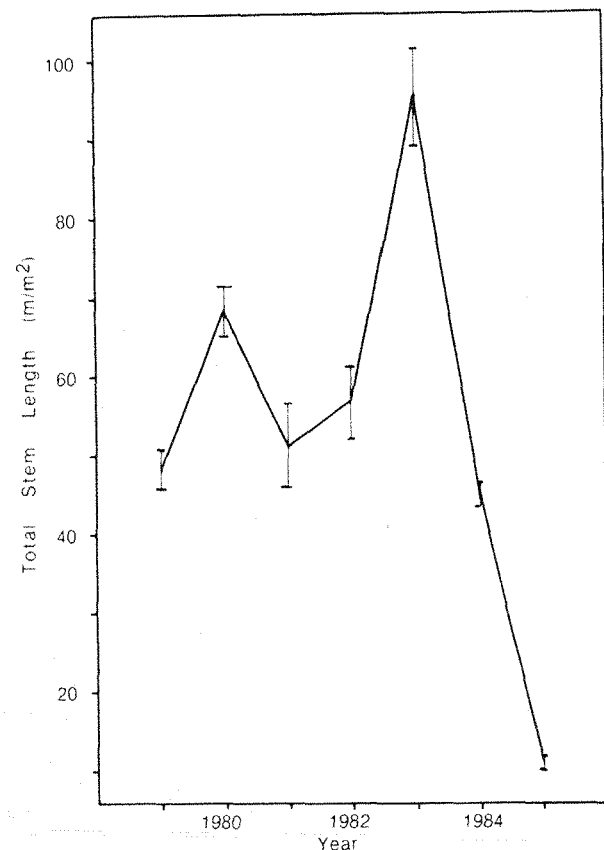
Figure 65. Changes in total stem length (a measure of biomass) for cordgrass. Means are from the quadrats in which cordgrass was present each year (Figure 62); vertical bars are ±1 standard error.

and height were lower than ever before recorded. The delayed reaction of cordgrass tsl measurements was due to the longevity of the plant. Individual stems live 1.5-2.0 years, and the 1984 measurements included stems with some live

material from the previous growing season. By 1985, there were few plants from the previous year and few individuals from 1985, even though tidal flushing had been reinstated throughout the entire growing season.

To interpret these variations in cordgrass growth requires consideration of the effects of hydrological change on pickleweed, because pickleweed is the competitive dominant (Zedler 1982; Covin 1984) and its distribution overlaps with cordgrass throughout most of the lower marsh. Years of high pickleweed cover were 1979, 1981, and 1984-85 (Table 26). These same years had low cordgrass biomass. Cordgrass tsl can be high when two conditions are met. First, there must be appropriate salinity, nutrients, and soil moisture; and second, there must be reduced competition from pickleweed. The latter condition appears to be associated with reduced drainage, that is, increased inundation. Several experimental tests of these hypotheses have been initiated.

Figure 66. Changes in average height of cordgrass. Means are based on the total number of stems measured each year.

5.4.1 Hydrology and Salinity Experiments

An experimental field study was initiated in 1984 to determine how coastal wetlands would respond to increased streamflow caused by treated wastewater. The data provide a test of the above hypotheses concerning cordgrass responses to salinity reductions at different times of the year. A brief summary and pertinent findings follow from the work of Beezley and Beare (SDSU, unpubl. data).

Figure 67. Changes in the maximum height of cordgrass. Means are from the number of quadrats in which cordgrass was present each year (Figure 62).
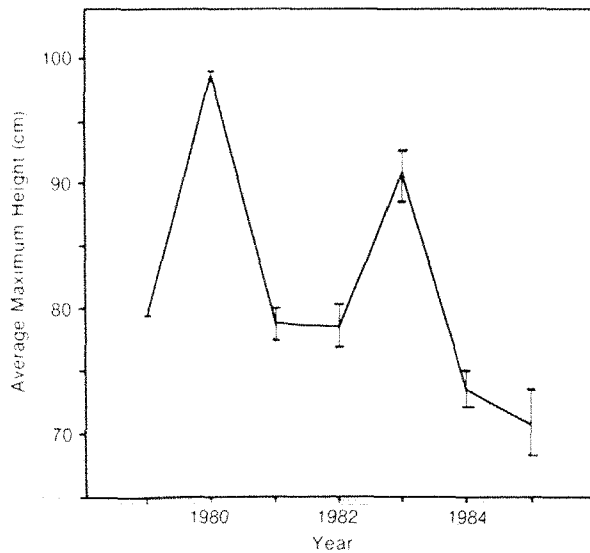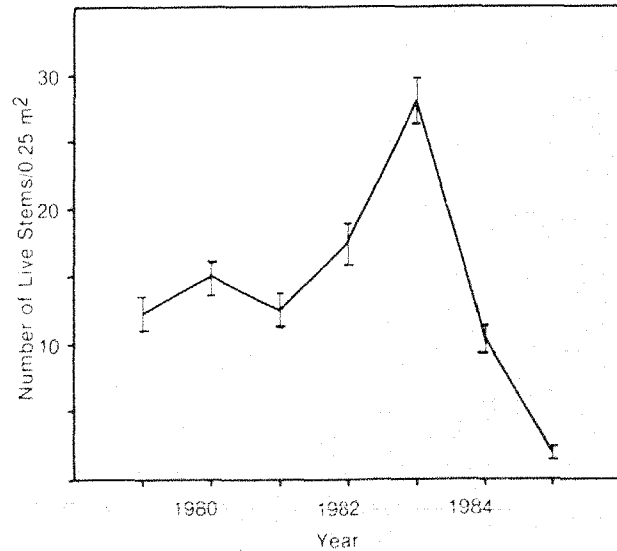

Figure 68. Changes in the density of cordgrass stems. Means are from the number of quadrats in which cordgrass was present each year (Figure 62).

An experiment was designed to determine the effect of year-long, winter, and summer irrigation with fresh water, all for comparison with unwatered control plots. A block experimental design was set up with replication in both cordgrass and pickleweed habitats. City water was piped to the marsh and used to fill meter-square cylinders that surrounded salt marsh vegetation. Watering began early in January 1984 and continued approximately biweekly for 7 months until the drought disturbed the experiment. Late in the experiment, watering changed soil moisture as well as the soil salinity. The drying of marsh soils, following estuary closure and high rates of evaporation created deep cracks throughout the experimental area, and the cylinders would no longer hold water. In late May, the winter-watering treatment ended and the summer-watering treatment began. Cordgrass responses were measured as in the monitoring program; pickleweed growth was measured as increased length of tagged stems.

Four hypotheses developed for cordgrass can be tested with results from the irrigation experiment. For the most part, these predictions were upheld.

a. From the results of prolonged streamflow in 1983 (Figure 65), we predicted that cordgrass growth should increase wherever watering took place and maximum biomass should occur with continuous watering. Plots had 394-761 cm/m^2 of cordgrass stems prior to watering (Table 28). Unwatered controls increased the least amount (mean = 834 cm/m^2) by late June, and then decreased with drought-caused mortality. Year-long and summer-watered plots continued to increase, on the average, throughout the experiment, while winter-watered plots declined along with controls.

b. From the effects of the 1980 flood on cordgrass (Figure 66), we predicted that winter watering should result primarily in increased height. Average height of cordgrass was 40 cm prior to watering in January, and controls increased 10 cm by late June. The height response was greater with watering, but the results were not quite as predicted. By August, year-long plots had increased 56 cm and summer-watered plots 52 cm, compared to 30 cm in winter-watered plots and 18 cm in controls. Winter-watered plots should have matched the year-long plots, if timing of freshwater influence were the only controlling factor. The growth response is complex and possibly modified by the unusual summer drought.

c. The increased density of cordgrass with streamflow during summer 1983 (Figure 68) led us to predict that summer watering should increase plant density. Increases in cordgrass density were greatest in the summer-watered plot (22/quadrat/6 months), as predicted, while year-long and winter-watered plots were similar to controls.

Table 28. Effects of irrigating cordgrass marsh in situ (from Zedler, Beezley, and Beare unpubl.).

		Watering treatment[a]			
	Block	Control	Year-Long	Winter	Summer
Jan.-June Increase in Total Stem Length (cm/0.125 m^2)	Block 1	694	1649	1009	1858
	Block 3	975	1651	1168	1841
Jan.-June Increase in Mean Height (cm)	Block 1	6	31	15	28
	Block 3	14	36	32	26
	Average	10	34	24	27
Jan.-Aug. Increase in Mean Height (cm)	Block 1	6	58	16	50
	Block 3	29	54	45	53
	Average	18	56	30	52
Jan.-June Density Change (#/.25 m^2)	Block 1	11	17	14	22
	Block 3	13	14	12	23
	Average	12	16	13	22
June-Aug. Density Change (#/.25 m^2)	Block 1	9	-5	-7	-2
	Block 3	-4	-8	-7	-16

[a]Watering began January 9, 1984, and continued approximately biweekly through August 7, 1984; winter watering ended and summer watering began on May 31; control plots were unwatered. Drought affected all plots from July onward.

d. High cordgrass mortality in 1984 (Figure 65) suggested that watered plants, i.e., those that did not experience gradual decrease in soil moisture, should be highly susceptible to drought. Thus, winter- and summer-watered plants should have higher mortality after the irrigation ended than plants in unwatered control plots. All treated plots experienced cordgrass mortality in the last 5 weeks of the experiment, when soils dried out between waterings. However, one control plot increased in density. While evidence is scanty, there is at least a suggestion that infrequently wetted areas withstand drought better, and differential rooting depths might explain differential survival. Studies of below-ground plant growth at different intertidal elevations are needed to explain the high creek-edge mortality seen during the 1984 drought.

The importance of seedling recruitment was not addressed in these year-long experiments. Most of the dynamics of cordgrass have resulted from changes in vegetative growth. Although we expected to see some seedlings appear in plots watered all year, such invasions were insignificant, perhaps because of the small size of the quadrats and short duration of the experiment.

The hypotheses that grew out of the monitoring program withstood experimental testing, and we provide a conceptual model of the control of cordgrass growth as follows: Cordgrass is commonly under stress due to hypersaline soils. Freshwater influxes to the marsh stimulate increased growth. If the influx occurs in winter, plants are able to respond by increasing their height. If the influx occurs in summer, during the peak of the growing season, plants respond by increasing vegetative reproduction. From the standpoint of an individual plant, it is a matter of carbon allocation; the later that fresh water is applied, the less likely the plants can respond by increasing in height. Increased production late in the season will be channeled primarily to new shoots.

5.4.2 Nutrient Addition Experiments

From the first year on, the annual censusing of cordgrass documented considerable spatial variability from quadrat to quadrat and transect to transect. While strong year-to-year differences have been explained, local variations have only recently been investigated. It is now clear that nutrients and insects add to both spatial and temporal changes.

As discussed in Chapter 4, Covin (1984) found that soil nitrogen was important to cordgrass growth. His experimental manipulations showed that urea increased cordgrass growth in pure stands (although in different amounts for the two sets of plots), but not in stands mixed with pickleweed. The influence of urea on cordgrass thus depended in part on the presence of its most frequent co-occurring species, with pickleweed the better competitor for urea.

Nutrient-addition experiments also suggested that insect grazing has significant impact on cordgrass growth and densities. Covin's urea-addition plot at TJE-28 produced cordgrass with higher tissue nitrogen content than at TJE-31, and a late-season dieback occurred on those plants. Patches of cordgrass died along that same transect after the 1980 flood. Because pickleweed was lacking, we know that competition was not the cause. If nitrogen inputs are commonly high at TJE-28, nitrogen uptake should be high, which should increase the probability of insect attack. We have yet to identify patterns of nitrogen influx to different transects or quadrats, and we need to evaluate directly the relationship between insect grazing and nutrient additions to help explain spatial heterogeneity in the salt marsh vegetation. Research with other wetland (Onuf et al. 1977) and grassland (McNeil and Southwood 1978) vegetation has shown that insects are attracted to plants with high nitrogen concentrations and that herbivory is greater on leaves with augmented nitrogen. Clearly, these secondary effects of added nitrogen can have important effects in nature.

CHAPTER 6

MANAGEMENT CONSIDERATIONS

Tijuana Estuary has two management programs; it serves as an endangered species refuge and a sanctuary for research and education. The northern part of the estuary (428 ha; 1,056 acres) is the Tijuana Slough National Wildlife Refuge, which is managed by the U.S. Fish and Wildlife Service. The specific goal is to protect three endangered species, the light-footed clapper rail, the California least tern, and salt marsh bird's beak. An area including the refuge, Border Field State Park (160 ha), and adjacent lands (a total of 1,125 ha) was designated as a National Estuarine Sanctuary in 1982. It joins 14 other estuaries within the United States that are set aside for research, education, and interpretation. A management plan for the sanctuary (Dobbin Associates 1985) was recently developed and adopted by the Tijuana National Estuarine Sanctuary Management Authority and associated agencies. The stated goals are resource protection, research, interpretation, land acquisition, and facility development.

6.1 RESEARCH NEEDS AND OPPORTUNITIES

In order to accomplish the main purposes of the refuge and sanctuary, the native biota of Tijuana Estuary must be maintained. A brief history of research activities and a discussion of the most important management problems will show how this estuary contributes to the overall understanding of regional wetlands.

Since the 1970's, there has been a continuing research interest in Tijuana Estuary, with emphasis on the salt marsh vegetation. The research projects have directly followed the challenges posed by environmental changes and ecosystem responses. Studies have progressed from descriptions of species occurrences and measurements of wetland processes to long-term comparisons of the effects of disturbances. There has been a growing emphasis on the experimental determination of cause-effect relationships. The

types of projects have shifted as the estuary experienced new and different environmental assaults.

With different management problems have come new opportunities for research support. In 1976, research funding was provided by Sea Grant to test paradigms of wetland plant productivity and export that were developed in Georgia and to determine how disturbance affected wetland productivity. Associated studies of endangered species habitat were supported by the U.S. Navy and U.S. Fish and Wildlife Service. The finding that disturbance dramatically alters marsh productivity then led Sea Grant to support development of wetland restoration techniques and, later, studies of how altered hydrology (amount and timing of freshwater influx) affects estuarine functioning. The frequent sewage spills of the 1980's and the threat of continuous wastewater discharge from Tijuana, Mexico, led to the analysis of streamflows, estuarine salinities, and biological impacts of year-round discharges (Environmental Protection Agency support through Section 205(j) of the Clean Water Act). The designation of Tijuana Estuary as a National Estuarine Sanctuary allowed funding of specific management-related research projects through the Sanctuary Programs Division of the National Oceanic and Atmospheric Administration (NOAA). Several problems, including wastewater effects on channel algae and cordgrass, dune revegetation and exotic species management, and recovery of plant populations from the 1984 drought, are now being addressed.

Tijuana Estuary, as a system subject to multiple disturbances, provides a rich laboratory for science. It is unusual in that a vegetation-monitoring program has been in place since 1979 and several distinct disturbance events were documented by that program. In many cases, however, the changes went unquantified (e.g., effects on benthic invertebrates and fishes),

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because the monitoring program was narrow in its focus. Monitoring will be extended to include channels, with regular sampling of benthic invertebrates and fishes in 1986. Bird studies need to be added as well. Long-term systematic sampling focused to identify cause-effect relationships is an appropriate approach for an estuary that is subject to a highly variable environment. The long-term data track in turn provides an excellent backdrop for specific studies of population, community, and ecosystem dynamics.

The Pacific Estuarine Research Laboratory (PERL) provides a second major opportunity for estuarine science. This facility (Figure 69), located on abandoned agricultural land at the southern edge of Tijuana Estuary, provides small artificial wetlands in replicate for controlled experimentation. Again, the disturbances to Tijuana Estuary catalyzed the shift toward manipulative experimentation. Attempts to do experimental work in situ at the estuary proved difficult because background conditions were unpredictable. Tests to assess the effects of increased freshwater on the salt marsh were initiated in 1984, when the normal tidal flows became blocked. That year, treatments that were intended to alter only soil salinity also altered soil moisture. Thus, the need for a highly controlled experimental facility was recognized and pursued. The NOAA Sanctuary Programs Division and California State Resources Agency have cosponsored the development of the outdoor laboratory, which is operated by San Diego State University (Figure 69).
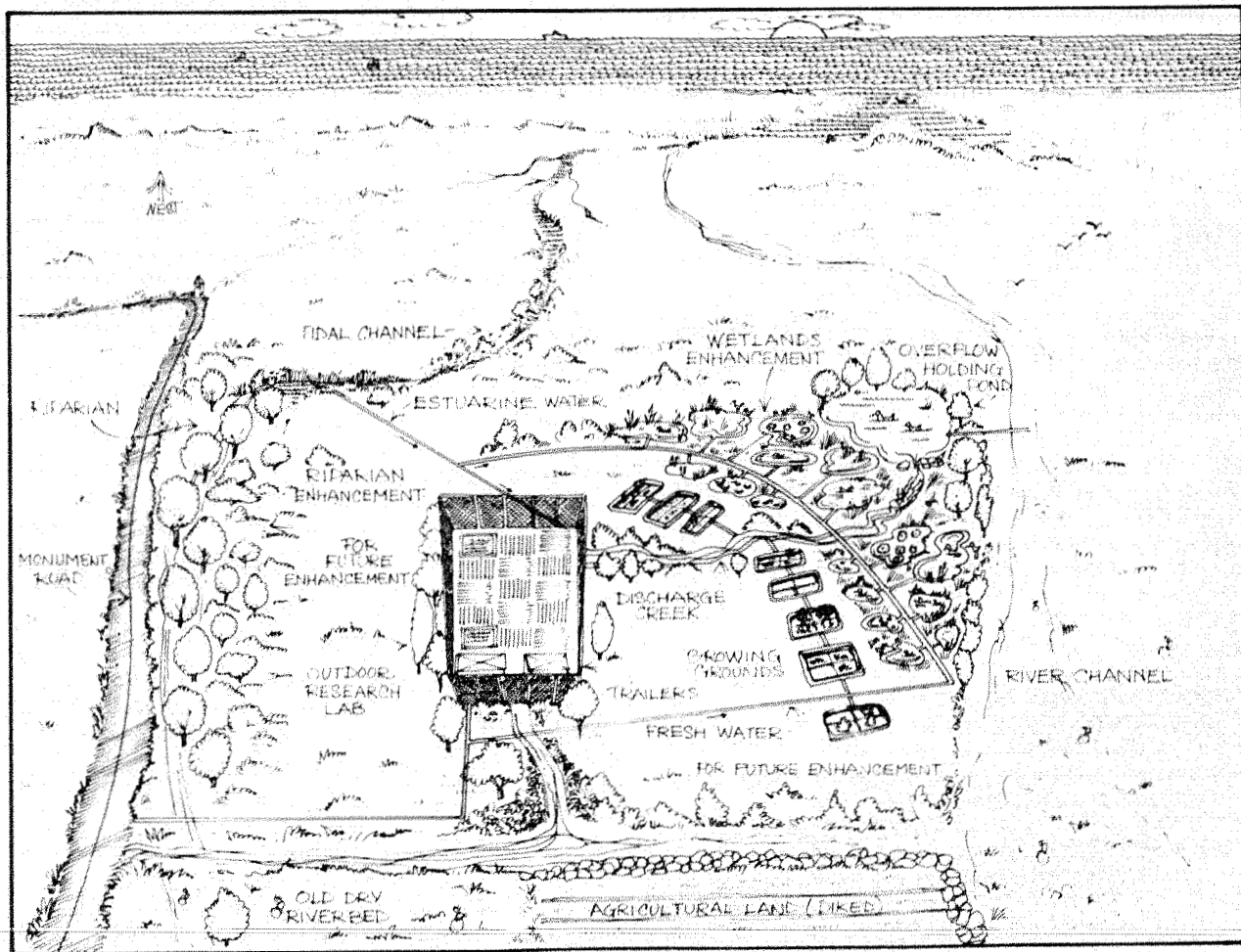
Figure 69. Conceptual drawing of the Pacific Estuarine Research Laboratory (center, fenced) and surrounding habitat improvements, looking west. The area of riparian/estuarine channel enhancement is on the left; artificial wetlands are on the right, and nurseries (growing grounds) are shown as rectangular gardens. Area drawn in foreground is about 28 ha (70 acres), with Tijuana Estuary on the horizon and the Tijuana River to the right.

Closely associated with the research activities at PERL are three projects that will create artificial wetland habitat, provide nurseries for wetland plants, and enhance an existing riparian/estuarine channel (Figure 69). The State Resources Agency (Environmental License Plate Fund) and the State Coastal Conservancy are sponsoring these activities. Fresh, brackish, and saline impoundments of several sizes will be constructed to provide alternative habitats for estuarine species. As Boland's (1981) research on shorebirds has shown, alternative wetland types can subsidize the estuarine populations. In many cases, these wetlands may provide essential refuges during times of whole-ecosystem perturbation.

The nurseries will be used to propagate wetland plants for transplantation to restoration projects within the region. One potential use will be the development of a living collection of plant species and gene pools from the region's wetlands, so that biological diversity can be maintained in the face of continuing wetland disturbance. The local extinction of annual pickleweed and sea-blite indicate the need for such a collection. When the region's few whole ecosystems continue to be subjected to catastrophic disturbances (both natural and human), the need to take an active role in preserving gene pools becomes urgent.

Enhancement of a riparian/estuarine channel will serve a variety of wetland species. The area that once carried part of the Tijuana River flow south along the bluffs (Figure 4) is now mostly dry. The riparian, or riverine, portion is dry because the river has been rerouted; the estuarine portion is dry because sediments have reduced tidal action. Enhancement will consist of removing exotic vegetation, planting native species, and removing recent sediments. Habitat for estuarine channel organisms will be increased.

These activities are management oriented, yet each will ultimately enhance our understanding of Tijuana Estuary. The artificial wetlands will attract wildlife and help to determine how salinity and vegetation influence animal usage. The nurseries will contribute information on what conditions optimize growth of different plant species. Finally, the enhanced channel will provide a demonstration of our ability to restore disturbed habitats. As with almost all of our studies at Tijuana Estuary, research and management will go hand in hand. With understanding has come the ability to modify the system to achieve desired management goals, a process that we call "ecotechnology." There is a very real need for such active management at Tijuana Estuary.

6.2 MANAGEMENT NEEDS

Tijuana Estuary is an urban estuary subject to the chronic and acute impacts of an enormous human population. The city of Imperial Beach surrounds the northern arm of the estuary. Agricultural lands and a large system of levees for flood control have modified the Tijuana River floodplain. Just upstream, the city of Tijuana, Mexico, includes over 2 million inhabitants, most of whom do not even have access to a sewer system. The watershed above Tijuana is scheduled for rapid and extensive development. At the same time, the downstream estuary is supposed to serve as a sanctuary for research and education, a refuge for endangered species, and a State park.

Management of Tijuana Estuary is the responsibility of several agencies that either own property within the estuary or have legal jurisdiction there. These include the U.S. Fish and Wildlife Service, the U.S. Navy, the California Department of Parks and Recreation, the California Coastal Commission, the California State Coastal Conservancy, the County of San Diego, and the Cities of Imperial Beach and San Diego. All of these agencies interact under the umbrella of the Tijuana River National Estuarine Sanctuary Management Authority. A recently adopted management plan for the sanctuary (Dobbin Associates 1985) details the roles of each participating agency and outlines a wide range of issues. Those that bear directly on estuarine ecology are examined here.

Management problems are numerous, but four stand out as having the greatest impact on estuarine ecology: sedimentation of channels, erosion of the beach and dunes, inputs of sewage, and modification of streamflow. Each problem has multiple causes. Increased sedimentation follows disturbance of soil-stabilizing vegetation both within the watershed and on the beach. The beach and dunes erode when storms and high sea levels coincide. Sewage spills are almost entirely traceable to breaks in Mexican sewage lines, although local leaks are not unknown. Streamflow augmentation is associated with reservoir and wastewater discharges; their effect is greatest during summer, when the river might otherwise be dry.

These many disturbances are interrelated: dune sands contribute sediment to channels, and sewage spills alter streamflows. The causes of these problems must often be dealt with separately; for example, dunes can be stabilized with fencing or vegetation to resist storm damage, but nothing can control sea levels. Mitigation of impacts, on the other hand, requires a

comprehensive approach, because altering habitat in one area can potentially affect the entire ecosystem. For an estuary that is managed primarily for its native wetland communities and endangered species, passive management (leaving nature alone) might seem preferable to active manipulation of environmental conditions. But disturbances have had significant impacts on the estuary, and the issue is not whether, but how much, intervention is required to maintain native species. More important, we need a rationale for planning those interventions when our ecological understanding is inadequate. A program of adaptive management (Walters and Hilborn 1978), with experimentation, evaluation, and progressively improved treatments, must be adopted in order to correct the problems at Tijuana Estuary.

In this profile, we provide recommendations for management of sedimentation, dune and beach erosion, sewage inputs, streamflow, and maintenance of the natural diversity of habitats. These are the main environmental problems for which ecological information can alleviate the problem or facilitate restoration of disturbed habitats.

6.2.1 Sedimentation Problems

Throughout southern California, estuaries and lagoons have been filling in rapidly, as hillsides within their watersheds are disturbed and developed. Vegetation that might slow erosion is sparse in Mexico, where grazing and fires are more frequent in the landscape (Minnich 1983). The extremely erodable soils move downstream with winter rains, and catastrophic sedimentation occurs at the coast. Mugu Lagoon lost 40% of its low-tide volume with cumulative sedimentation during the floods of 1978 and 1980 (Onuf, in press). Sedimentation is a natural process, but the rates have accelerated, and the system's ability to respond by changing its configuration has been constrained by peripheral developments.

The management goal should be to maintain the natural habitat diversity at Tijuana Estuary while still allowing year-to-year variations in environmental conditions, which are so characteristic of the region. The dilemma is that flooding, sedimentation, and sluggish tidal exchange are all part of the natural environment, but their impacts are accumulating at Tijuana Estuary and in the region's coastal wetlands as a whole. Other natural events that counter the impacts of sedimentation may also be augmented by human activities. For example, the greenhouse effect may be accelerating sea-level rise and somewhat compensating for sediment accretion. However, the average rise in sea level cannot begin to keep up with catastrophic sedimentation, and the net effect is for coastal wetlands to fill in more rapidly than they would naturally.

The management questions are several: Should maintenance dredging seek to retain a specific estuarine physiography and, if so, what configuration of channels should be maintained? How should the negative impacts of maintenance dredging be mitigated? Where should dredge spoils be deposited? What regime of tidal flushing is desired? What degree of tidal flushing will prevent mouth closure but not be detrimental to macroalgae, phytoplankton, cordgrass, and other organisms that flourish with reduced tidal flow?

Preliminary answers to the complex questions raised here can be provided on the basis of current ecological knowledge. However, the final analysis must be based on a thorough hydrological evaluation of the estuary and simulations of how it would change with different regimes of maintenance dredging. The State Resources Agency and the State Coastal Conservancy have recently provided funding to map the entire sanctuary using 30-cm contours and to develop the required hydrologic model. This project (P. Williams, SDSU, in prog.) will evaluate the tidal prism and entrance configuration. Until then, we suggest the following:

a. Maintenance dredging should restore tidal channels to their historic configurations wherever possible, with depths based on the hydrologic analysis. However, channels that were historically close to the dunes (i.e., west of the former islands, Figures 9-12) may not be restorable because of the retreating beach line. Also, in the mouth area, dredging efforts are unlikely to be effective because sediment movement is so dynamic (Williams, pers. comm.).

b. Dredging is necessary to restore channels, but the process disrupts benthic and peripheral habitats. At present, we don't know what species are being affected. Thorough studies of the benthos and fish communities, to compare composition before and after dredging, as well as in areas with and without good tidal flushing, are urgently needed. Some of this work is underway (Nordby, in prog.; Dexter, in prog.). The most obvious change that occurs with dredging is the destruction of creek-side vegetation. Associated with losses in plant cover are modifications of marsh soils and infauna. To the extent possible, areas of native vegetation should be avoided; where unavoidable, a salvage and revegetation program is needed. Studies to compare recovery rates with and without revegetation would help to evaluate the necessity for labor-intensive management practices. Vegetation should be held at PERL if it cannot be maintained on site during construction. Any organisms that cannot be salvaged should be made available for research projects at PERL.

c. Dredging at Tijuana Estuary will generate spoils that differ in quality, depending on the source of sediments (sand dunes or bluffs) and proximity to sewage spills. Sandy spoils should be used to rebuild the dunes, but spoils of low quality should be taken off the site. The desirability of using fine sediments to replenish the dune needs further evaluation (Williams, pers. comm.).

d. The tidal flushing regime needed to maintain the natural diversity of habitats is difficult to define, because there are few records of tidal action within the estuary. The studies of marsh vegetation suggest that there should be continual but not necessarily vigorous tidal flushing. Cordgrass is not recovering rapidly from the 1984 drought; in fact, it continued to decline in 1985. We suspect that sluggish tidal action may be necessary at times to reduce pickleweed vigor in order for cordgrass to have a competitive advantage.

6.2.2 Beach and Dune Erosion

Winter storms that coincide with high sea levels erode the dunes and beach. Summer is the rebuilding phase in an annual cycle of removal and replenishment. However, if the replenishing sands are intercepted in their transport along shore or downstream, the beach and dunes show a net loss (Inman 1985). In addition to the annual cycle, there is a long-term trend for an increase in mean sea level, which means that the beach will gradually move inland.

It may be impossible to prevent beach and dune erosion at Tijuana Estuary; however, slowing the losses and restoring dune plant and animal communities are achievable management goals. Disturbance of beach vegetation has contributed to the destabilization of the dunes, and replanting is desirable. However, because initial attempts to reconstruct and replant the dune north of the estuary mouth have failed, a new approach is called for. The dune south of the mouth will be restored in late summer 1986, after the period of least tern nesting. Dunes will be rebuilt in two rows, to create a double barrier to storm erosion. Plans for this second phase of dune reconstruction incorporate four experimental treatments that will be replicated along the dune and evaluated over at least a 2-year period:

a. *Dune rebuilt by bulldozers and fenced with a sand-trapping web.* This combination is expected to be most effective in stabilizing the dune, and the largest length of dune will be assigned to this treatment. Several areas within this treatment will be planted with native vegetation to encourage natural stabilization of the substrate. Revegetation alone is probably insufficient to control erosion; there is no native grass and plant cover is patchy.

The expense of growing and transplanting the native perennials requires that plants should be protected with fencing.

b. *Dune rebuilt but not fenced.* Segments of dune will be left unfenced to evaluate the effectiveness of fencing.

c. *Existing topography left; fencing added.* The role of fencing in helping to build up the dune will be evaluated by comparing this treatment with the next.

d. *Existing topography unaltered.* These "control plots" will serve two purposes, a comparison for other treatments and a refuge for native organisms. Patches along the beach where native plants remain will be included in these plots. Dune insects are expected to flourish in these refuges and to expand onto the restored dunes.

As the effects of each treatment become clear, the management program can be modified to incorporate the most effective measures. Measures of dune profiles, vegetative expansion, and insect colonization will insure that restoration of the total dune ecosystem is assessed and that revised plans are based on a broad data base.

6.2.3 Streamflow Modifications

Reservoirs can modify estuarine hydrology by reducing total volume of streamflow, by delaying the start of floodflows, or by prolonging the period of wet-season flows. In the United States portion of the Tijuana River watershed, Barrett and Morena Reservoirs trap streamflow and presumably modify the timing and volume of floodflows. Water can be discharged from Morena to Barrett, but the gates of Barrett Reservoir cannot be opened once water is impounded; thus, drawdown is not possible. In Mexico, Rodriguez Reservoir has gates that can be used to lower water levels, and the prolonged discharges of 1983 indicate the magnitude of streamflow change that can occur as a result of reservoir drawdown. Record flows for 10 months (March through December) occurred during periods of little rainfall and usual low streamflows (Table 29). At such times, salinities are lowered (Chapter 5), tidal regimes are probably muted, and nutrient concentrations increase (Covin 1984).

There are several scenarios under which streamflow into Tijuana Estuary might be altered by wastewater discharges. The city of Tijuana, Mexico, is directly upstream of the estuary, and the land slopes northward towards the United States. At present, the largest influxes occur as sewage spills, when Mexican pipelines, designed to carry sewage west and south to an intertidal outfall,

Table 29. Streamflow data (acre-ft) for the Tijuana River at the United States-Mexico border. All 1983 flows were augmented by discharges from Rodriguez Dam; flows for March-December 1983 were maximum for the period of record (from IBWC 1983).

Month	1983 Flows	Average Flows
January	5,236	2,824
February	35,849	10,141
March	293,494	13,875
April	62,938	3,584
May	42,599	1,979
June	9,696	519
July	9,242	366
August	17,092	541
September	978	74
October	1,237	87
November	4,377	250
December	6,705	501

cannot handle increased volumes from Mexico, so the alternatives are for the United States to construct a new plant to treat Mexican wastewater or for Mexico to treat its own sewage.

The first alternative would allow the United States to control the ultimate discharge point for treated wastewater (e.g., tertiary treatment and recycling, impoundment and timed release to Tijuana River to minimize ecological impacts, or disposal through an ocean outfall), but cost estimates were over $700 million. The second alternative, for Mexico to treat its own wastewater, was favored by Mexico and the State Department, and current plans suggest that initial increases in wastewater would be routed to an intertidal outfall several kilometers south of the border, while later discharges (over 30 MGD) would undergo primary treatment and be discharged to Tijuana River. It is not surprising that sewage disposal has stimulated international controversy over the past several years.

For the estuary, the ecological impacts of wastewater influx are two-fold: reduced salinities and increased nutrient concentrations. Unlike most regions of the United States, where wastewater influxes are of concern primarily because estuaries undergo eutrophication, the greater problem in the arid southwest is altered hydrology. Riverflow is normally low and confined to winter; wastewater discharges would change an intermittently flowing stream into a permanently flowing river. A recent evaluation of how increased streamflow would affect the estuary (Zedler et al. 1984a,b) identified impacts on fishes, invertebrates, vascular plants, and algae (Table 30) and led to recommendations on how to reduce negative impacts (Zedler et al. 1984c).

break. Flows exceeding 7,000 m^3 per day (over 2 MGD) have occurred at various unpredictable intervals.

Plans have been developed for a major sewage interception system, wherein flows from four canyons will be collected and piped to the San Diego treatment plant (R. Donally, City of San Diego Utilities Division, pers. comm.). In the interim, however, raw sewage continues to flow directly into the estuary on a daily basis. Reasons for the long delays in solving this problem are largely political. The United States has no jurisdiction for preventing the flows; government agencies can only deal with the sewage once it crosses the international border. Local residents and estuary managers have called for an end to the sewage pollution, but solutions are slow to come. Direct evidence for a detrimental impact on the estuary and its endangered species is lacking. Attempts to determine if toxic materials were present in estuarine organisms have been unsuccessful, in part because so many of the fishes and invertebrates died out in 1984 (Jorgensen, pers. comm.). While some species of bivalve molluscs reestablished in 1985, reasons for their absence in 1986 are unknown.

In the future, other wastewater management practices may lead to greater continuous flows. At present the city of San Diego receives approximately 20 MGD from Tijuana through a sewage pipe that leads to a primary treatment plant and ocean outfall in the United States. As Tijuana continues to grow and additional freshwater supplies become available from the Colorado River aqueduct, the volume of wastewater is expected to exceed 30 MGD. The San Diego treatment plant

A model of estuarine salinity was developed to predict dilution with discharges of 12.5, 100, and 200 MGD. The 41-year record includes 10 years of "heavy" flow (greater than 10,000 acre-ft/yr), 13 years of intermediate flow (100-10,000 acre-ft/yr), and 18 years of low flow (0-100 acre-ft/yr). Monthly averages were then computed for intermediate-flow years. Wastewater discharges of 30-35 MGD, indicated in one potential plan, would exceed these intermediate-year flows six-fold in winter and much more in summer. The quantity of water that would reach Tijuana Estuary would be sufficient to reduce water salinities and affect marine species substantially (Zedler et al. 1984b). Measurable dilution was possible with only 12.5 MGD (Figure 70). During neap tides, salinities would drop much more than during spring tides, so a wide range of conditions would result. It was predicted that the estuary would become slightly brackish at 12.5 MGD and fresh at 200 MGD. Review of the literature on salinity tolerances indicated that most species could tolerate briefly

Table 30. Predicted impacts of reduced salinity due to artificially augmented streamflows (from Zedler et al. 1984b).

Condition	Vascular plants	Algae	Invertebrates	Fishes
Status quo	Halophytes produce 40-60% of food base	Algal mats produce 40-60% of food base	Feed on algae; take up dissolved organic carbon	Feed on the invertebrates and on algae and detritus; 40 species on record
Brief reduction to brackish conditions	Halophyte growth stimulated; algal mats shaded	Reduced algal mat productivity	Some species lost; commercial-recreational species included	None lost
Prolonged reduction to brackish conditions	Halophyte growth stimulated; some species shift boundaries; cord-grass may expand its distribution	Low-salinity tolerant species (e.g. greens) invade, but shading limits productivity	Some species lost; commercial-recreational species included	Of the 40 species, 16 are likely to persist
Brief reduction to fresh conditions	Halophyte growth stimulated; some glycophytes invade	Algal mat productivity reduced	Most species in channels would die; survivors would have altered density and size distributions	Only 5 species are likely to persist; halibut and turbot would probably die or leave
Prolonged period of freshwater influence	Marsh shifts from halophytes to glycophytes; eventually canopy becomes tall and dense	Composition shifts to low-salinity tolerant species; overall productivity greatly reduced	None of the original species survive	Mullet, staghorn sculpin, and killifish would persist

brackish conditions, but that prolonged periods of freshwater conditions would have substantial negative impacts on the invertebrates, fishes, and vegetation.

Management recommendations were developed (Zedler et al. 1984c) to reduce impacts of augmented streamflow, should regulatory agencies decide to allow wastewater discharge to Tijuana River. It was suggested that wastewater be utilized selectively within Tijuana Estuary (1) to restore disturbed habitat, where soils were excessively saline; and (2) to enhance riparian habitat. Large-volume river flows over long periods of time should not be permitted; rather, a system of impounding and discharging wastewater with the outgoing high tide might be required to maintain the marine character of Tijuana Estuary.

The second ecological impact of wastewater discharge is nutrient influx. Effects of nitrogen additions to lower marsh vegetation were examined by Covin (1984, 1986) and Beezley (in prep.); nitrogen is clearly limiting and plant growth increases with fertilization, but enrichment can also stimulate insect herbivory and reverse the stimulating effect on plant biomass. Studies to determine the effect of wastewater on macroalgae and phytoplankton were initiated in 1985 by

Rudnicki (1986) and Fong (1986; Chapter 4). In general, nutrient addition stimulates both algal groups, but there is a strong interaction with salinity. Growth increases with fertilization, but the types of species that "bloom" are determined by salinity. Further testing to determine levels of nitrogen and phosphorus that stimulate nuisance algal blooms are underway for the Regional Water Quality Control Board.

In the overall environmental assessment of wastewater discharge, the impacts of increased freshwater flow are outweighed by concerns for water quality. The Regional Water Quality Control Board ranks disease risks and potential for eutrophication (potential nuisance algal blooms and fish kills) more highly. The Environmental Protection Agency is analyzing environmental problems associated with riverine discharge, ocean disposal, and intertidal discharge south of the United States-Mexico border (L. Fondall, EPA, pers. comm.). Hydrologic planning (Williams, in prog.) will include an evaluation of how streamflows can be used to enhance riparian habitat in the Tijuana River Valley.

The development of plans to manage long-term, large-volume discharges should include simulations of the effects of each alternative on
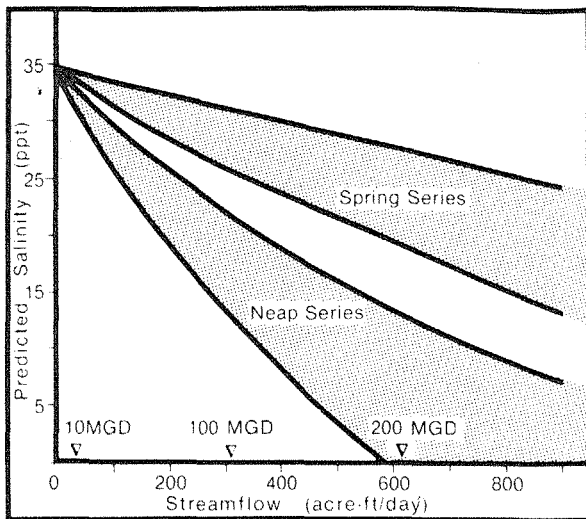
Figure 70. Salinity reductions predicted by a simulation model (Zedler et al. 1984a). Salinities were calculated iteratively, by alternating constant high and low tide levels until the salinity at low tide remained constant. The upper line represents the highest salinity value predicted during a 24-hour period in the spring series; the lower line represents the lowest predicted salinity during a 24-hour period in the neap series. The spring and neap tidal series are representative of average high and low amplitude tidal prisms. Therefore, salinity values should range between upper and lower lines when the assumptions of the model are met (reprinted from Zedler et al. 1984b).

estuarine sediment dynamics and salinities. An estuarine circulation model is needed to determine how wastewater discharges will move throughout the channels, tidal creeks, and intertidal habitats. Then, an analysis of how those changes in circulation and salinity affect estuarine organisms should be done. While some work has tested the tolerance of estuarine invertebrates (D. Kyle, SDSU, in prog.), more research is needed to determine how reduced salinities affect critical life history stages of various estuarine organisms.

6.2.4 Habitat Management

Decades of disturbance to the estuary and its watershed have substantially altered the environmental factors that control habitats. The physiographic and hydrologic conditions that led to the pre-1900 ecological communities have been irreversibly changed. Since 1900, some communities have been lost entirely (e.g., woody beach vegetation), and other new ones have developed (e.g., brackish ponds and marshes). With the recently accelerated sedimentation rates and the threat of greatly altered streamflows, it is

no longer possible to recommend passive habitat management of Tijuana Estuary. Careful, well-planned management procedures are required to insure that the recognized values of Tijuana Estuary are maintained.

Several management recommendations follow from the habitat values identified in Chapter 3. The overall management goal should be to maintain the natural variety of habitats (Zedler 1984), recognizing that increasing the area of any one habitat type should not reduce habitat for another. Single-species management is not desirable, because procedures that might benefit one species might negatively affect another. We list here the recognized values of each habitat type, identify management problems, and suggest management objectives.

a. *Transition from upland to wetland.* This is a diminishing habitat in southern California; it is valued for its rarity, its function as a buffer between wetlands and urbanized areas, and as a foraging ground for bird species. Species of concern include sensitive birds (e.g., short-eared owls, black-shouldered kites) and the horned lizard. The latter have been collected for pets and reduced to extremely low numbers. *Frankenia palmeri* is a potential member of the habitat, but it has not been recorded at Tijuana Estuary.

The generic problem facing the transition habitat is urban encroachment, which occurs as fill, trash disposal, trampling, and invasion by dogs and cats. Associated impacts are invasions by exotic weeds and altered densities of native animals.

Recommended management objectives are to remove fill, revegetate trails, control dumping of trash, control feral and domestic animals, control exotic plants, and plant native perennials that are likely to have occurred in this habitat. Suitable plants to consider include lemonadeberry, laurel sumac, *Frankenia palmeri* (on an experimental basis), box-thorn, and native succulents. Ideal locations for transition restoration projects are (1) the slope at the corner of Imperial Beach Boulevard and Third Street, (2) the abandoned gravel mounds near the gravel pit ponds, and (3) abandoned agricultural land near Monument Road.

Finally, within this transitional habitat, the upper limit of wetland needs to be designated for legal purposes. An official wetland boundary determination will facilitate enforcement of Section 404 of the Clean Water Act, which regulates fill in wetlands.

b. *Salt marsh.* The most widely valued attribute of the salt marsh is the habitat it provides for endangered species. The cordgrass-dominated marsh is nesting and foraging habitat for the light-

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footed clapper rails; the pickleweed-dominated areas are important to Belding's Savannah sparrows; and the upper marsh is the sole habitat for salt marsh bird's beak. In addition, the marsh is essential to a variety of other organisms, including nonendangered birds, insects and invertebrates, as a place to feed, seek cover, and reproduce. Overall, the salt marsh contributes substantially to the primary productivity base that supports estuarine food chains.

Recent disturbances have reduced the natural diversity of plant communities; cordgrass populations have declined drastically; annual pickleweed, sea-blite, and *Jaumea carnosa* have also declined. The marsh vegetation is converting to the pickleweed-dominated community that characterizes the region's lagoonal wetlands. These events affect salt marsh animals, as indicated by the loss of the light-footed clapper rail population. It dropped from about 40 pairs to zero, and at present, only two individuals are known to occur in the entire estuary. In addition, the endangered salt marsh bird's beak is highly vulnerable because of its location adjacent to urban development. Among the threats to its habitat are trampling, filling, and (along Seacoast Drive) ornamental plantings. An annual, salt marsh bird's beak is conspicuous only during the spring and summer, making enforcement of the Endangered Species Act difficult. If the species' habitat disappears when plant are present only as seeds, there is little evidence that a "taking" of an endangered species (as prohibited by the Act) has occurred.

Overall, the habitat management goal should be to restore the natural diversity of ecological communities in the intertidal marsh. While dredging to maintain good tidal flushing is the usual recommended procedure, there is concern that too much dredging will not allow recovery of these populations. The hydrological plan (Williams, in prog.) will be done with ecological input to evaluate alternatives. Studies are in progress at PERL to provide management recommendations for recovery of cordgrass and annual pickleweed. Direct disturbances, such as trampling and filling must be prevented. On a limited basis, plants such as salt marsh bird's beak should be grown from seed at PERL as a gene bank and to provide material for experimental work. Finally, the salt marsh monitoring program that began in 1979 needs to be funded on a permanent basis.

The potential conflict between resource management and visitor access needs to be confronted, with clear priorities developed. Access to salt marsh habitats needs to be carefully controlled to protect resources, but visitors may not be satisfied with views from a distance. Data on responses of birds to disturbance (e.g., White, in

prog.) need to be incorporated into planning for trails. The initial plans for identifying and marking specific foot paths (Dobbin Associates 1985) should be implemented with one exception. The construction of a bridge that would open to traffic the salt marsh west of the inland lagoon should be reevaluated. The ecological communities and endangered species that will be affected by increased human use have not yet recovered from past traffic and denudation.

c. *Salt pannes.* The natural values of salt pannes are not often recognized, and, in many wetlands, proposals are made to convert them to other uses. During both the wet and dry phases, salt pannes are important areas for insects, including rove beetles and mudflat tiger beetles. When inundated, the areas serve as feeding grounds for migrant and resident birds. Species associated with the intertidal salt marsh and the transition to upland also use these areas.

Lack of quantitative information about their habitat value is thus a management problem. Another continuing problem in salt pannes is the compaction of soils caused by vehicle and foot traffic. In the southern part of the estuary, a horse track that was abandoned in the 1960's still has soils that appear too dense for colonization by burrowing insects and too dense or too saline for vegetation reestablishment.

We recommend that research be initiated to quantify the communities of organisms that use salt pannes throughout the annual cycle of wet and dry conditions, and that compacted and noncompacted areas be compared further, building on the preliminary work of Nordby (1984). Methods of reaerating the soils that are effective, but not too disruptive, should be developed. An experimental approach with several alternative treatments is recommended.

d. *Brackish marsh.* Areas that have reduced salinities throughout most of the year are currently maintained by rainfall and urban runoff. Although artificial in this sense, they do support an ecosystem with species native to the area. Elsewhere in the region, brackish marshes are valued for their augmentation of habitat for populations of clapper rails, black-necked stilt, snowy egrets, and other birds. They also increase habitat diversity at the estuary and attract species that would not otherwise occur there (e.g., red-winged blackbirds).

The management problem associated with brackish marsh is their potential expansion at the expense of saline wetlands. With increased freshwater runoff, soils are leached of salts, and the brackish marsh species displace those of the

salt marsh. Where exotic weeds (such as brass buttons) and horticultural escapes establish, the expansion of brackish conditions detracts from the basic habitat management goal of maintaining natural habitats.

We recommend maintaining the point source urban runoff that exists south of the inland lagoon and monitoring the flow volume and water quality. A basic characterization of the region's brackish marshes is needed. At Tijuana Estuary, distribution limits of brackish marsh plants should be monitored in relation to flows in order to establish levels that allow expansion into the salt marsh. We recommend eliminating the point sources of street runoff at the northern end of the marsh. Discharges need to be redirected away from the marsh to discourage invasion of exotic plants and to restore and retain habitat for endangered species, such as salt marsh bird's beak.

If expansion of native brackish marsh species is desired, it should be promoted in areas where salt marshes and other natural estuarine ecosystems cannot be restored. Suitable sites exist within the Tijuana River and in abandoned agricultural lands. Several brackish ponds and marshes will be created at the PERL site. The use of treated wastewater should be encouraged for creation and maintenance of artificial brackish marshes. Wildlife use of these artificial wetlands should then be carefully documented.

e. *Channels and creeks.* The channel habitats at Tijuana Estuary are important to nearly all estuarine animals; they are recognized for their value in support of the food chain. All of the endangered birds use channel and creek areas for feeding. In previous years, there have been recreational shellfisheries and commercial bait fisheries. At present, both shellfish gathering and fishing are prohibited in the estuary.

The problems that affect the channels and creeks ultimately have an impact on the entire estuary, because the estuarine waters move throughout the system. Tidal closure, sedimentation, disturbance from dredging, and reduced water quality (wastewater input, nuisance algal blooms, reduced salinity) all require active management. The impacts of tidal closure are detailed in Chapter 5. Increased sedimentation rates have an impact on benthic organisms, and the associated turbidity affects water-column species. Dredging to remove accumulated sediments and restore tidal flushing in turn creates turbidity and alters the substrate. We know little of the impacts of dredging at Tijuana Estuary, because monitoring did not begin until spring 1986. The nutrient and salinity effects of wastewater discharges have been examined experimentally (Rudnicki 1986; Fong 1986), and the influence of

future freshwater flows from Mexico has been predicted (Zedler et al. 1984a,b,c); however, it is not clear how the existing sewage flows affect channel invertebrates and fishes, nor exactly how reduced salinities alter the normal channel populations. The current lack of bivalves in channels near the mouth is unexplained.

The management goal should be to reestablish and maintain the tidal flushing regime required to support the variety of estuarine communities present in 1977. The extent to which this is possible and the procedures required should be determined in the ongoing hydrological study (Williams, in prog.). Management of tidal flushing should be done with the minimum necessary disturbance due to dredging operations.

A monitoring program for channel fishes and invertebrates has begun with start-up funding from NOAA (Nordby, in prog.); it needs to be continued through years of different flow regimes. Salinity and water-quality relationships of these same species need to be determined. Reasons for the decline in benthic species and measures to facilitate their reinvasion need to be determined.

f. *Sandflats and mudflats.* The intertidal flats are closely associated with tidal channels and creeks, and the impacts of disturbance and considerations for management are similar. The primary values attributed to these sites are their habitat for shorebird loafing and foraging and feeding areas for the light-footed clapper rail and Belding's Savannah sparrow. It is important to determine if artificial impoundments can compensate for the loss or reduced quality of feeding areas in the estuary. Toward this goal, a variety of artificial wetlands will be constructed near PERL, and their use by shorebirds will be assessed.

g. *Beach and dunes.* The esthetic quality of beaches makes them the habitat most highly valued by the public. Consequently, human use is extensive year round. Ecologically, the habitats are valued for their support of native animals, including the globose dune beetle, sandy beach tiger beetle, sand dune tiger beetle, wandering skipper, and two nesting birds, the California least tern and snowy plover. Other species, such as Belding's Savannah sparrow, feed on dune and beach insects. The native plants are especially important to the ecosystem, because they stabilize the dunes, which in turn protect the estuary from sea storms.

The major problem facing the beach and dunes is coastal erosion. Substantial losses of sand occur each winter, but not all is replenished each summer; a continual net loss is obvious from aerial photos from 1928 through 1985. The height and location of dunes has changed with recent storm

overwashes, and stabilization is needed. In addition, exotics (sea rocket and ice plant, *Carpobrotus edulis*) have invaded. Experimental work that was initiated on the dunes has been plagued with vandalism as well as trampling. Sewage contamination sometimes leads to closure of the beach to swimmers; this management problem does not have an ecological solution.

Fencing should be installed along the ocean side of the dunes to prevent trampling of California least tern and snowy plover nests, as well as the native vegetation. Interpretive signs should be located away from the fence to prevent people from approaching too closely. Fences should be made to keep people, dogs, and horses away from the colonies, and posts should be topped with a tuft of wire to prevent perching by raptors.

It is widely agreed that dune reconstruction and stabilization is the preferred management objective, and a first attempt was made north of the mouth in 1985. Although the reconstructed dune helped protect estuarine channels from overwash during the 1986 storms, there was substantial erosion on the seaward side and dune crest, and most of the transplanted dune species died. Dune restoration south of the mouth has been designed as an experiment to determine how best to stabilize the habitats. At the same time, research on the role of the exotic sea rocket (Wood, in prog.) and the environmental requirements of several native plants (Fink, in prog.) will help to develop the best revegetation plan.

h. *River channels.* There are no descriptions of the Tijuana River where it meets the estuary. A riparian ecosystem developed after the 1980 flood, and dense vegetation is now present within the sanctuary. Species composition and use by wildlife remain unquantified. Many of the future hydrologic changes that will occur at Tijuana Estuary may have their greatest impact on this habitat type. As sewage spills come under control, streamflows will decline; if Mexico begins to discharge treated wastewater into the river, streamflows may increase to 30 or more million gallons per day.

Preliminary recommendations for the management of increased streamflow have been made (Zeder et al. 1984c), and Williams (in prog.) is evaluating a variety of problems and management solutions associated with the river corridor between the estuary and the Mexico border. Research is badly needed to characterize the riparian species and their habitat requirements. Determining the best management practices for this international river remains a major challenge.

In summary, the individual disturbances that have altered each of the above habitats may seem minor. Collectively, however, they have shifted many features of the estuary. It would have been difficult to predict that trampling the dunes would contribute to the demise of clapper rails. Yet the cumulative impacts of denudation, sedimentation, mouth closure, drought, hypersalinity, and sewage spills have acted to alter the estuary so much that it bears little resemblance to its condition in 1982. Tijuana Estuary was once a resilient system; it was capable of recovering even from catastrophic flooding. At present, however, changes in hydrology (e.g., the tidal prism) and shifts in several populations (e.g., the loss of the rail population and the dominance by pickleweed) may preclude recovery of the variety of ecological communities that were once present.

Those few changes that have been observed or identified through analysis of our monitoring data are just symptoms of a changing ecosystem. There is so much more that we do not understand about this estuary and its responses to disturbance. The task of recommending management procedures on the basis of the relatively small amount of knowledge we possess is humbling. We cannot expect all of our recommendations to be right or to work in restoring what has been lost. We do expect that continuing research will be useful in revising the above management recommendations as new information becomes available.

We suggest that managers be given the time and resources required to adopt a new philosophy of estuarine management, and not just to adopt this list of recommended projects. For each problem that arises, the approach should be to (1) review what is already known about that type of problem at Tijuana Estuary and elsewhere, (2) lay out alternatives for treating problems, (3) set up experiments that can test various solutions, (4) evaluate the successes and failures, (5) identify their causes insofar as is possible, and (6) document all phases so that future management will benefit. In other words, management should be based on a scientific approach, replacing trial and error with ecotechnology.

6.3 MITIGATION — SUCCESSES AND FAILURES

Throughout southern California, poorly defined mitigation projects are conceived and implemented. Their success or failure is rarely assessed, and quantitative documentation is lacking. Most of the projects are carried out in order to mitigate the impacts of dredging or filling more wetland acreage. Actually, few mitigation projects increase habitat area; rather, they change one type of wetland habitat into another. The process purports to justify further wetland destruction. The myth that changes in habitat quality can compensate for reduced wetland area is perpetuated — not by

demonstrated successes but by the absence of documented failures (Zedler, in press b).

At Tijuana Estuary, the restoration of badly-disturbed areas is needed, and enhancement of less-disturbed sites would be useful. First, however, the specific goals of restoration and enhancement must be laid out, and criteria for judging their achievement established. With a full-scale plan for future projects, the Management Authority would be able to respond to opportunities for funding such projects. Tijuana Estuary has already been selected for two off-site mitigation projects, both to mitigate habitat losses within San Diego Bay. In the absence of a comprehensive restoration plan, piecemeal alterations of Tijuana Estuary to take advantage of mitigation funds can be more harmful than beneficial.

For example, in 1983, it was suggested that two dikes within the abandoned sewage lagoons be breached in order to improve tidal flushing and isolate one dike segment as an island, and that sand be placed on that island to create least tern nesting habitat. The proposed enhancement was intended to mitigate an earlier, non-permitted fill operation in San Diego Bay. However, the proposed excavations would have created stagnant pools; the excessive dredging would have lowered water quality by exposing buried sewage sludge; the proposed use of rock to stabilize cut slopes would have introduced foreign substrates to the wetland, and valued cordgrass habitat would have been unnecessarily eliminated. Just prior to implementation, an alternative excavation design was recommended and enforced by the Fish and Wildlife Service. Unfortunately, specific goals were not enumerated, and no mechanism was provided for monitoring changes or assessing the success of the "enhancement." After dike breaching, the northernmost sewage lagoon did have increased tidal flushing, but isolation of the dike system did not stop canine or human intruders (a second mitigation will now attempt to accomplish that objective). Furthermore, deposition of sand on top of the dike island stimulated, rather than precluded, vegetative invasion of intended tern nesting islands.

In another restoration project, weedy vegetation in the disturbed upland transition northwest of the inland lagoon was to be eradicated and replaced with native species. Burning was attempted but fires did not spread over the site; thus, about 10 acres of habitat were disked and sown with native plant seeds. However, weedy species reinvaded rapidly, and only a few native plants became established. Later, the upland transition just north of the inland lagoon was cleared of debris and weeds and replanted with native vegetation. In this case, a bulldozer scraped the site and encroached upon patches of native vegetation. Again, weedy species quickly reinvaded, plus some pickleweed was damaged. It is clear from both of these attempts to restore the wetland-upland transition, that we know too little about the control of exotic plants and the establishment of native species.

In the above cases, there were benefits, in that trash and debris were removed from the wetland. Still, the restoration goals were not achieved. Experimentation with careful field supervision is needed. For future projects, we recommend that a scientific approach be used, so that there is greater potential to understand how and why restoration measures succeed or fail.

Tijuana Estuary has an important role to fulfill within southern California. The goal of research is to provide the information needed to improve management of the region's precious wetland resources. By understanding how environmental conditions affect species distributions and abundance, we hope to specify how ecosystems can be manipulated to achieve desired results. Passive management will not be sufficient to maintain the natural diversity of habitats and their native species. The need for ecotechnology is clear.

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50272-101

REPORT DOCUMENTATION PAGE	1. REPORT NO. Biological Report 85(7.5)	2.	3. Recipient's Accession No.

4. Title and Subtitle

The Ecology of Tijuana Estuary, California: An Estuarine Profile

5. Report Date June 1986

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10. Project/Task/Work Unit No.

11. Contract(C) or Grant(G) No.

(C)

(G)

12. Sponsoring Organization Name and Address

U.S. Fish and Wildlife Service
National Coastal Ecosystems Team
1010 Gause Blvd.
Slidell, LA 70458

13. Type of Report & Period Covered

14.

15. Supplementary Notes

16. Abstract (Limit: 200 words)

Tijuana Estuary in southern California is characterized by a high degree of environmental variability resulting primarily from unpredictable freshwater inputs. Tijuana Estuary is unusual for its international setting (three-fourths of its watershed is in Mexico); its diversity of ecological communities, which provide habitat for a variety of rare and endangered species; and its history of ecological study, yielding extensive data from years with and without catastrophic disturbances. The estuary is areally dominated by emergent wetlands (salt marshes, brackish marshes, and salt pannes); estuarine channels, tidal creeks, intertidal flats, dunes, and beaches are also major habitat types.

This report discusses these habitats and synthesizes data amassed on the vegetation, algae, invertebrates, fishes, and birds found in the estuary, their ecological interrelationships, and relationships of the biota with the physical environment. Also discussed are responses of biotic components to changes resulting from major storms, closure of the estuarine mouth, prolonged inundation of emergent wetlands, and prolonged drought.

Portions of Tijuana Estuary are managed as a National Wildlife Refuge and a National Estuarine Sanctuary. Management issues for this ecosystem include erosion, streamflow alterations and sewage wastewater discharges, and mitigation of impacts due to catastrophic events.

17. Document Analysis   a. Descriptors

Estuaries, ecology, geology, hydrology, climate, nitrogen, nekton, algae, biological productivity

b. Identifiers/Open-Ended Terms

Wetlands, energy flow, nutrient cycling, emergent vascular plants

c. COSATI Field/Group

18. Availability Statement	**19. Security Class (This Report)** Unclassified	**21. No. of Pages** 104
Unlimited release	**20. Security Class (This Page)** Unclassified	**22. Price**