

SALT MARSH VASCULAR PLANT DISTRIBUTION
IN RELATION TO TIDAL ELEVATION, HUMBOLDT BAY, CALIFORNIA

by

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ABSTRACT

The relationship between tidal elevation and the distribution of salt marsh vascular plants was investigated in Humboldt Bay, California. Plant species composition and cover were assessed and elevation surveyed in 148 one-square-meter plots in July-August, 1985, within five salt marsh study sites around northern and central Humboldt Bay. Elevations were surveyed with reference to the National Geodetic Vertical Datum (NGVD) and converted to a mean lower low water (MLLW) scale based on National Ocean Service (NOS) calculations for the relationship between NGVD and MLLW.

Twenty-two plant species were encountered in the sampling, including the three rare plant species: Orthocarpus castillejoides var. humboldtiensis, Cordylanthus maritimus ssp. palustris and Grindelia stricta ssp. blakei. Direct gradient analysis was used to illustrate the change in species composition with elevation. Using cluster analysis, the samples were grouped on the basis of floristic similarity into three major vegetation types: Salicornia virginica marsh, Spartina densiflora marsh and mixed marsh, of which the mixed marsh type was most floristically diverse.

At the four study sites associated with North Humboldt Bay, salt marsh vegetation ranged from 5.7 to 8.4

ft. MLLW. Tidal characteristics were notably lower at the fifth study site, Elk River, with salt marsh vegetation occurring between 3.9 and 6.1 ft. MLLW. Through discriminant analysis, tidal elevation data for North Bay were assessed as 60.0 percent effective in predicting the class memberships identified by cluster analysis. While there was overlap in their elevation distribution, each of the salt marsh types was most common within a particular range of elevation. Salicornia marsh was most prevalent below 6.9 ft. MLLW, Spartina marsh between 6.9 and 7.3 ft. MLLW and mixed marsh above 7.3 ft. MLLW.

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INTRODUCTION

Salt marshes are found in the upper intertidal zone of sheltered, temperate coastlines worldwide. Salt marsh species occur only within a specific range of tidal elevation, but the limits for this parameter previously have not been established for Humboldt Bay, California. This lack of information has been a hindrance in planning local salt marsh restoration projects. If an area is too low, the frequency and duration of tidal inundation may be too stressful to support vascular plant growth. If too high, upland plants may outcompete salt marsh species. A primary goal of this study was to determine the range of elevations suitable for salt marsh establishment in Humboldt Bay, based on the distribution of natural populations.

Zonation patterns of vegetation in salt marshes have been correlated with tidal elevation (Johnson and York 1915, Chapman 1938, Purer 1942, Hinde 1954, Adams 1963, Eilers 1975, Claycomb 1983), suggesting another application for tide level-plant species information in salt marsh restoration. It may be possible to favor a certain type of salt marsh community by manipulating elevation. With this ability, restoration projects could be designed with specific objectives such as providing habitat for particular species or mitigating for the loss

of a certain type of salt marsh. In this study, elevation ranges are presented for 22 plant species within Humboldt Bay salt marshes, vegetation types are classified, and the feasibility of discriminating among these vegetation types on the basis of tidal elevation is assessed. The influences of tidal inundation, salinity, soil aeration, nutrient availability and substrate type on plant distribution are discussed.

LITERATURE REVIEW

Overview

The classic treatise on the world's salt marshes and salt deserts was written by Chapman (1960, 1974), who has since edited another volume on the same subject (1977). Other major works on the general biology and ecology of salt marsh communities include Ranwell (1972), Waisel (1972), Reimold and Queen (1974), Pomeroy and Wiegert (1981) and Long and Mason (1983). Overviews on the vegetation of North American Pacific coastal marshes have been provided by Macdonald (1969, 1977_a, 1977_b) and Macdonald and Barbour (1974). Community profiles are available for tidal marshes of the Pacific Northwest (Seliskar and Gallagher 1983), of San Francisco Bay (Josselyn 1983) and of southern California (Zedler 1982) through a series published by the United States Fish and Wildlife Service.

A central theme in salt marsh field investigations has been to describe and explain plant distribution patterns. The vegetation of European salt marshes has been described by Chapman (1939, 1959), Corre (1985) and de Jong and de Kogel (1985); Australian salt marshes by Clarke and Hannon (1967); North American east coast marshes by Johnson and York (1915), Miller and Egler (1950), Adams (1963) and Niering and Warren (1980);

southern California marshes by Purer (1942), Vogl (1966), Zedler (1977) and Neuenschwander et al. (1979); San Francisco Bay marshes by Hinde (1954); Oregon marshes by Jefferson (1974) and Eilers (1975); and Canadian marshes by Glooschenko (1978).

Humboldt Bay salt marsh vegetation has been described by Macdonald (1967), Claycomb (1983) and Newton (1985a, 1985b, 1986a). Claycomb documented vegetation changes at a salt marsh restoration site. Other local studies containing information on salt marsh vegetation at restoration sites include Stopher et al. (1981), Miner and Moore (1982-1986) and Koplín et al. (1984). Newby (1980) assessed the distribution of cordgrass and pickleweed in relation to nutrient availability on an island in Humboldt Bay. Rogers (1981) measured the productivity of selected salt marsh species in Humboldt Bay.

Josselyn (1982) provided an overview of wetland restoration in California. Zedler (1984) prepared a guidebook for salt marsh restoration in southern California, and Josselyn and Buchholz (1984) a guide for San Francisco Bay, containing information on state-of-the-art techniques in marsh restoration, guidelines for planning and monitoring, revegetation considerations and recommendations for defining project goals. Newton (1986b) discussed management considerations for three rare plant species in Humboldt Bay salt marshes.

Race and Christie (1982) discussed the ethics of mitigation strategies and the role of marsh creation in coastal management.

Zonation

Zonation is a characteristic feature of salt marsh communities (Chapman 1960, Macdonald 1977a). The non-uniformity of the vegetation is obvious upon first glance, but the delineation, description and explanation of vegetation units within the salt marsh have been the subject of much research. Frequently, the vegetation is envisioned as a series of belts spanning the intertidal zone, distinguished by reference to tide level with terms such as low, middle and high or upper marsh (Johnson and York 1915, Purer 1942, Adams 1963, Neuenschwander et al. 1979, Claycomb 1983). The names of dominant species have also been used to distinguish vegetation units, generally with some reference to their position on the shore (Hinde 1954, Clarke and Hannon 1967, Ewing 1983, de Jong and de Kogel 1985). Others have described the pattern of vegetation units as a mosaic (Miller and Egler 1950, Burg et al. 1980, Niering and Warren 1980, Corre 1985).

The delineation of vegetation units within the salt marsh remains imprecise. Nearly always, some species transcend the bounds of floristic units, and exceptions can be found for every environmental delineation of zones.

Some investigators have questioned the concept of zonation in the salt marsh, in turn describing a vegetation continuum, with species composition and dominance changing gradually across the environmental gradient (Vogl 1966, Boorman 1971, Zedler 1977).

Tide-Elevation Complex

Clarke and Hannon (1969) used the term "tide-elevation complex" to describe a set of interrelated factors including tidal inundation, soil and water salinity, soil aeration and nutrient availability. These factors all exhibit patterns that can be referenced to tidal elevation, and all are influential in governing plant distribution. Zedler (1977) demonstrated that elevation provides a good index of environmental patterns, with lower elevations having more inundation, higher salinity and higher soil organic matter.

Within the tide-elevation complex, the impact of any one factor may vary with species, timing or location. In general, it appears that tidal inundation is most influential at low elevations, and that salinity becomes more important at high elevations (Ranwell 1972, Corre 1985, Niering and Warren 1980).

Tidal inundation affects plant distribution through wave action, flushing, and the frequency and duration of submergence periods. At its lower extent, the salt marsh

experiences both submergence and emergence daily. The upper marsh is inundated less frequently, with periods of emergence sometimes exceeding a month.

Wave action disrupts the substrate, increases turbidity and uproots seedlings (Macdonald 1977a). Wiehe (1935) suggested that tidal scour acts as an important factor limiting the lower distribution of Salicornia europea by inhibiting seedling establishment.

Tidal flushing can be important in lowering groundwater salinity, especially at higher elevations, where evaporation sometimes leads to the development of hypersaline conditions. In San Francisco marshes, Balling and Resh (1983) attributed the vigorous plant growth and high species diversity near mosquito ditches to the lowering of extreme soil salinities by tidal flushing.

Prolonged submersion in seawater is stressful for vascular plants in a number of ways. Photosynthesis may be reduced by a diminished carbon supply and a reduction in the amount of incident light, or by an alteration in the light's spectral composition. Transpiration and respiration may be reduced by stomatal closure and a diminished oxygen supply. Wet soils are prone to anaerobic conditions because oxygen has a low solubility in water, and because microbial activity (and hence oxygen consumption) is higher under moist conditions. Soil anaerobiosis can induce toxic levels of iron, manganese

and sulphide, and interfere with nutrient uptake by plants (Mahall and Park 1976b, Macdonald 1977a, Zedler 1984, Groenendijk 1985).

In the Netherlands, Groenendijk (1985) tested plant tolerances to prolonged seawater immersion. He found considerable interspecific variation, though he could not correlate these differences with the positions of species on the shore. Experiments testing the sensitivity of generative parts to prolonged tidal immersion did suggest that reduced reproductive success may be important in the distribution of some species.

Prolonged emergence can stress plants through soil desiccation and the development of hypersaline conditions. Hypersalinity is less common north of Point Conception, California, than along the southern California coast, where it is promoted by low rainfall and high evaporation rates (Macdonald 1969). Nutrient availability can become limiting during an extended emergence period, as tidewaters are the major source of nutrients in the salt marsh (Macdonald 1977a).

Several attempts have been made to correlate patterns of tidal inundation with patterns of plant distribution. There is general agreement that inundation patterns exhibit a discontinuity at the lower limit of salt marsh establishment. At this level, usually near mean lower high water (MLHW), the duration of submersion periods

decreases markedly. Analyses based on annual hours of submersion indicate a pattern that declines steadily with increasing elevation (Hinde 1954, Zedler 1977). Analyses based on the number and length of continuous submergence and emergence periods suggest a second major discontinuity in the inundation pattern (Macdonald 1969, Eilers 1975, Claycomb 1983). Near the elevation of mean higher high water (MHHW), there appears to be a marked increase in the maximum duration of continuous exposure periods.

Macdonald (1969) stated that south of Point Conception, the MHHW level is easily recognized in the field by the vertical distribution of floral groups, and that north of Point Conception, the division is indistinct.

In calculating niche parameters for salt marsh species, Russel et al. (1985) assessed tidal inundation using three related measurements: tidal elevation, number of submergences per year and the longest period of continuous exposure. While the three measurements did not exhibit linear relationships to one another, they did produce similar results in the analysis of niche parameters.

Recently, salinity has received increased attention as a major factor in determining salt marsh plant distribution (Mahall and Park 1976a, Nestler 1977, Ungar and Riehl 1980, Zedler 1982, Corre 1985, Jaworski and Tedrow 1985). A basic model of the salinity regime in

salt marshes has been described by Mahall and Park (1976a) and Macdonald (1977a). Salinity gradually increases landward to a maximum level near mean high water (MHW), then declines. At low elevations, where oceanic influences predominate, soil profile salinity is more stable than at high elevations, where it is affected to a greater degree by rainfall and evaporation. Salinity tends to increase with soil profile depth during wet seasons, but decrease with soil profile depth during dry seasons, when evaporation produces concentrated soil salinities near the surface.

Adequate evaluations of salinity are complicated by a high degree of temporal and spatial variability. Salinity varies daily with the tide, seasonally with rainfall and evaporation, and with varying amounts of freshwater inflow. Zedler (1982) suggested that the year-to-year variations in salinity make it a good candidate for explaining yearly changes in salt marsh plant species composition. It is likely that salinity has its major impact on plant distribution through extreme conditions (Corre 1985).

A plant's response to salinity depends on its stage of development and the degree to which it is already under stress. Mahall and Park (1976a) suggested that salinity stress is most critical during late spring and summer, when plants are actively growing. Ungar and Riehl (1980)

concluded that salinity levels at the time of seed germination are crucial in determining plant distribution. Zedler (1984) described a "critical period" in the establishment of the rare annual, Cordylanthus maritimus ssp. maritimus, in which the seeds are dependent on either rainfall or flushing by high tides to provide moist, low-saline conditions for germination. Woodell (1985) found that while most salt marsh species tested required brackish or fresh water to germinate, the rate of germination was greatly enhanced by pre-soaking in seawater.

The influences of the tide-elevation complex tend to produce a linear banding of vegetation across the intertidal zone. This vertical pattern can be obscured where physical factors other than the tide-elevation complex exert overriding influences. Differences in soil texture from one location to another can alter zonation patterns. Soil moisture and salt retention characteristics affect salinity gradients. In coarse soils, percolation is rapid and salt is quickly leached from the soil surface. In clay soils, salts are retained better because of slow percolation rates and a higher cation exchange capacity (Gallagher 1977). Zonation patterns are also obscured by variations in distance from water sources (Clarke and Hannon 1967).

Chance also helps determine plant distribution

patterns. Storms, flooding, tidal debris buildup, hypersalinity, herbivory and trampling all cause local mortality, leading to patches of open space in the marsh. The chance establishment of one species or another in these open areas could partly determine later vegetation patterns (Miller and Egler 1950, Niering and Warren 1980, Zedler 1982).

Competition

Many salt marsh species appear to have wider ranges of tolerance to physical stress than they exhibit in the field (Gray 1985). Using Hutchinson's terminology, the realized niches of these species are smaller than their fundamental niches, suggesting that competition occurs among species for available space and resources. (Odum 1983).

The importance of competition in determining the distribution of salt marsh plants was suggested by Purer (1942) and Hinde (1954). Clarke and Hannon (1971) used a simulated elevation gradient to test the impact of competition on Australian salt marsh species. They concluded that four of the six species tested were influenced by competition at both their lower and upper limits, and that the other two were affected by competition at their landward limit.

Zedler (1977) used tests of abundance and association

to assess the role of competition among salt marsh species in the Tijuana Estuary in southern California. She hypothesized that Salicornia virginica is limited in the middle of its range by competition with either Batis maritima or Salicornia bigelovii, or both. Zedler also suggested that Triglochin maritimum, which blooms earlier than other salt marsh species, may avoid competition by a temporal partitioning of resource use.

Russel et al. (1985) measured niche breadths of salt marsh species in relation to tidal inundation. They found that mean niche overlaps are significantly smaller in areas with higher species diversity, presumably resulting from a greater intensity of competitive interactions in these areas.

Competition has more impact on species distributions at high marsh elevations, whereas physical factors tend to predominate at low elevations. The environmental stresses associated with tidal inundation appear to have an overriding influence on determining which species occupy the lower shore. More species can tolerate the environmental conditions of the high marsh, setting the stage for competitive interactions (Chapman 1960, Ranwell 1972, Zedler 1977, Russel et al. 1985).

Competition becomes even more intense landward of the intertidal zone, where physical conditions are more favorable for vascular plant growth. Laboratory tests

have shown that many salt marsh species grow better in brackish or fresh conditions than in saline conditions (Barbour 1970, Barbour and Davis 1970, Phleger 1971). Quite possibly, these species are restricted from non-saline habitats by their inability to compete. Relatively few vascular plants have evolved mechanisms for tolerating the stresses imposed by periodic tidal inundation. For those that have, the salt marsh environment represents an important refuge from competitors.

STUDY AREA

Location

Humboldt Bay is a large marine embayment occurring in Humboldt County, northern California. The bay is comprised of two shallow basins, North Bay (= Arcata Bay) and South Bay, and a deepwater section around the mouth called Entrance Bay (Fig. 1). Extensive mudflats are exposed during low tide in North and South Bays. Two narrow sand spits shelter the estuary from wave exposure, allowing the development of salt marsh in the upper intertidal zone.

According to Cowardin et al. (1979), Humboldt Bay salt marshes belong to the Columbian Province, estuarine system, intertidal subsystem, emergent wetland class and persistent subclass. The tidal regime varies from regularly to irregularly flooded. Water chemistry is haline to mixohaline.

Humboldt Bay represents the principal site of salt marsh between Coos Bay, 156 nautical miles to the north, and San Francisco Bay, 225 nautical miles to the south. The salt marsh community in Humboldt Bay is floristically unique. Spartina densiflora, a Chilean species of cordgrass presumably introduced during the 1850s, has risen to a position of dominance here. The species is not known to occur anywhere else in North America, except for

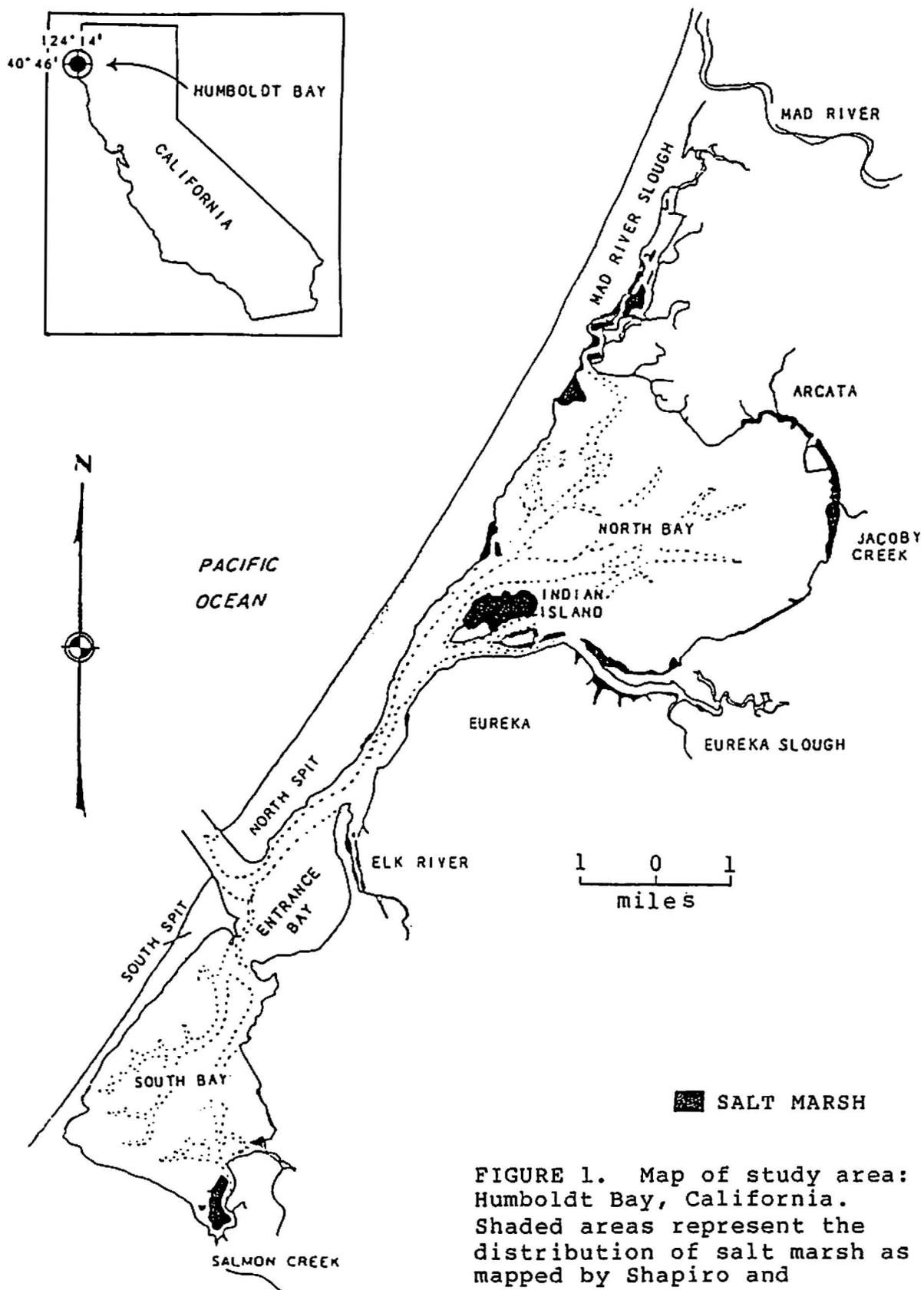


FIGURE 1. Map of study area: Humboldt Bay, California. Shaded areas represent the distribution of salt marsh as mapped by Shapiro and Associates (1980).

a small patch in San Francisco Bay, where it was introduced from Humboldt Bay in 1976. Chile imported lumber from Humboldt Bay during the 1850s while undergoing a period of rapid development. It is speculated that seeds of S. densiflora were transported inadvertently with ballast gathered from Chilean shorelines on lumber ships returning to Humboldt Bay (Spicher and Josselyn 1985).

Prior to taxonomic investigation by Spicher (1984), the Humboldt Bay cordgrass was believed to be a northern ecotype of Spartina foliosa (Pacific cordgrass), a species characterizing central and southern California coastal marshes. Aberrations in the habit and distribution of the cordgrass in Humboldt Bay were noted, but were attributed to higher rainfall and geographic isolation (Rogers 1981). Unlike S. foliosa, S. densiflora grows in tussocks, and it occupies a higher range of elevation in the intertidal zone than its California relative. S. foliosa reaches its northern limit just north of San Francisco Bay in Bodega Bay (Spicher and Josselyn 1985).

North of Humboldt Bay, salt marshes on the Pacific coast do not have Spartina (Eilers 1975), except for the introduction of exotic species in spots. S. anglica was introduced from England to Puget Sound, Washington, in 1961 or 1962 for controlling shore erosion (Spicher and Josselyn 1985). Kozloff (1983) reported that S.

alterniflora, a species native to the North American Atlantic coast, has firmly established in Willapa Bay, southern Washington. This same species has been found in several locations in Humboldt Bay within the past few years.

Another feature contributing to the floristic uniqueness of Humboldt Bay salt marshes is the presence of three rare plant species, two of which are endemic. Orthocarpus castillejoides var. humboldtiensis (Humboldt Bay owl's clover), Grindelia stricta ssp. blakei (Humboldt Bay gumplant) and Cordylanthus maritimus ssp. palustris (Point Reyes bird's beak) are all on List 1B of the California Native Plant Society Inventory as rare and endangered throughout their ranges (California Native Plant Society 1984). The owl's clover and gumplant are endemic to the Humboldt Bay area; Point Reyes bird's beak ranges from Coos Bay, Oregon, to Morro Bay, San Luis Obispo County, California (Newton 1986b).

Humboldt Bay salt marshes are further distinguished from northern marshes by the presence of Limonium californicum (sea lavender) and from southern marshes by the absence of Frankenia grandifolia and Suaeda californica (sea blite). Aside from these distinctions, Humboldt Bay shares a number of floristic components with other Pacific coast marshes. Species that range from British Columbia to southern California include Salicornia

virginica (pickleweed), Distichlis spicata (saltgrass), Jaumea carnosa, Triglochin maritimum (arrowgrass) and Cuscuta salina (marsh dodder) (Macdonald 1977a, 1977b).

Salt Marsh Distribution

Shapiro and Associates (1980) estimated a total of 970 acres of salt marsh remaining in Humboldt Bay (Fig. 1). This acreage represents less than 15 percent of the estimated 7000 acres present in 1850, when European settlers initiated the practice of marsh reclamation. Wet, unstable marshlands were "reclaimed" from the sea for agricultural use by building dikes that held back tidewaters. Today much of these former salt marshes are still pastureland. The salt marshes remaining in Humboldt Bay are protected by law. Recognition of the ecological and aesthetic values of coastal wetlands led to the establishment of the California Coastal Act of 1976, which deters further destruction of these habitats and requires mitigation when development is permitted.

Only about 140 acres of salt marsh remain in South Bay. About 40 acres border the Elk River Estuary. In North Bay, about 130 acres of salt marsh are associated with Mad River Slough, 120 acres with Eureka Slough, and there is a 195-acre parcel of salt marsh on Indian Island. The remaining salt marsh acreage is scattered around the periphery of North Bay (Shapiro and Ass. 1980) (Fig. 1)

Climate

The Humboldt Bay area has a temperate marine climate, with mild, wet winters and cool, dry, foggy summers. The mean annual temperature is 52 degrees Fahrenheit, with summer months averaging ten degrees warmer than winter months. The average annual precipitation is 38 inches, 90 percent of which occurs between October and April. Fog is a dominant feature of the area, especially in summer and early autumn, with resulting high humidity throughout the year. Winds prevail from the northwest in spring and summer and from the south in fall and winter (Elford and McDonough 1974, U. S. Army Corps 1979).

Tidal Regime

The tidal cycle in Humboldt Bay has a mixed semidiurnal pattern characterized by two high tides of unequal magnitude and two low tides of unequal magnitude each lunar day (Fig. 2, Table 1). The height of the tide varies from place to place around the bay perimeter in response to complex current patterns. These variations were assessed by the National Ocean Service (NOS) at twelve locations around the bay (Fig. 3, Table 2). Means were calculated for each stage of the tidal cycle, and expressed in relation to mean lower low water (MLLW) at each station (Table 3).

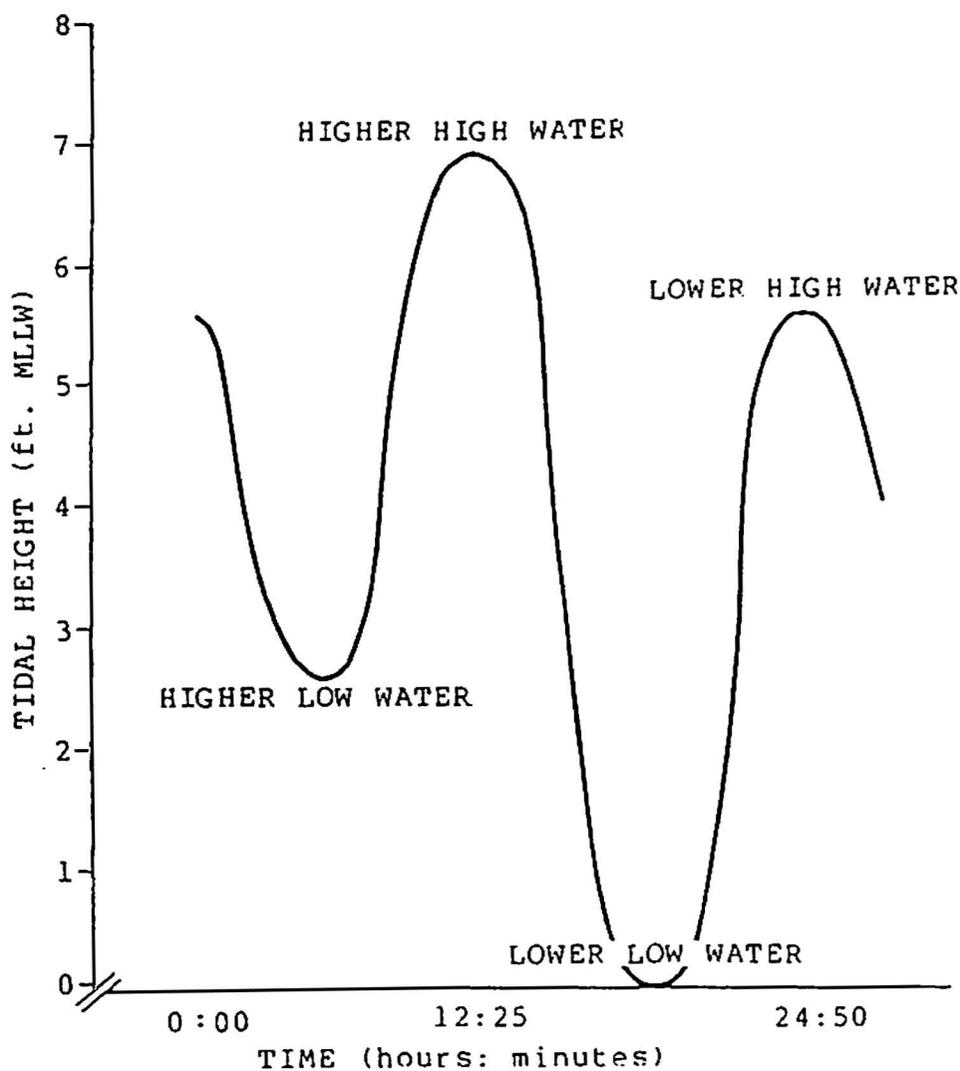


FIGURE 2. A typical tidal curve for Humboldt Bay, California. The pattern is mixed-semidiurnal, characterized by two high tides of unequal magnitude and two low tides of unequal magnitude each day. (A tidal day = 24 hours, 50 minutes.) Highs and lows also vary in magnitude from day to day. Tidal heights recorded over extended time periods are used in calculating means. Often such tidal datums are referenced to the height of mean lower low water (MLLW) by setting MLLW = 0 ft.

TABLE 1. Definitions of tidal datum terms (Harris 1981).

HHW = Higher High Water

MHHW = Mean Higher High Water

LLW = Lower Low Water

MLLW = Mean Lower Low Water

LHW = Lower High Water

MLHW = Mean Lower High Water

HLW = Higher Low Water

MHLW = Mean Higher Low Water

EHW = Extreme High Water

MHW = Mean High Water, a plane midway between MHHW and MLHW.

MLW = Mean Low Water, a plane midway between MHLW and MLLW.

MTL = Mean Tide Level, a plane midway between MHW and MLW.

MSL = Mean Sea Level, usually within a few 0.01 ft. of MTL. The MSL datum changes over time because the mean elevation of the sea surface is gradually rising relative to land.

NGVD = National Geodetic Vertical Datum, established in 1929 as a reference datum plane for geodetic leveling. It is intended to approximate MSL, however NGVD is a fixed surface that does not change over time.

Diurnal Range = MHHW - MLLW.

Mean Range = MHW - MLW.

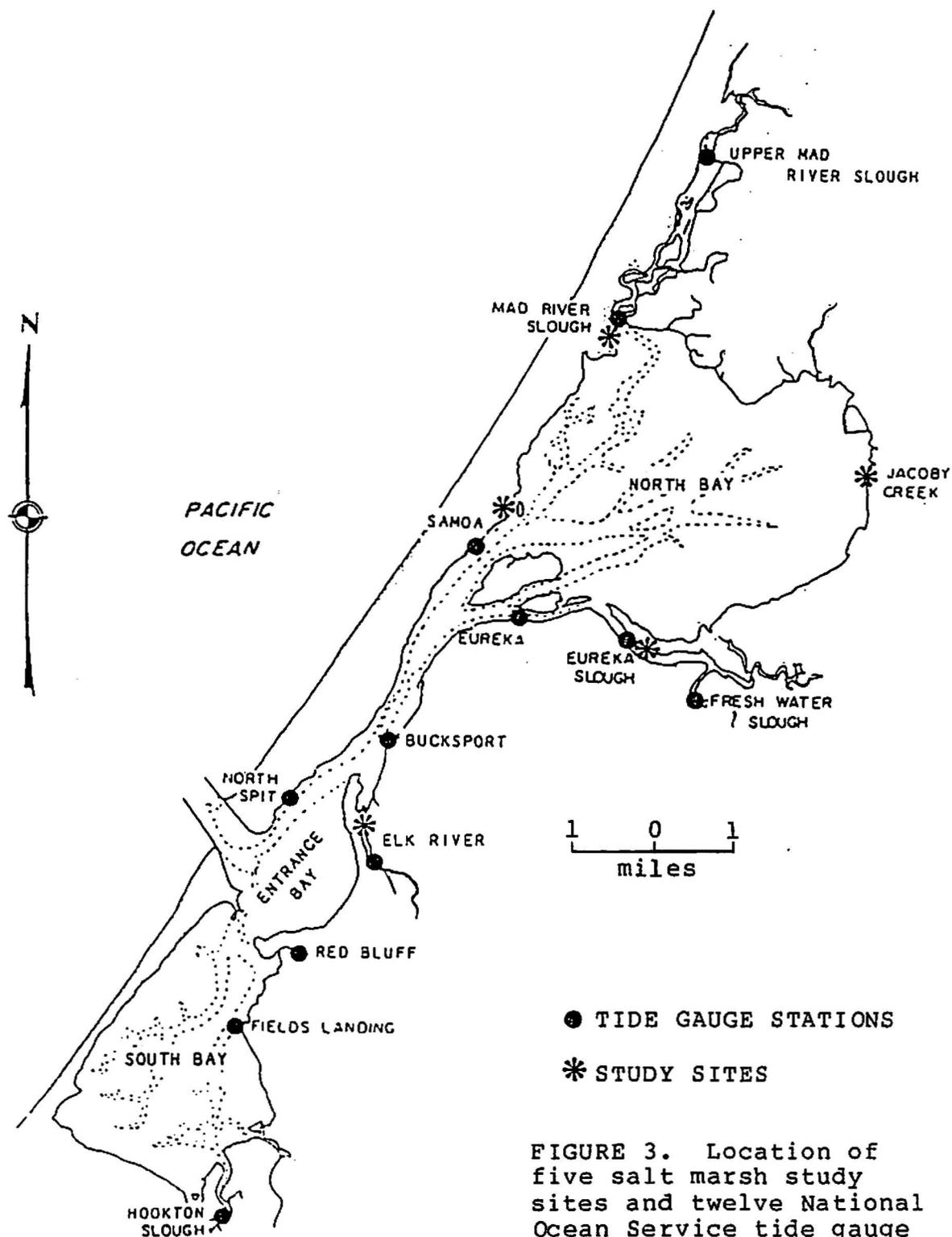


FIGURE 3. Location of five salt marsh study sites and twelve National Ocean Service tide gauge stations in Humboldt Bay, California.

TABLE 2. National Ocean Service tide gauge station locations and dates monitored, in Humboldt Bay, California.

TIDE GAUGE STATION	ABBREVIATION	DATES
941 8983 Upper Mad River Slough	UMR	7/78-1/79
* 941 8865 Mad River Slough	MRS	9/77-2/80
* 941 8817 Samoa	SAM	4/78-6/79
* 941 8802 Eureka Slough	EUS	3/78-6/79
941 8801 Eureka	EUR	8/77-2/80
941 8799 Freshwater Slough	FRS	3/78-1/79
941 8778 Bucksport	BS	8/77-2/80
* 941 8757 Elk River	ER	9/77,4/79
941 8767 North Spit	NS	8/77- Present
941 8739 Red Bluff	RB	4/78-1/79
941 8723 Fields Landing	FL	4/78-2/80
941 8686 Hookton Slough	HS	9/77-6/79

* Tide gauge stations near salt marsh study sites.

TABLE 3. Tidal datums calculated by the National Ocean Service (1981-1985) for twelve locations in Humboldt Bay, California.

HUMBOLDT BAY TIDAL DATUMS (ft. MLLW)										
GAUGE STATION	MLLW	MLW	MHLW	MTL	MLHW	MHW	MHHW	DIURNAL RANGE	MEAN RANGE	NGVD
UMR	0.00	1.30	2.60	4.26	6.51	7.22	7.93	7.93	5.92	N/A
* MRS	0.00	1.32	2.64	4.18	6.32	7.03	7.74	7.74	5.71	4.28
* SAM	0.00	1.27	2.54	3.95	5.91	6.62	7.33	7.33	5.35	3.99
* EUS	0.00	1.27	2.54	4.01	6.04	6.76	7.48	7.48	5.49	4.04
EUR	0.00	1.28	2.56	3.94	5.90	6.61	7.32	7.32	5.33	4.02
FR	0.00	1.08	2.16	3.78	5.78	6.49	7.20	7.20	5.41	N/A
BS	0.00	1.28	2.56	3.79	5.60	6.30	7.00	7.00	5.02	3.85
* ER	0.00	0.39	0.78	2.40	3.70	4.40	5.10	5.10	4.01	1.96
NS	0.00	1.25	2.50	3.73	5.52	6.22	6.92	6.92	4.97	3.72
RB	0.00	1.21	2.42	3.66	5.43	6.12	6.81	6.81	4.91	3.69
FL	0.00	1.23	2.46	3.69	5.45	6.15	6.85	6.85	4.92	3.70
HS	0.00	1.22	2.44	3.73	5.54	6.24	6.94	6.94	5.02	3.71

* Tide gauge stations near study sites.

N/A = Not Available

Generally, the mean tide level (MTL) and the amplitude of the tide increase with distance from the entrance in North Bay, though not in South Bay. At the North Spit tide gauge station, the MTL is 3.73 feet MLLW, the diurnal range is 6.92 feet and the mean range is 4.97 feet (National Ocean Service 1981-1985). There is extensive mixing in the bay as a result of its large tidal prism, large tidal range and limited freshwater input.

Soils

Salt marsh soils are comprised of the finest sediments in the bay. The particles are bound tightly together, forming a peat high in organic matter. Samples have revealed 63 to 72 percent of the soil content to be organic matter, mostly roots and dead vegetation (Burton 1972). In most cases, the marsh deposits are three to four feet thick, grading downward to clayey silts (Thompson 1971).

Tidal channels penetrate the marshes in dendritic patterns. Some channels are well-defined, with mud banks two to three feet high; others are bounded by gradual slopes covered with vegetation. Like the bay mudflats, the mud in the tidal channels is soft and black, with an odor of sulfur. In the vegetated portion of the marsh, plant roots help stabilize the substrate.

Both erosion and accretion are occurring within

Humboldt Bay, as indicated by aerial photographs, sediment core samples and recorded siltation measurements. Net erosion is apparent near the mouth of Eureka Slough, attributable to wave attack and to alterations in the drainage pattern of Freshwater Creek. Net accretion has been noted near the mouth of Jacoby Creek, a source of considerable sediment. At other areas along the bay shoreline, there appear to be seasonal cycles of erosion and accretion in response to shifting wind and wave conditions (Thompson 1971).

Study Sites

Study sites were selected on the basis of the following criteria: A. Presence of relatively undisturbed salt marsh. B. Proximity to an established benchmark, for ease in surveying. C. Proximity to a NOS tide gauge station, for accuracy in estimating tide levels. Five areas were selected: Mad River Slough, Jacoby Creek, Eureka Slough, the Samoa Peninsula, and Elk River (Fig. 3). The first four sites are associated with North Bay, and the Elk River site with Entrance Bay. The Jacoby Creek and Eureka Slough sites are part of the Humboldt Bay National Wildlife Refuge, managed by the United States Fish and Wildlife Service.

The Mad River Slough site is located on the southwest side of the mouth of the slough. This marsh was diked in

the early 1900s, but the dike was eroded and abandoned by 1927. Reportedly, the area had reverted to salt marsh by 1948 (Shapiro and Ass. 1980). Remnants of the old dikes are now vegetated primarily with salt marsh species.

The Jacoby Creek site is located on the eastern shoreline of North Bay, south of the mouth of Jacoby Creek. Here the marsh gradually slopes westward to the adjoining mudflats.

The Eureka Slough site is adjacent to the mouth of the slough, on the east side. Here the bayward margin of the marsh is a two to three-foot-high bank under active erosion by wave attack, with clumps of marsh mud and vegetation slumped onto the mudflat in places.

The Samoa site is located on the western shoreline of North Bay, near the intersection of the Samoa Bridge and Samoa Blvd. During the 1930s through the 1950s, log rafts were stored along this shore. The marsh bank is steep in most places.

The Elk River site is located on the spit extending from the river mouth, west of the river channel. Formation of Elk River Spit first became apparent in the 1930s. The mechanism for sediment deposition in this area was provided by stabilization of the bay entrance and by deepening of navigation channels (Costa 1982). Much of the spit is covered by sand dunes, with pockets of salt marsh bordering Elk River.

METHODS

Sampling

In July, 1985, 148 sample plots were established. Transects were run perpendicular to the shoreline, from randomly-selected points on the edge of the mudflat to the upper marsh boundary. Sample plots were placed at twenty-meter intervals along the transects, with additional plots in segments showing obvious contour and/or vegetation changes. Thirty-eight plots were sampled at Samoa, 31 at Eureka Slough, 28 at Mad River Slough, 28 at Elk River, and 23 at Jacoby Creek.

At each plot, vegetation characteristics were assessed within a one-square-meter area defined by a portable quadrat frame. All plant species occurring inside the frame were recorded and their percent cover estimated visually. Cover is defined as the vertical projection of the species crown area to the ground surface. Cover is considered to have greater ecological significance as a measure of plant distribution than density or frequency of individuals (Mueller-Dombois and Ellenberg 1974). Visual estimates of cover were facilitated by the placement of central crossbars, breaking the frame into four 0.25-square-meter subsections. In addition, the arms of the frame and the crossbars were marked off in decimeters. Cover was

estimated to the nearest ten percent, with additional cover classes for species having one to five percent cover, and for those with less than one percent cover. Voucher specimens of all species were collected and filed at the Humboldt State University Herbarium. Taxonomic nomenclature used follows Smith and Sawyer (1986).

After vegetation characteristics were recorded, the center of each sample plot was marked with a wooden stake. In August, 1985, these points were surveyed with reference to the National Geodetic Vertical Datum (NGVD), using U. S. Coast and Geodetic Survey benchmarks as reference points (Table 4). Elevations were translated to a scale based on mean lower low water (MLLW), using National Ocean Service calculations for the relationship between NGVD and MLLW (Table 3).

No tidal records were available for the Jacoby Creek area. Based on distance from the bay entrance and circulation patterns within the Bay (Shapiro and Ass. 1980), records for the Mad River Slough station were considered the best estimates available of tidal conditions at the Jacoby Creek salt marsh. On three occasions in February, 1986 (under calm conditions), the height of high tide was monitored simultaneously at all study sites by using plastic tidepoles smeared with a water-sensitive, color-coded paste ("Kolor Kut"). Heights at the Mad River Slough and Jacoby Creek sites were within

TABLE 4. United States Coast and Geodetic Survey benchmarks used as reference points in surveying elevation at five salt marsh study sites in Humboldt Bay, California.

STUDY SITE	BENCHMARK	ELEVATION (ft. NGVD)
Samoa	# Z 1091 1967	12.35
Mad River Slough	# J 735 1970	11.68
Jacoby Creek	# G 75 1955	8.91
Eureka Slough	# J 75 1942	22.03
Elk River Slough	# S 1087 1967	9.51

0.1 foot of each other on all three occasions. Variations among the other sites were consistent with the figures established by NOS.

Analysis

Data were interpreted using direct gradient analysis, cluster analysis and discriminant analysis. Direct gradient analysis is a form of ordination; cluster and discriminant analyses are forms of classification. Ordination and classification techniques are often combined as complementary tools in the description and explanation of vegetation patterns (Whittaker 1973, Gauch 1982).

In direct gradient analysis (Whittaker 1967, 1973), the samples were arranged according to their position on the tidal elevation gradient. Sample plots were grouped into 0.25-foot elevation classes. Within each elevation class, mean percent cover and percent frequency were calculated for each species.

The samples were grouped on the basis of floristic similarity in cluster analysis, carried out in the computer program package CLUSTAN (Wishart 1978). The plots were clustered by Ward's method of hierarchical fusion (Ward 1963), using a squared Euclidean distance matrix as demonstrated by Wishart (1969). This method is designed to minimize the loss of information in passing

from each level of the hierarchy to the next. At each stage in the fusion process, the objective is to join whichever two clusters have the least variance between them, as measured by squared Euclidean distance. Euclidean distance is called a dissimilarity coefficient because it measures distances apart, but fundamentally it fulfills the same function as a similarity coefficient. The only distinction between dissimilarity and similarity coefficients is in which direction the scale runs (Clifford and Stephenson 1975, Romesburg 1984).

Two objectives were achieved by means of discriminant analysis, using the SPSS computer program, procedure DISCRIMINANT (Hull and Nie 1981). First, discriminant analysis was used to measure the validity of the classification derived by cluster analysis, through a procedure outlined in Romesburg (1984). A discriminant function was developed using the floristic attributes of the plots as independent variables and the class memberships given by cluster analysis as the dependent variable. The percentage of plots placed by the discriminant function into the same classes as by the cluster analysis is a measure of secondary validity for the classification.

Second, using the same class memberships as the dependent variable, tidal elevation data were submitted as the independent variable. The percentage of class

memberships correctly identified indicates how well the vegetation classes can be delineated on the basis of tidal elevation.

RESULTS

Direct Gradient Analysis

Elevations sampled at the Elk River study site were notably lower than at any of the four North Bay sites. Salt marsh vegetation was found between 3.9 and 6.1 ft. MLLW at Elk River and between 5.7 and 8.4 ft. MLLW in North Bay (Table 5). Tidal data collected at Elk River were excluded from general tide analyses because of the site's uniqueness.

Twenty-two vascular plant species were encountered in the study (Appendices A and B). Seventeen species were recorded at the Jacoby Creek site, 16 species at the Samoa site, 15 species at the Eureka Slough site, 15 species at the Elk River site, and 14 species at the Mad River Slough site. Ten species were common to all five sites, and five species were recorded at only one of the five sites.

Orthocarpus castillejoides var. humboldtiensis appeared in samples only at Jacoby Creek, Deschampsia caespitosa only at Elk River, and the three species Carex lynqbyei, Scirpus maritimus and Juncus lesueurii only at Samoa (Table 5).

The North Bay samples were grouped into ten 0.25-ft. elevation classes (Table 6). Most samples occurred at intermediate elevations. Species composition and abundance changed with elevation (Fig. 4). Salicornia

TABLE 5. Distribution of salt marsh plants by elevation at five study sites in Humboldt Bay, California, July-August, 1985. Species ranges at the four North Bay sites were combined to provide a composite list. Ranges are in ft. MLLW.

	NORTH HUMBOLDT BAY STUDY SITES				NORTH BAY (composite)	ELK RIVER
	SAMOA	MAD R. SLOUGH	JACOBY CREEK	EUREKA SLOUGH		
<i>Salicornia virginica</i>	5.7-7.5	6.4-7.7	5.9-8.4	6.4-7.9	5.7-8.4	3.9-6.1
<i>Spartina densiflora</i>	5.9-7.7	6.1-7.7	5.9-7.6	6.4-7.9	5.9-7.9	3.9-6.1
<i>Jaumea carnosa</i>	6.5-7.4	7.1-7.7	7.1-8.4	7.0-7.9	6.5-8.4	4.7-5.6
<i>Triglochin maritimum</i>	6.5-7.7	7.1-7.4	6.3-8.4	7.4-7.5	6.3-8.4	3.9-4.9
<i>Triglochin concinnum</i>	7.0-7.3	7.1-7.7	7.7-8.4	7.4-7.8	7.0-8.4	---
<i>Spergularia canadensis</i>	7.2-7.4	7.1	---	7.5-7.7	7.1-7.7	---
<i>Cordylanthus maritimus</i> ssp. <i>palustris</i>	7.0-7.4	7.4	7.7-8.4	7.5-7.8	7.0-8.4	5.4
<i>Atriplex patula</i> ssp. <i>hastata</i>	7.0-7.4	7.4	7.9	7.7-7.8	7.0-7.9	4.9-5.0
<i>Distichlis spicata</i>	7.0-7.4	7.1-7.7	6.6-8.4	7.4-7.8	6.6-8.4	4.3-6.1
<i>Limonium californicum</i>	7.0-7.3	7.1	7.7-8.4	7.4-7.8	7.0-8.4	5.6
<i>Plantago maritima</i> var. <i>juncoides</i>	7.2-7.3	7.7	7.7-8.2	7.5-7.8	7.2-8.2	5.4
<i>Cuscuta salina</i>	7.2-7.4	7.7	8.4	7.8	7.2-8.4	5.4

Table 5. Elevation ranges of salt marsh species, in ft. MLLW (continued).

	NORTH HUMBOLDT BAY STUDY SITES				NORTH BAY (composite)	ELK RIVER
	SAMOA	MAD R. SLOUGH	JACOBY CREEK	EUREKA SLOUGH		
<i>Carex lyngbyei</i>	7.4-7.7	---	---	---	7.4-7.7	---
<i>Grindelia stricta</i> <i>ssp. blakei</i>	---	---	7.4-8.4	7.5-7.8	7.4-8.4	4.7-6.0
<i>Scirpus cernuus</i> <i>ssp. californicus</i>	7.5	---	7.7-7.9	---	7.5-7.9	---
<i>Spergularia macrotheca</i>	---	7.7	7.6-8.4	---	7.6-8.4	5.6
<i>Scirpus maritimus</i>	7.7	---	---	---	7.7	---
<i>Juncus lesueurii</i>	7.7	---	---	---	7.7	---
<i>Parapholis</i> spp.	---	---	7.7-7.9	7.8	7.7-7.9	5.4
<i>Orthocarpus castillejoides</i> <i>var. humboldtiensis</i>	---	---	7.7-8.4	---	7.7-8.4	---
<i>Deschampsia caespitosa</i>	---	---	---	---	---	4.9-5.0
TOTAL RANGE SALT MARSH	5.7-7.7	6.1-7.7	5.9-8.4	6.4-7.9	5.7-8.4	3.9-6.1
NUMBER OF SPECIES	16	14	17	15	22	15
NUMBER OF SAMPLES	38	28	23	31	120	28

TABLE 6. Elevation classes used in direct gradient analysis of the North Humboldt Bay samples.

ELEVATION (ft. MLLW)		
RANGE	MIDPOINT	NUMBER OF SAMPLES
5.75-6.00	5.88	2
6.01-6.25	6.13	6
6.26-6.50	6.38	7
6.51-6.75	6.63	13
6.76-7.00	6.88	9
7.01-7.25	7.13	31
7.26-7.50	7.38	26
7.51-7.75	7.63	16
7.76-8.00	7.88	8
8.01-8.40	8.20	2
		TOTAL: 120

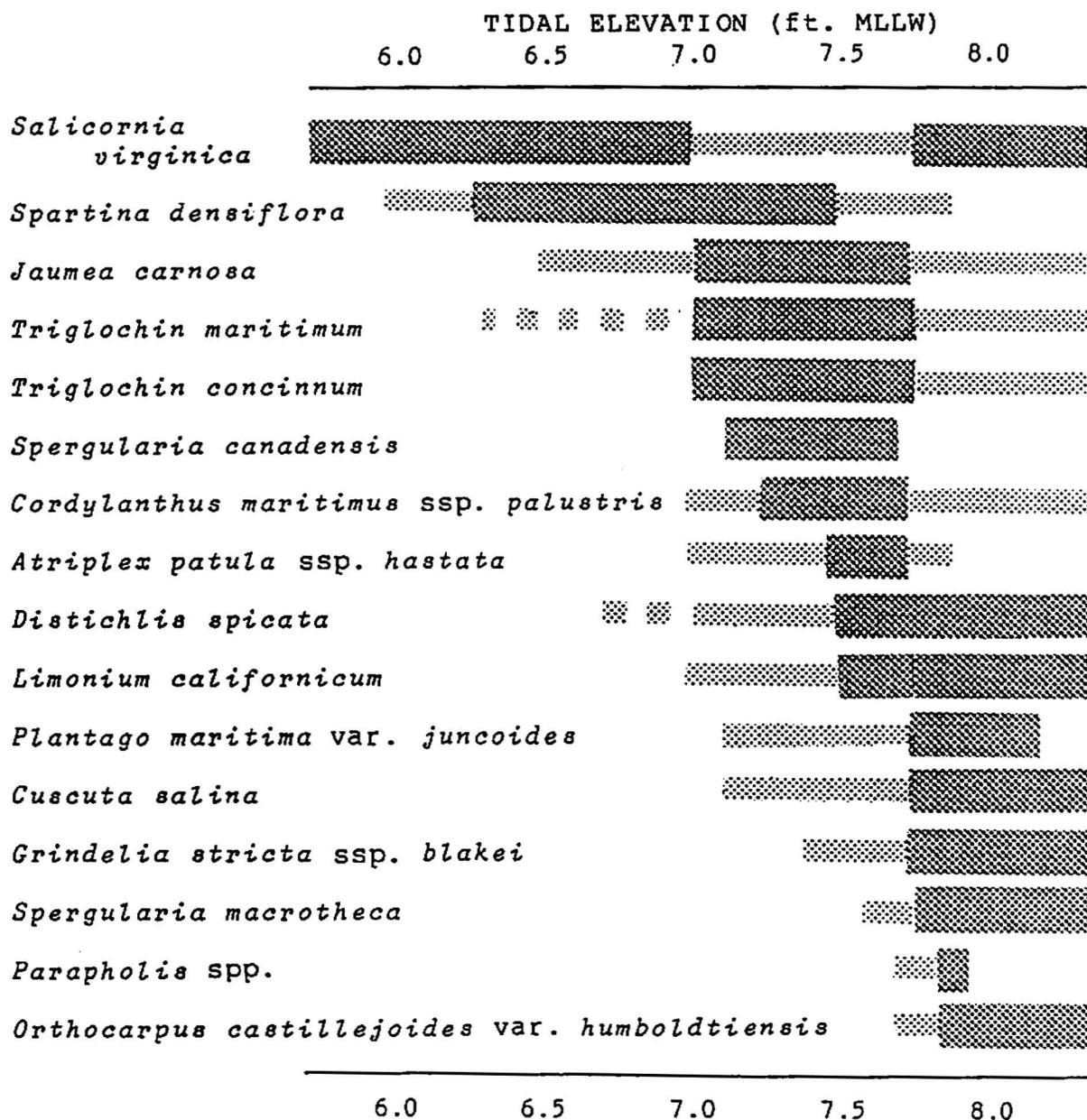


FIGURE 4. Distribution of major salt marsh plant species across the tidal elevation gradient in North Humboldt Bay, California. Wider bands indicate the range in which each species had its peak cover, as assessed within 0.25-foot elevation classes. Broken bands indicate sporadic occurrence.

virginica (pickleweed), a low-growing succulent, extended to the lowest elevation and had the broadest elevation range of any species. It was found throughout the entire range of tidal elevations sampled (Table 5). Salicornia was more abundant at the low and high ends of its elevation range than at mid-levels, as indicated by its bimodal cover and frequency curves (Figs. 4 and 5).

The decline of Salicornia at intermediate elevations corresponded with a peak in the abundance of Spartina densiflora (cordgrass). The tall, coarse grass extended almost as low as Salicornia, but had less cover at low elevations. At high marsh elevations, the frequency and cover of Spartina dropped off as those of Salicornia rose (Table 5, Figs. 4 and 5).

Distichlis spicata (saltgrass) occurred sporadically at the lower end of its range, and its frequency and cover increased steadily with elevation. Jaumea carnososa, a trailing succulent, occupied an elevation range similar to that of Distichlis, but Jaumea reached its peak cover and frequency lower, declining slightly at the highest marsh elevations (Table 5, Figs. 4 and 6).

Two species of arrowgrass, Triglochin maritimum (common arrowgrass) and T. concinnum (slender arrowgrass) occur in Humboldt Bay. Triglochin maritimum extended to a lower tidal elevation, though with sporadic occurrence. Both species occurred at high marsh elevations, and were

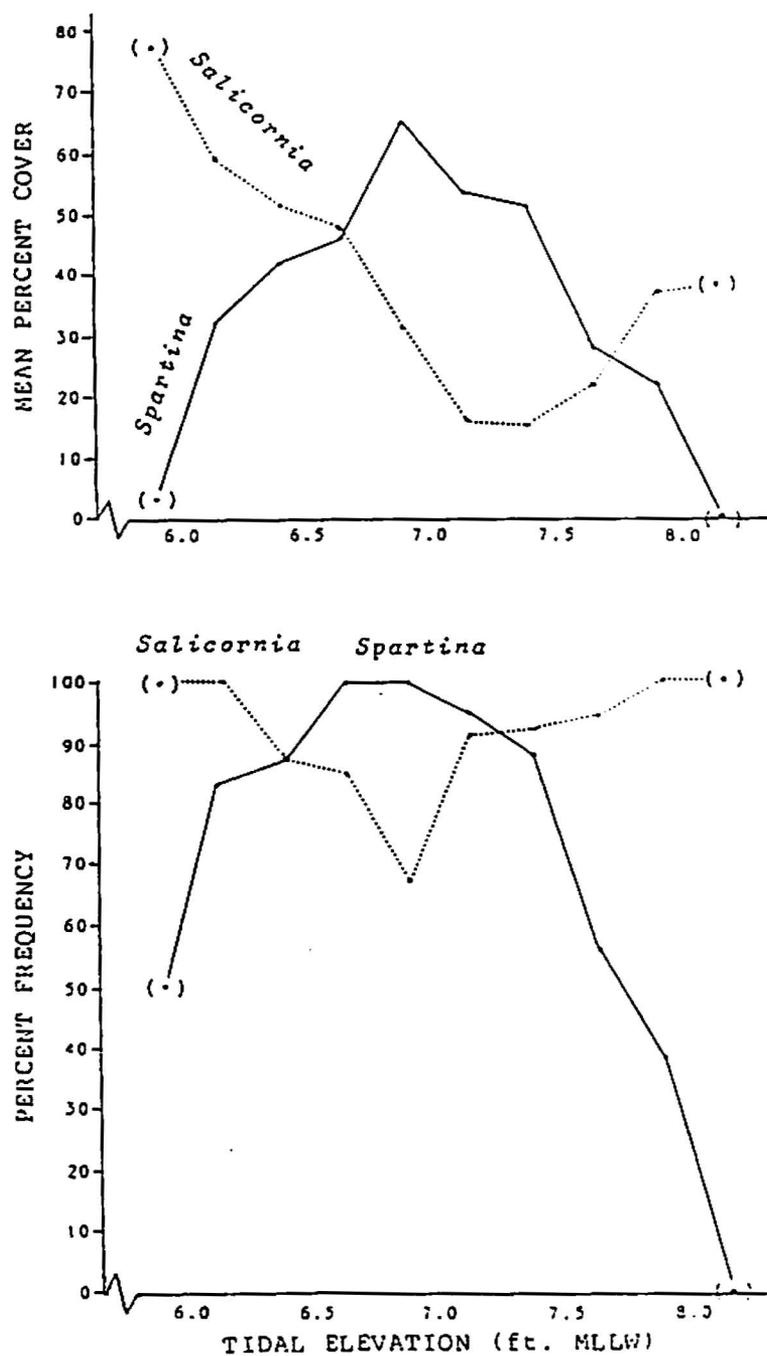


FIGURE 5. Cover and frequency of Salicornia virginica and Spartina densiflora over the tidal elevation gradient in North Humboldt Bay, California, based on 0.25-foot elevation classes. The decline of Salicornia at intermediate elevation corresponded with peaks in the cover and frequency of Spartina. Points based on less than five samples are in parentheses.

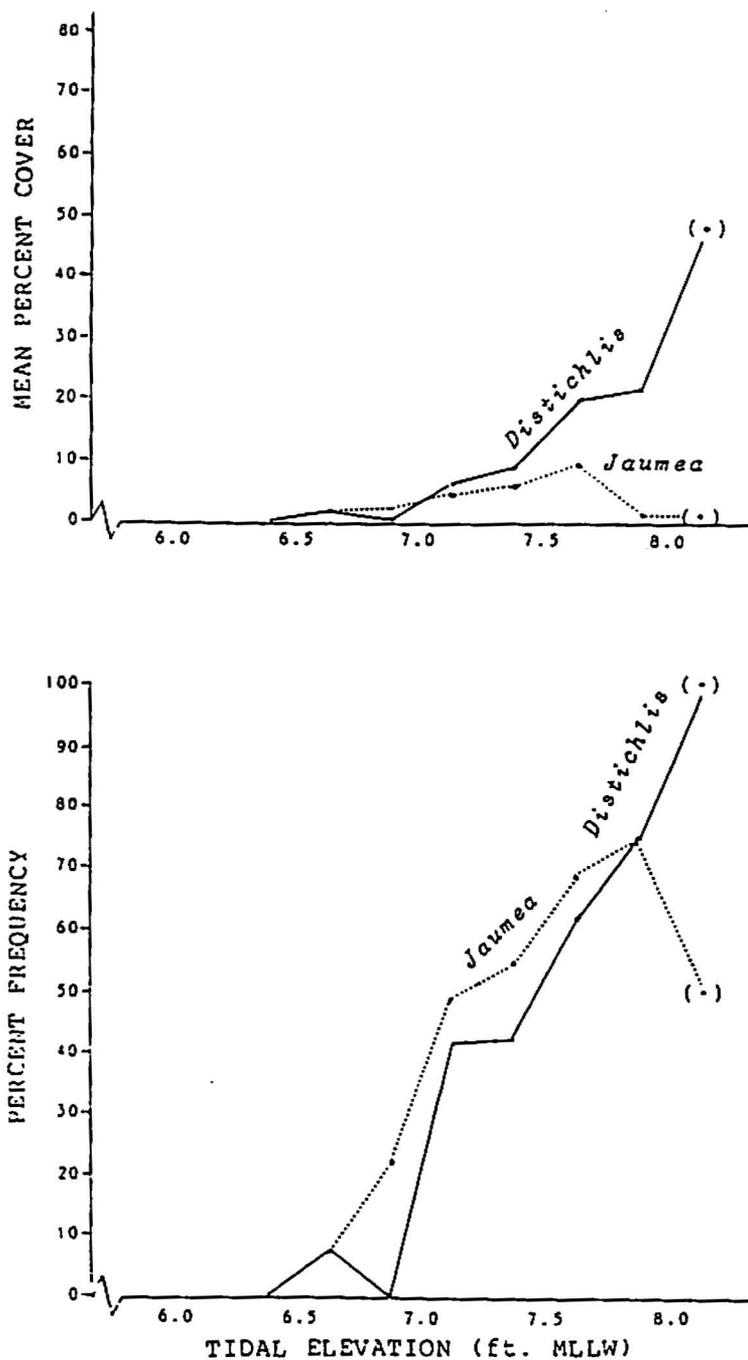


FIGURE 6. Cover and frequency of *Distichlis spicata* and *Jaumea carnosa* over the tidal elevation gradient in North Humboldt Bay, California, based on 0.25-foot elevation classes. The two species had similar ranges, but *Jaumea* reached its peak cover and frequency lower than *Distichlis*. Points based on less than five samples are in parentheses.

roughly equivalent in terms of frequency and cover (Table 5, Figs. 4 and 7).

The three rare salt marsh plant species in Humboldt Bay were all associated with high elevation marshes. Cordylanthus maritimus ssp. palustris (Point Reyes bird's beak) was found at all of the study sites, occurring at elevations of 7.0 ft. MLLW or higher in North Bay, and at 5.4 ft. MLLW at Elk River. Orthocarpus castillejoides var. humboldtensis (Humboldt Bay owl's clover) was encountered only at Jacoby Creek, and only at elevations of 7.7 ft. MLLW or higher. Grindelia stricta ssp. blakei (Humboldt Bay gumplant), in samples at three sites, occurred at elevations over 7.4 ft. MLLW in North Bay, and over 4.7 ft. MLLW at Elk River (Table 5, Figs. 4 and 8). None of the three species had more than one percent cover within any elevation class. Within a single one-square-meter plot, cover was as high as five percent for each Cordylanthus and Orthocarpus, both small annuals. General observations indicated that sampling conducted earlier in the growing season of Orthocarpus might have yielded slightly higher cover estimates than those reported here. Grindelia, a woody perennial, had as high as twenty percent cover within a single plot.

None of the remaining species had greater than five percent cover within any elevation class. Generally, these species were restricted to elevations over 7.0 ft.

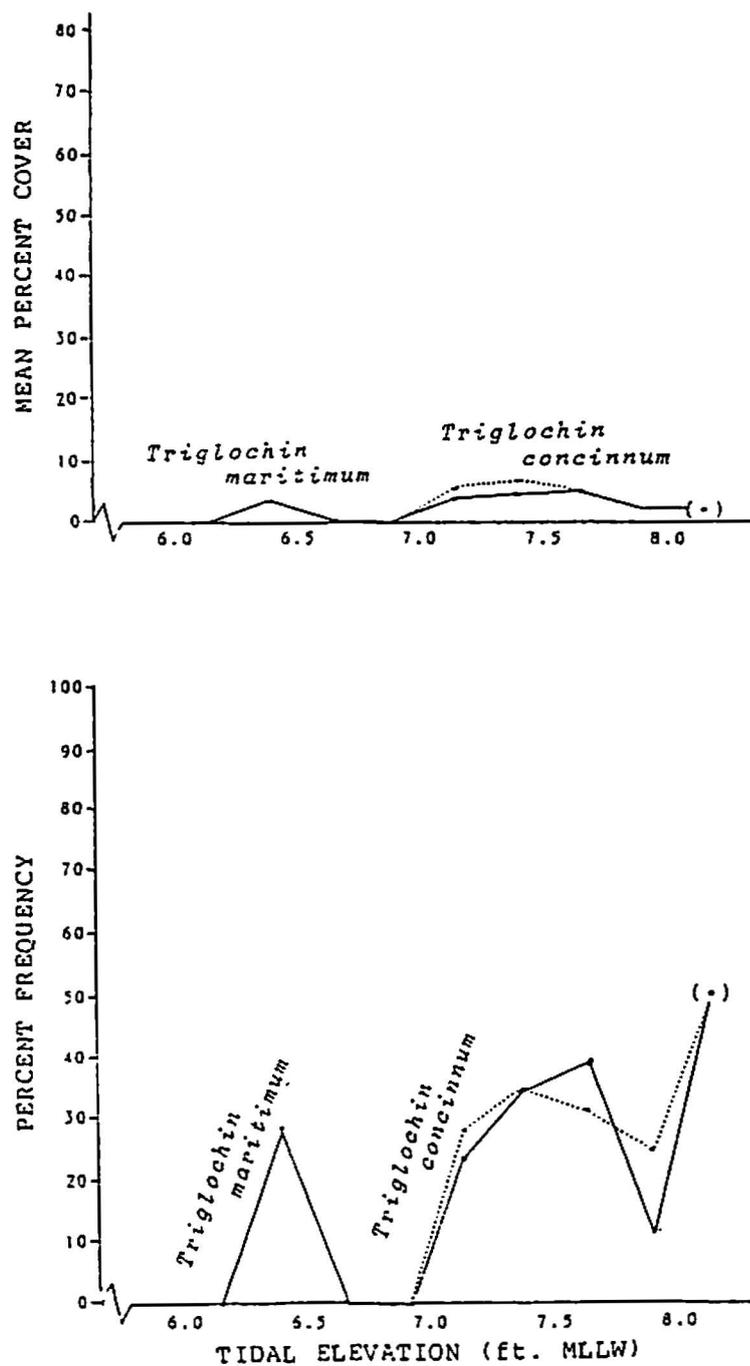


FIGURE 7. Cover and frequency of *Triglochin maritimum* and *Triglochin concinnum* over the tidal elevation gradient in North Humboldt Bay, California, based on 0.25-foot elevation classes. *T. maritimum* extended lower than *T. concinnum*, but with sporadic occurrence. At high elevations, the two species had roughly comparable cover and frequency. Points based on less than five samples are in parentheses.

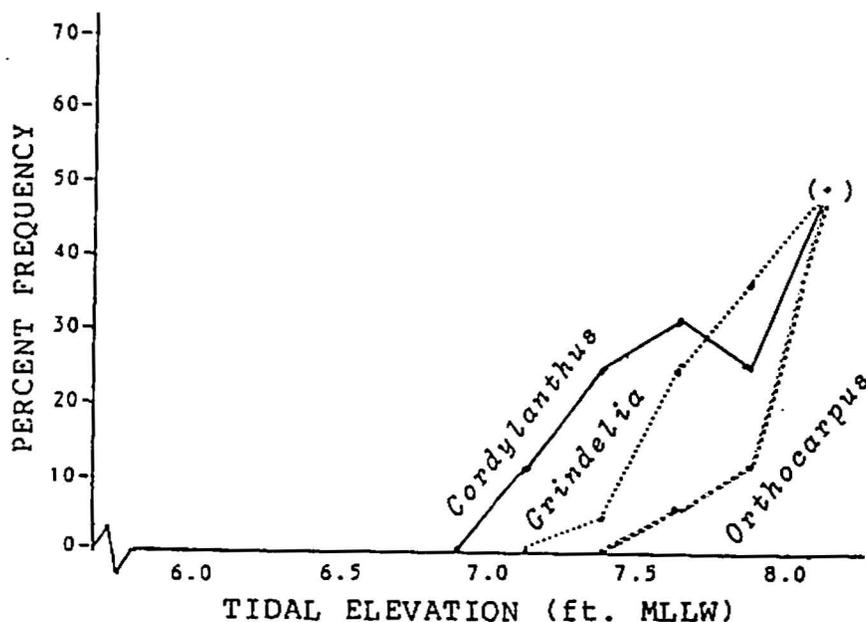


FIGURE 8. Frequency of three rare salt marsh plant species over the tidal elevation gradient in North Humboldt Bay, California, based on 0.25-foot elevation classes. Orthocarpus castillejoides var. humboldtiensis, Cordylanthus maritimus ssp. palustris and Grindelia stricta ssp. blakei all increased in frequency with elevation. Orthocarpus had the lowest frequency, as it was sampled at only one study site. None of the three species had greater than one percent mean cover within any elevation class. Points based on less than five samples are in parentheses.

MLLW in North Bay and over 4.7 ft. MLLW at Elk River, and they all tended to increase in abundance with elevation (Table 5, Fig. 4).

Cluster Analysis

The samples were grouped on the basis of floristic similarity, using cluster analysis, into three major vegetation types (Fig. 9). Salicornia virginica, Spartina densiflora, Distichlis spicata, Jaumea carnosa and Triglochin maritimum were present in all three marsh types, but with markedly different levels of abundance (Fig. 10, Tables 7 and 8). The groups can be characterized as:

- A. Salicornia marsh.
- B. Spartina marsh.
- C. Mixed marsh.

The 36 samples classified as Salicornia marsh and the 53 samples classified as mixed marsh were more alike one another floristically than either group was to the 59 samples classified as Spartina marsh (Fig. 9). The mixed marsh type had a higher species diversity than either Salicornia or Spartina marsh types, both in terms of species richness and relative cover. Salicornia marsh had only five species. Two of these, Salicornia and Spartina, together occupied over 95 percent cover. Spartina marsh had ten species, but again about 95 percent cover was

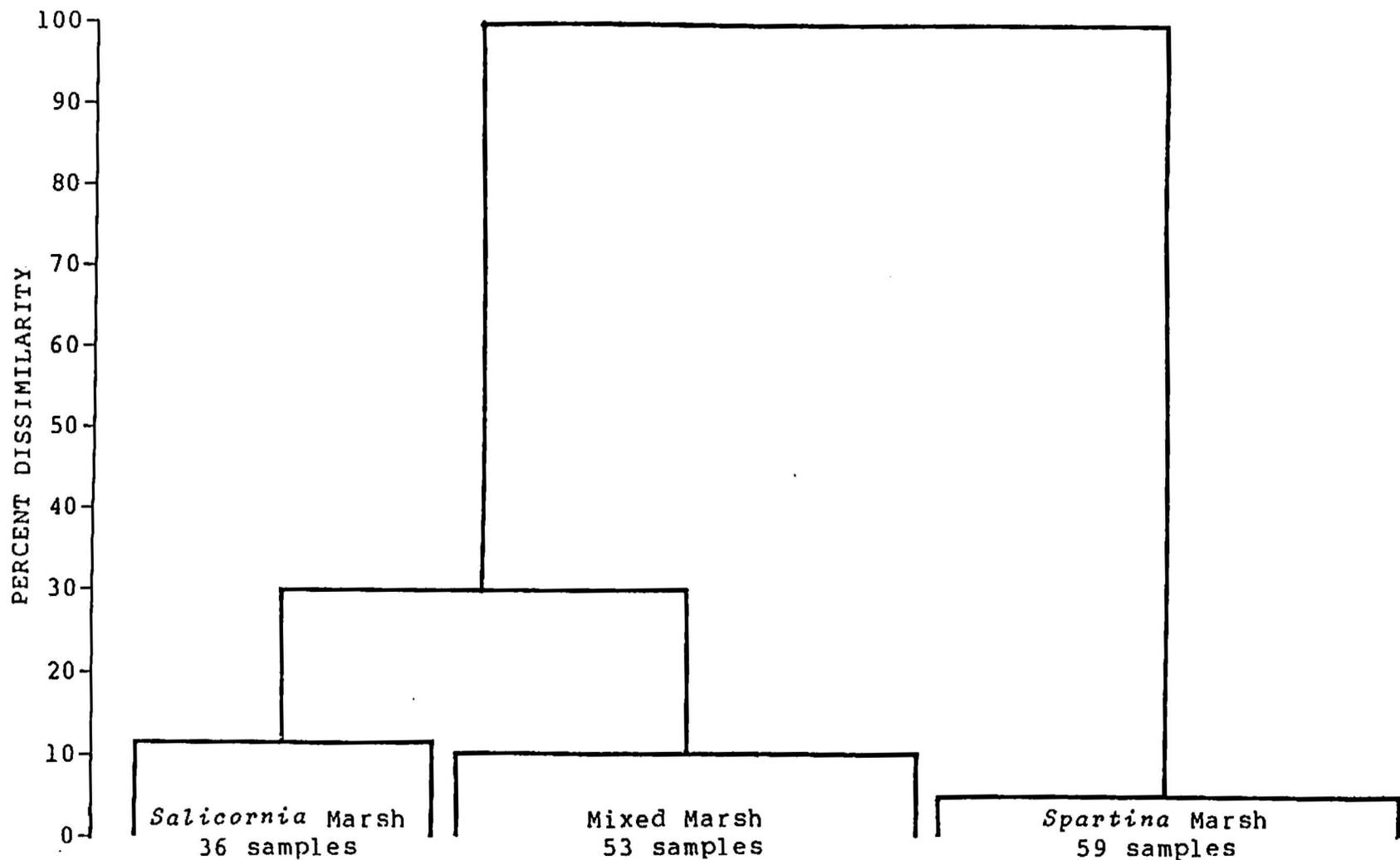


FIGURE 9. The samples were grouped on the basis of floristic similarity, through cluster analysis, into three major types: Salicornia marsh, Spartina marsh and mixed marsh. The samples representing the Spartina marsh type were floristically distinct from all other samples. In relation to this level of distinction, the Salicornia and mixed marsh types were more alike, and all three marsh types demonstrated high levels of within-group similarity.

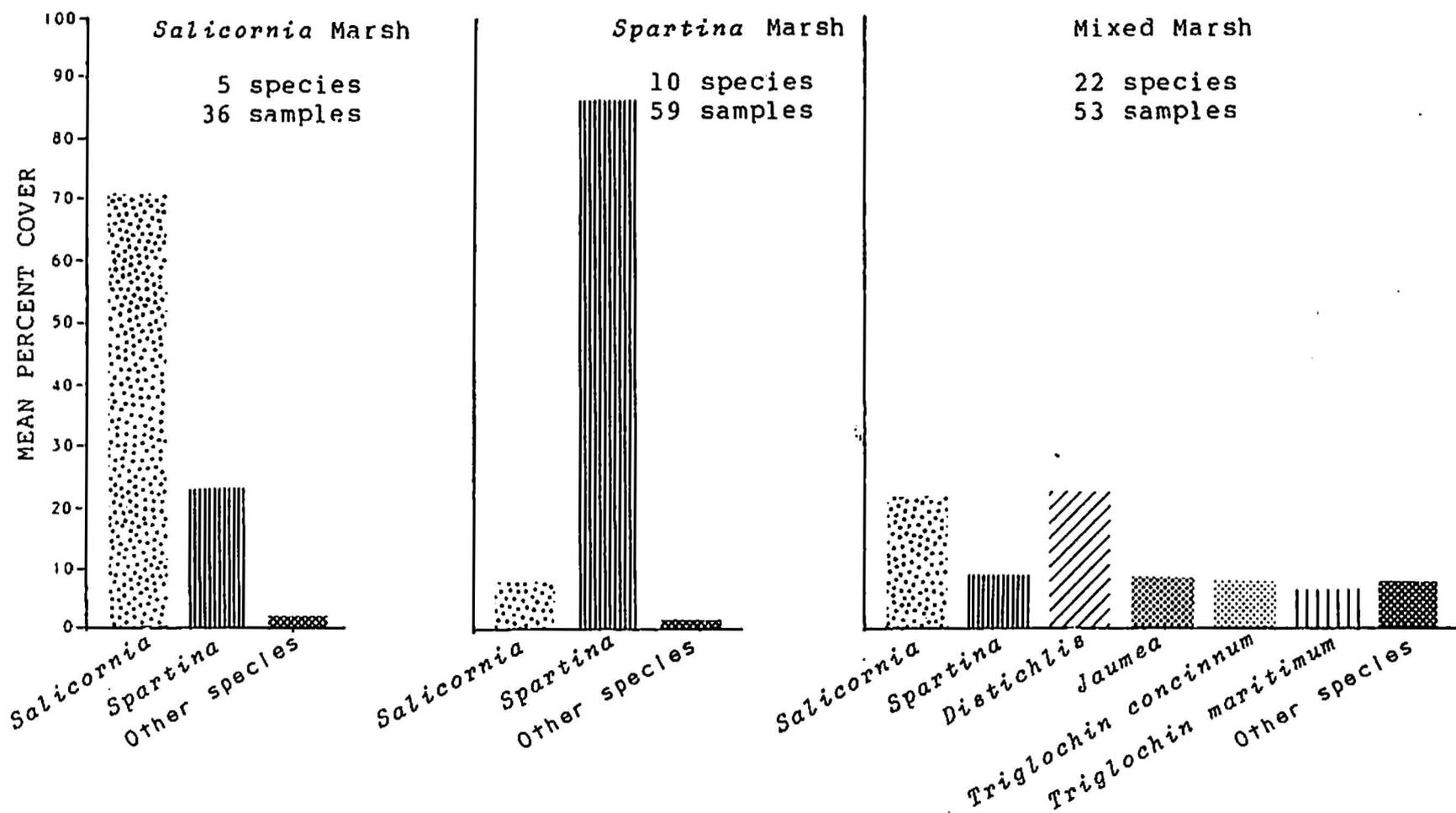


FIGURE 10. Cover of dominant species within each of three salt marsh types, in Humboldt Bay, California.

TABLE 7. Cover of species in three salt marsh types.

MARSH TYPE: NUMBER OF SAMPLES:	PERCENT COVER: MEAN (RANGE)		
	<i>Salicornia</i>	<i>Spartina</i>	<i>Mixed</i>
	36	59	53
<i>Salicornia virginica</i>	70.6 (40-100)	7.7 (0-40)	21.5 (0-50)
<i>Spartina densiflora</i>	23.3 (0-50)	87.0 (30-100)	9.1 (0-50)
<i>Distichlis spicata</i>	X (0-10)	X (0-10)	22.0 (0-80)
<i>Jaumea carnosa</i>	X (0-10)	X (0-5)	8.4 (0-50)
<i>Triglochin maritimum</i>	1.1 (0.10)	X (0-10)	6.5 (0-50)
<i>Triglochin concinnum</i>		X (0-5)	7.8 (0-60)
<i>Atriplex patula</i> ssp. <i>hastata</i>		X (0-1)	X (0-30)
<i>Limonium californicum</i>		X (0-1)	2.3 (0-30)
<i>Grindelia stricta</i> ssp. <i>blakei</i>		X (0-10)	X (0-20)
<i>Deschampsia caespitosa</i>		X (0-5)	X (0-10)
<i>Cordylanthus maritimus</i> ssp. <i>palustris</i>			X (0-5)
<i>Plantago maritima</i> var. <i>juncoides</i>			X (0-10)
<i>Cuscuta salina</i>			X (0-20)
<i>Spergularia canadensis</i>			X (0-5)
<i>Spergularia macrotheca</i>			X (0-5)
<i>Parapholis</i> spp.			X (0-10)
<i>Orthocarpus castillejoides</i> var. <i>humboldtiensis</i>			X (0-5)
<i>Scirpus cernuus</i> ssp. <i>californicus</i>			X (0-5)
<i>Scirpus maritimus</i>			X (0-1)
<i>Carex lyngbyei</i>			X (0-50)
<i>Juncus lesueurii</i>			X (0-1)

X = Present, with less than one percent mean cover.

TABLE 8. Frequency of species in three salt marsh types.

MARSH TYPE: NUMBER OF SAMPLES:	PERCENT FREQUENCY		
	<i>Salicornia</i> 36	<i>Spartina</i> 59	<i>Mixed</i> 53
<i>Salicornia virginica</i>	100.0	81.4	96.3
<i>Spartina densiflora</i>	91.7	100.0	61.1
<i>Distichlis spicata</i>	8.3	10.2	79.6
<i>Jaumea carnosa</i>	11.1	20.3	70.4
<i>Triglochin maritimum</i>	19.4	13.6	46.3
<i>Triglochin concinnum</i>		3.4	46.3
<i>Atriplex patula</i> ssp. <i>hastata</i>		3.4	11.1
<i>Limonium californicum</i>		1.7	38.9
<i>Grindelia stricta</i> ssp. <i>blakei</i>		1.7	22.2
<i>Deschampsia caespitosa</i>		1.7	1.9
<i>Cordylanthus maritimus</i> ssp. <i>palustris</i>			42.6
<i>Plantago maritima</i> var. <i>juncoides</i>			27.8
<i>Cuscuta salina</i>			16.7
<i>Spergularia canadensis</i>			16.7
<i>Spergularia macrotheca</i>			11.1
<i>Parapholis</i> spp.			7.4
<i>Orthocarpus castillejoides</i> var. <i>humboldtiensis</i>			5.6
<i>Scirpus cernuus</i> ssp. <i>californicus</i>			5.6
<i>Scirpus maritimus</i>			1.9
<i>Carex lyngbyei</i>			1.9
<i>Juncus lesueurii</i>			1.9

attributable to the same two species: Spartina and Salicornia. Twelve species were unique to the mixed marsh type, with a total of 22 species. Overall no single species had greater than 25 percent cover, and six species had between five and 25 percent cover in the mixed marsh type (Fig. 10, Table 7).

In the Salicornia marsh type, Salicornia was present in 100 percent of the samples, with a mean cover of 70.6 percent (Tables 7 and 8). Dense pickleweed mats, two to three decimeters high, commonly bordered tidal channels and intertidal flats where the slope was gradual. Individual tussocks of Spartina were often interspersed among the pickleweed mats. Occasionally Jaumea, Distichlis or Triglochin maritimum were found in this marsh type, but with minimal cover. The number of species per sample ranged from one to four.

In the Spartina marsh type, Spartina was present in 100 percent of the samples, with a mean cover of 87.0 percent (Tables 7 and 8). The stiff cordgrass formed thick, nearly homogenous stands six to ten decimeters high. Salicornia was scattered sparsely in the understory, growing in an elongate form. The other eight species listed as occurring in this marsh type were generally associated with the occasional openings in cordgrass stands or along the margins of the stands. The number of species per sample ranged from one to six.

In the mixed marsh type, Distichlis and Salicornia were co-dominants. Although Salicornia was more widely dispersed, the two species were approximately equivalent in terms of cover, with Distichlis tending to form thick cover in spots. Salicornia had a 96.3 percent frequency with 21.5 percent mean cover, and Distichlis had a 79.6 percent frequency with 22.0 percent mean cover (Tables 7 and 8). Generally the mixed marsh appeared as a low-growing meadow of grasses, succulents and small herbs, with occasional taller plants. The number of species per sample ranged from three to eleven. Jaumea was commonly interspersed in these meadows, but with less cover than either of the two dominants. Occasionally Jaumea formed pure, dense cover in small patches, typically within slight depressions. Spartina occurred in the mixed marsh type, but with less regularity and less cover than in either of the other two marsh types. In the mixed marsh, Spartina individuals tended to be shorter and less vigorous, appearing stunted in form. Both species of arrowgrass occurred in the mixed marsh type. Triglochin maritimum tended to grow in dense tufts up to one meter tall. The shorter, more delicate T. concinnum was commonly interspersed with Salicornia and Jaumea.

The three rare plant species Cordylanthus maritimus ssp. palustris, Orthocarpus castillejoides var. humboldtiensis and Grindelia stricta ssp. blakei were all

found primarily in the mixed marsh type. Orthocarpus blooms early in the spring, forming large pink patches in some areas. I found a white form of Orthocarpus near Jacoby Creek, also noted by Newton (1986b) as occurring in Second Slough, Eureka. Orthocarpus was found typically in open areas where Spartina was either absent or occurred as small individuals with low coverage. Orthocarpus was associated most frequently with Salicornia, Triglochin concinnum, Jaumea and Distichlis. Cordylanthus occurred in the same type of association, but it did not form large patches like Orthocarpus. Cordylanthus blooms in late spring to early summer. Grindelia was distributed within a wider range of plant associations. It was found growing on the edges of Spartina stands and on the sides of dikes with Deschampsia caespitosa (tufted hairgrass), as well as within Salicornia - Distichlis - Jaumea meadows.

Scattered throughout these low-growing meadows were individuals of Limonium californicum (sea lavender) and Plantago maritima var. juncoides (sea plantain). Two species of sand spurrey were present. The tiny annual Spergularia canadensis was typically associated with Triglochin concinnum, Salicornia and Jaumea. Spergularia macrotheca, a more stout perennial, tended to occur in slightly higher, drier sites with Distichlis and Salicornia. Cuscuta salina (marsh dodder), an orange, vine-like plant, was found parasitizing Salicornia and

occasionally other species in high elevation marshes. Scirpus cernuus ssp. californicus (slender clubrush) occurred infrequently and with low cover in the mixed marsh type. Atriplex patula ssp. hastata, an exotic annual from Europe, occurred irregularly within the study marshes, exhibiting more vigorous growth in bordering disturbed areas.

Two species of sea hard-grass occurred, but they were not distinguished in the field, and results are here presented for the two together as Parapholis spp. Until the recent discovery of P. strigosa in Humboldt Bay by T.P. Worley (pers. comm. 1986) P. incurva was the only member of the genus reported in North America. Both species are native to Europe, and they are distinguished primarily on the basis of anther size.

Scirpus maritimus (saltmarsh bulrush), Juncus lesueurii (salt rush) and Carex lyngbyei (Lyngby's sedge) were found growing in patches in the upper margin of salt marsh at Samoa. Although not sampled elsewhere, these three species were observed near other study sites, often in association with one another. All three species are characteristically associated with brackish conditions.

Discriminant Analysis

Discriminant analysis provided a secondary validation for the preceding classification. A discriminant function

developed on the basis of the floristic attributes of the samples placed 98.7 percent of the samples into the same groups as the cluster analysis.

The floristic classification could best be described by differences in the abundances of Spartina, Salicornia and Distichlis. On the basis of cover data for these three species alone, 95.3 percent of the samples were placed into the same groups as established by cluster analysis.

A weak correlation between tidal elevation and marsh type was indicated by discriminant analysis. Using North Bay data, a discriminant function developed solely on the basis of tidal elevation placed 60.0 percent of the samples into the same groups as the cluster analysis (Table 9). Sampling intensity at Elk River was considered inadequate for accurate evaluation of the relationship between vegetation patterns and elevation.

Supplied with the elevation data for the North Bay samples, the DISCRIMINANT program formulated a basic prediction:

- Below 6.9 ft. MLLW,
the marsh type is Salicornia.
- Between 6.9 and 7.3 ft. MLLW,
the marsh type is Spartina.
- Over 7.3 ft. MLLW,
the marsh type is mixed.

TABLE 9. Results of discriminant analysis for North Humboldt Bay, California, showing the number of samples predicted in each salt marsh type on the basis of tidal elevation in relation to the class memberships derived by cluster analysis on the basis of floristic similarity, with correct predictions underlined. The total number of correct predictions was 72/120, or 60.0 percent.

FLORISTIC CLASSIFICATION		PREDICTION BASED ON TIDAL ELEVATION		
		<i>Salicornia</i> marsh	<i>Spartina</i> marsh	Mixed marsh
	<u>Class total</u>			
<i>Salicornia</i> marsh	29	<u>19</u>	4	6
<i>Spartina</i> marsh	48	10	<u>23</u>	15
Mixed marsh	43	1	12	<u>30</u>
TOTALS:	120	30	39	51

Of the 30 plots with elevations below 6.9 ft. MLLW, 63.3 percent (19/30) were correct predictions, i.e. they actually were Salicornia marsh. Spartina marsh occurred in 33.3 percent (10/30) of the low-elevation plots, and mixed marsh in 3.3 percent (1/30) of the plots. At intermediate elevations, between 6.9 and 7.3 ft. MLLW, 59.0 percent (23/39) of the plots were correctly predicted to be Spartina marsh, 10.3 percent (4/39) were actually Salicornia marsh, and 30.7 percent (12/39) actually mixed marsh. At higher elevations, over 7.3 ft. MLLW, 58.8 percent (30/51) of the plots were correctly predicted as mixed marsh, 11.8 percent (6/51) were Salicornia marsh and 29.4 percent (15/51) Spartina marsh (Table 9, Fig. 11).

The efficacy of the mean high water (MHW) tidal datum in predicting marsh type was also assessed. All elevations were converted to a scale of MHW = 0. Discriminant analysis revealed a 52.5 percent correct prediction rate for the MHW elevations, using North Bay data.

While there was overlap in their elevation ranges, each marsh type was most prevalent within a different elevation zone (Fig. 11). Salicornia marsh occurred primarily at low tidal elevations, Spartina marsh at intermediate elevations, and mixed marsh at high elevations. In North Bay, the mean elevation was 6.7 ft. MLLW (standard deviation: 0.56) for the Salicornia marsh

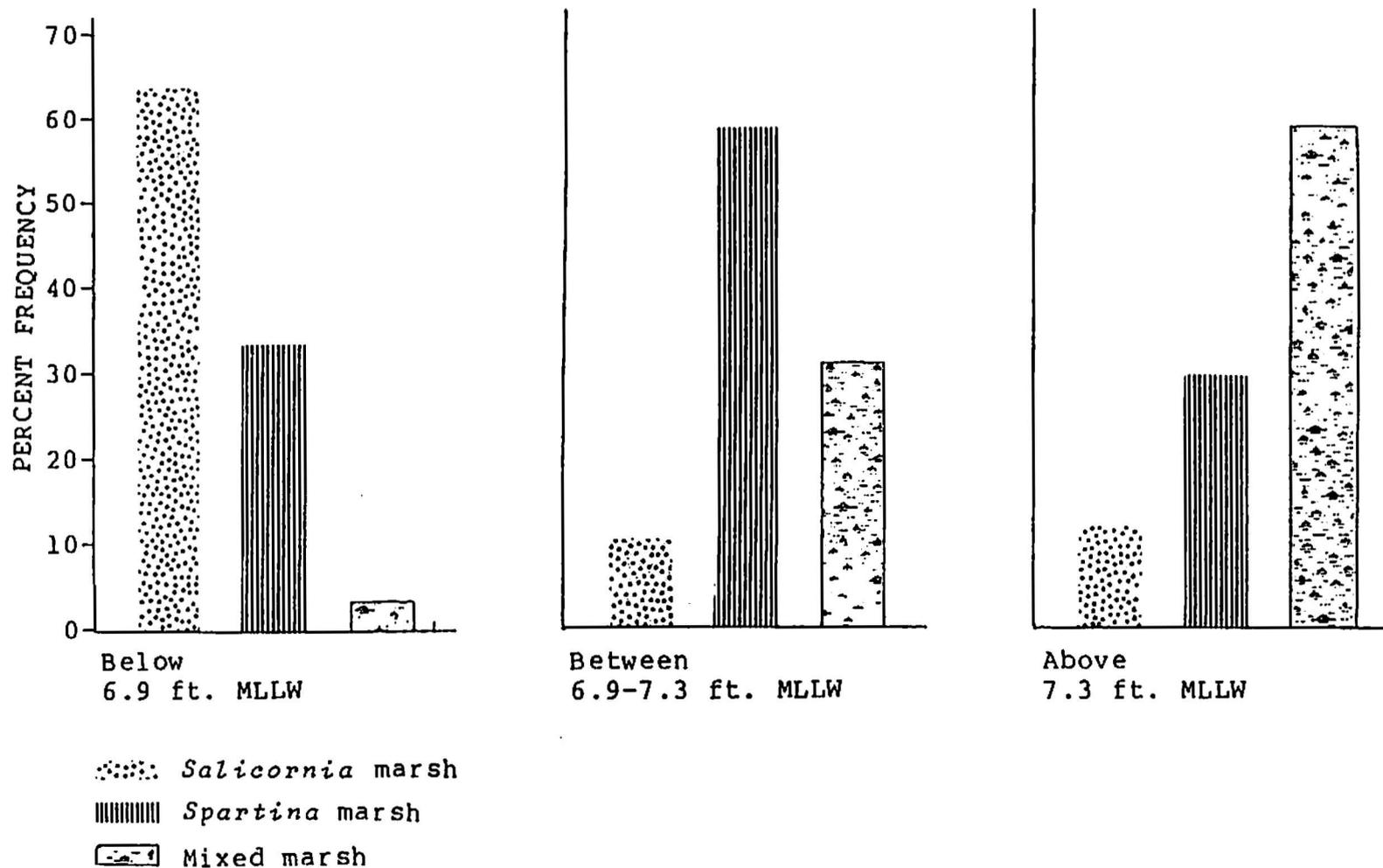


FIGURE 11. Frequency of three salt marsh types within different ranges of elevation in North Humboldt Bay, California. While there is overlap in their distribution, each marsh type is most common within a different range of tidal elevation.

type samples, 7.0 ft. MLLW (0.37) for the Spartina marsh type samples, and 7.4 ft. MLLW (0.41) for the mixed marsh type samples.

At the Samoa study site, the mixed marsh type occurred in a narrow band along the bayward margin of the marsh, on a bank 2.5 to 3.5 feet above the adjacent mudflats. About five meters from the marsh edge, the vegetation changed from the meadows of Salicornia, Jaumea, Triglochin concinnum and Distichlis to stands of Spartina. The transition was fairly abrupt, notable because of the change in plant height. The Spartina stands extended landward to the upper margin of the marsh, where the brackish species Carex lyngbyei, Juncus lesueurii and Scirpus maritimus occurred in small patches. The southern section of the study site was dominated by Salicornia mats which were visibly lower than the Spartina stands and generally separated from them by tidal channels.

The vegetation pattern was similar at Eureka Slough. Most of the marsh in this area was covered by thick stands of Spartina. The mixed marsh type occurred primarily on high banks bordering the mudflats. Salicornia mats occurred landward of the railroad tracks, in areas protected from wave attack and receiving tidal inundation by way of Eureka Slough.

At the Mad River Slough site, the mixed marsh type occurred on the dike remnants bordering the bay and along

the edge of the slough, bounded on the landward side by tidal channels. The marsh proper was a mosaic in which Spartina stands predominated and Salicornia mats occurred in open areas, typically bordering tidal channels.

At the Jacoby Creek site, the mudflat-marsh interface was a gradual slope rather than a steep bank. Salicornia was the primary colonist, occurring in small patches on the mudflat and gradually progressing to larger mats. Short individuals of Spartina also occurred along the mudflat edge. The Spartina marsh type was restricted to a narrow strip bordering a tidal channel that cut through the marsh roughly parallel to the shoreline. The Salicornia - Distichlis - Jaumea meadows representing the mixed marsh type were more extensive at this site than at any of the other areas sampled.

At the Elk River site, tall tufts of Triglochin maritimum occurred locally with Salicornia as colonizers of the mudflat. Spartina stands bordered the slough, with Grindelia and Deschampsia appearing in spots along the edge. The mixed marsh type occurred in small pockets bordering the adjacent sand dunes.

DISCUSSION

Zonation

Three major floristic types within Humboldt Bay salt marshes have been described in terms of species composition and abundance. Each marsh type was associated primarily with a different range of tidal elevation, but there were no distinct elevation demarcations between types. Salicornia virginica marsh was most common at low elevations, Spartina densiflora marsh at intermediate elevations and mixed marsh at high elevations. The Salicornia and Spartina marsh types were each represented by a single dominant. Both species also occurred in lesser abundance outside their zones of dominance. In this sense the vegetation pattern could be interpreted as a continuum, with individual species ranges overlapping across the elevation gradient and with the marsh types representing changes in species dominance.

In contrast to the uniformity of the Salicornia and Spartina marsh types, the mixed marsh type exhibited greater heterogeneity, with a number of species distributed in mosaic patterns. Variations in the dominance of certain species could be used as a basis for further subdivisions within this type, though no discrete associations were revealed by cluster analysis. Most salt marsh plants are perennials and many reproduce primarily

by vegetative means. This often results in patchy, irregular distributions. The uniformity of vegetation at low elevations with increasing diversity, complexity and variability at higher elevations is a common characteristic of salt marsh communities (Vogl 1966, Macdonald 1977a, Ewing 1983, Russel et al. 1985).

Cluster analysis did not reveal any patterns of clustering by site, as would be expected if any of the sites were floristically unique. Major species were present at all five sites. Each marsh type was represented at all sites, though with differences in abundance. The Jacoby Creek marsh was the only study site with large areas covered by the mixed marsh type and with minimal coverage by the Spartina marsh type. At the other four sites Spartina stands were a predominant feature and the occurrence of the mixed marsh was more restricted. The Elk River marsh was the only study site where large patches of Triglochin maritimum colonized the mudflats. This pattern is characteristic of Oregon coastal marshes, which tend to be brackish (Macdonald 1977b), and here may reflect the freshwater influence of Elk River.

Tidal Elevation

The tidal characteristics at Elk River were unique. The tidal range and mean tidal height here were several feet lower than in other areas of the bay, attributable to

Elk River's history of shoaling, sand bars and other topographic features (J.R. Hubbard pers. comm. 1986). As a result, salt marsh vegetation occurred within a lower elevation range at this site than elsewhere in Humboldt Bay (Table 5).

Generally, salt marsh vegetation extended slightly below the level of mean lower high water (MLHW). The lowest elevation recorded was 0.4 feet below MLHW at Jacoby Creek and 0.2 feet below MLHW at each Samoa and Mad River Slough. The lowest elevation recorded at Eureka Slough was 0.4 feet above MLHW, but I suspect that increased sampling intensity in this area would reveal salt marsh occurrence at lower elevations, with a low extent likely comparable to the other North Bay sites. At Eureka Slough, vegetation characteristic of low marsh was restricted to areas sheltered from erosive wave attack, and no samples were taken in these protected spots. The erosion occurring in Eureka Slough marshes is apparently related to alterations in the drainage of the Freshwater/Eureka Slough system. Diking of tidal channels and canal-dredging have reduced the load of sediment which once may have stabilized these marshes (Rogers 1981). At Elk River, the lowest elevation recorded was 0.2 feet above MLHW (Tables 3 and 5).

Overall, the lowest extent of salt marsh vegetation that I recorded was 3.9 ft. MLLW at Elk River and 5.7 ft.

MLLW in North Bay, at Samoa. Claycomb (1983) recorded a low point of 1.5 meters (4.9 feet) MLLW at his Bay Street (North Bay) salt marsh study site in 1981. In 1980 he surveyed the same point at 1.7 meters (5.4 feet) MLLW, and it was his only sample point below 1.8 meters (5.9 feet) MLLW.

The highest elevations recorded in this study should not be regarded as the upper limits of these species nor the potential upper extent of salt marsh vegetation in Humboldt Bay, since no natural marsh-upland transitions were available for sampling. At Elk River, there was a fairly abrupt transition from salt marsh to sand dune vegetation around 6.1 ft. MLLW. The study sites in North Bay were all abruptly terminated at their upper boundaries by dikes. The highest elevation I sampled in North Bay was 8.4 ft. MLLW, at the Jacoby Creek marsh. Claycomb (1983) reported salt marsh extending to 8.8 ft. MLLW, but his Bay Street study area in North Bay also lacked a natural marsh-upland transition. Investigators in other areas have reported salt marsh vegetation extending to the level of extreme high water (EHW) (Macdonald 1969, 1977a, Jefferson 1974, Macdonald and Barbour 1974). For most of North Bay, EHW is estimated at 10.5 ft. MLLW, and for Elk River at 9.0 ft. MLLW. (National Ocean Service 1981-1985). Harvey et al. (1978) reported that the upper limit of California salt marshes occurs at about three

feet above mean high water (MHW), which would be at about 9.5 to 10.0 ft. MLLW for North Bay, and at about 7.5 ft. MLLW for Elk River (Table 3).

In addition to elevation range, the related factors of slope, tidal circulation and drainage are important considerations in assessing the suitability of an area for salt marsh establishment. A slope of one to two percent appears optimal (Zedler 1984). If too flat, drainage may be inadequate and the impounded tidewaters will inhibit vascular plant growth, even at seemingly suitable elevations. Likewise, a high elevation that supports salt marsh vegetation in an area with adequate tidal circulation may be unsuitable where tidal flow is restricted or the slope is too steep. The maximum slope that can support salt marsh vegetation is unknown.

Within the zone occupied by salt marsh the nature of the vegetation changed with elevation. Each of the three vegetation types identified was most common within a different elevation range, although there was overlap in their distribution (Fig. 11). Tidal elevation data were 60.0 percent effective in delineating the vegetation types described (Table 9). Tidal elevation has been discussed as an index of a complex set of environmental gradients. While there is a general pattern, these factors do not always change in a linear fashion. In addition, different factors may be most critical at different times, at

different locations or even on different regions of the shore. Overlap in the elevation distribution of salt marsh vegetation types could be attributable to variations in salinity, substrate type, accretion and erosion, patterns of vegetation establishment or competitive interactions.

Competition

The impacts of competition were not tested in this study, but a few speculations can be made regarding competitive interactions among salt marsh species in Humboldt Bay. The lower limits of Salicornia virginica and Spartina densiflora and the absence of most species from the lower marsh are probably attributable to environmental tolerance levels rather than competition. Few species can tolerate the frequency and duration of tidal immersion associated with these low elevations.

It is likely that Salicornia is limited in the middle of its distribution by competition with Spartina, as the bimodality of Salicornia's abundance curves cannot readily be explained by environmental limitations. Presumably, intermediate elevations provide optimal environmental conditions for Spartina growth, and here the species out-competes Salicornia. Salicornia appears to have a wider range of environmental tolerance; it flourishes at low and high elevations, where not out-competed by

Spartina. The growth form of Salicornia is more elongate and woody where the species occurs with Spartina at intermediate elevations. Dense Spartina establishment not only reduces the abundance and vigor of Salicornia, but apparently precludes the occurrence of most other species, few of which can compete with the thick growth of the tall cordgrass.

The growth and flowering of Triglochin spp. early in the season here may represent an example of competition avoidance through a temporal partitioning of resources, as suggested by Zedler (1977) for T. maritimum in the Tijuana Estuary, southern California.

Competition for space may be important to the establishment of high marsh annuals. Newton (1986b) noted that the opening of space associated with slight disturbance favors the growth of the rare species Cordylanthus maritimus ssp. palustris in Humboldt Bay. Numerous other competitive interactions could be occurring among species in the high salt marsh. This topic warrants further investigation.

Future Research

With the information presented here, it might be possible to favor the establishment of a particular vegetation type in salt marsh restoration by manipulating elevation, but further steps are needed to increase the

reliability of the outcome. A desired vegetation type could be encouraged by planting selected species. For example, if a project's objective is to provide habitat for the three rare salt marsh plant species in Humboldt Bay, than a Salicornia - Jaumea association would be desirable. This type of marsh would be favored at elevations of 7.3 ft. MLLW or higher in North Bay, however there is still a chance that Spartina stands could establish at these high elevations (Fig. 11). Planting Salicornia might be effective in giving this species a competitive edge over Spartina establishment. Experimentation along these lines is encouraged.

Reliability of restoration outcomes could also be enhanced by a clearer understanding of the causes of overlap in the elevation distribution of these vegetation types. Future research should focus on determining the importance of salinity, substrate type, accretion and erosion, patterns of vegetation establishment, competitive interactions and vegetation dynamics over time.

An adequate assessment of soil and water salinity requires frequent, widely-distributed samples. It is important to know the ranges of salinity in the field and seasonal distributions as well as averages. Critical times for sampling the extremes include the end of the dry season and after heavy rains. Plant phenology should be considered in assessing the impacts of seasonal variations

in salinity.

Specific patterns of accretion or erosion and of vegetation establishment in an area may be more important in determining plant distribution than previously recognized (Macdonald 1977a). A better understanding of these factors would help in assessing the suitability of potential restoration sites and in deciding whether or not to plant.

Whenever feasible, long-term vegetation studies in natural salt marsh are encouraged. In evaluating the causes of distribution patterns, it is important to know how these patterns change temporally as well as spatially.

Controlled experimentation and annual monitoring in salt marsh restoration projects could help clarify which factors are most critical in the distribution of salt marsh species. Furthermore, long-term monitoring is essential for evaluating the effectiveness of restoration attempts. The practice of restoration is a relatively new concept in land management, and it remains to be seen whether man-made marshes can actually develop to the functional equivalents of natural wetland ecosystems.

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APPENDIX A: Plant Species List

<u>SCIENTIFIC NAME</u>	<u>FAMILY</u>	<u>COMMON NAME</u>
<u>Atriplex patula</u> L. ssp. <u>hastata</u> (L.) Hall & Clem.	CHENOPODIACEAE	orache, saltbush
<u>Carex lyngbyei</u> Hornem.	CYPERACEAE	Lynqby's sedge
<u>Cordylanthus maritimus</u> Nutt. ssp. <u>palustris</u> (Behr) Chuang & Heckard	SCROPHULARIACEAE	Point Reyes bird's beak
<u>Cuscuta salina</u> Engelm.	CUSCUTACEAE	marsh dodder
<u>Deschampsia caespitosa</u> (L.) Beauv. ssp. <u>beringensis</u> (Hult.) Lawr.	GRAMINEAE	tufted hairgrass
<u>Distichlis spicata</u> (L.) Greene	GRAMINEAE	saltgrass
<u>Grindelia stricta</u> DC. ssp. <u>blakei</u> (Steyerm.) Keck	COMPOSITAE	Humboldt Bay gumplant
<u>Jaumea carnosa</u> (Less.) Gray	COMPOSITAE	jaumea
<u>Juncus lesueurii</u> Bol.	JUNCACEAE	salt rush
<u>Limonium californicum</u> (Boiss.) Heller	PLUMBAGINACEAE	sea lavender, marsh rosemary
<u>Orthocarpus castillejoides</u> Benth. var. <u>humboldtiensis</u> Keck	SCROPHULARIACEAE	Humboldt Bay owl's clover

APPENDIX A: Plant Species list (continued).

<u>SCIENTIFIC NAME</u>	<u>FAMILY</u>	<u>COMMON NAME</u>
<u>Parapholis incurva</u> (L.) Hubb.	GRAMINEAE	curved sea hard-grass, sicklegrass
<u>Parapholis strigosa</u> (Dum.) Hubb.	GRAMINEAE	sea hard-grass
<u>Plantago maritima</u> L. var. <u>juncoides</u> (Lam.) Gray	PLANTAGINACEAE	sea plantain
<u>Salicornia virginica</u> L.	CHENOPODIACEAE	pickleweed
<u>Scirpus cernuus</u> Vahl ssp. <u>californicus</u> (Torr.) Thorne	CYPERACEAE	slender club rush
<u>Scirpus maritimus</u> L.	CYPERACEAE	saltmarsh bulrush
<u>Spartina densiflora</u> Brong.	GRAMINEAE	cordgrass
<u>Spergularia canadensis</u> (Pers.) Don var. <u>occidentalis</u> Rossb.	CARYOPHYLLACEAE	sand-spurrey
<u>Spergularia macrotheca</u> (Hornem.) Heynh.	CARYOPHYLLACEAE	sand-spurrey
<u>Triglochin concinnum</u> Davy	JUNCAGINACEAE	slender arrowgrass
<u>Triglochin maritimum</u> L.	JUNCAGINACEAE	common arrowgrass

Nomenclature is consistent with Smith and Sawyer (1986).

APPENDIX B: Plant Species Descriptions

CARYOPHYLLACEAE

Spergularia canadensis (sand spurrey): a tiny, inconspicuous annual, 0.5-2 dm., blooming in mid-spring with pale pink, 5-merous flowers 5-7 mm. across. The opposite leaves are light green and slightly fleshy.

Spergularia macrotheca (sand spurrey): a larger, sprawling perennial, 1-4 dm., with succulent light-green stems and whorled leaves tinged with red. The rose-pink flowers are up to one cm. across.

CHENOPODIACEAE

Atriplex patula ssp. hastata (orache): an exotic annual from Europe, 3-10 dm., characterized by the arrowhead shape of its soft-green, opposite leaves. Young foliage has a scurfy coating. Leaf-like bracts enclose the small, inconspicuous flowers. Pistillate flowers occur below staminate flowers in the same spike.

Salicornia virginica (pickleweed): a perennial, 2-3(6) dm., with decumbent, somewhat woody lower stems and erect, succulent branches. The leaves are reduced to small scales, and the minute flowers are sunken in cavities of the internodes. The pale-green plant grows vegetatively in spring, flowers in early to mid-summer, and takes on a red, senescent form in autumn.

PLANTAGINACEAE

Plantago maritima var. juncoides (seaside plantain): an evergreen perennial, 1-3 dm., with narrow, basal leaves that are fleshy and curved. The small, greenish, 4-petaled flowers are concentrated in spikes raised up on scapes.

PLUMBAGINACEAE

Limonium californicum (sea lavender): a rather showy perennial, 2-5 dm., closely related to the horticultural statice. Blooming from mid-summer into the fall, the tiny lavender flowers are clustered at the ends of a much-branched scape, with leathery, spatulate leaves growing in a basal rosette. Limonium is a salt-excreter, and salt crystals are often evident on

the undersides of the leaves. The species occurs along much of the California coast, reaching its northern limit in Humboldt Bay.

CUSCUTACEAE

Cuscuta salina (marsh dodder): an obligate parasite commonly associated with Salicornia; other hosts observed include Jaumea and Triglochin. Cuscuta is believed to be related to morning-glories. The plant is bright orange, and it is virtually all tendril, having no chlorophyll, no roots and drastically reduced leaves. An annual, its life as an individual plant consists of a short period after germination, before attaching to a host. In June, tiny yellow buds open to white, shallow-campanulate flowers, 2-3 mm. in size.

SCROPHULARIACEAE

Cordylanthus maritimus ssp. palustris (Point Reyes bird's beak): a delicate branched or unbranched annual, 1-4 dm., listed by the California Native Plant Society as rare and endangered. The common name "bird's beak" refers to the shape of the flower, and so does the generic name (Cordylanthus = "club-flower"). The flower has a tubular corolla 1.5-2 cm. long, with two lips approximately equal in length. The lower lip is shallowly three-lobed, and the upper one curved at the apex. The flower is white, with a yellowish base and a deep purple margin. The flower is surrounded by glaucous green bracts. The bird's beak is a facultative parasite. It forms haustoria, which penetrate the roots of other species. The haustoria could provide an alternate source of water during periods of long emergence. C. maritimus ssp. maritimus is a southern California species of bird's beak, also listed as rare and endangered. There is some question as to whether these two species are truly distinct taxonomically (Dunn in Zedler 1984).

Orthocarpus castillejoides var. humboldtiensis (Humboldt Bay owl's clover): a small annual, 1-3 dm., listed by the California Native Plant Society as rare and endangered. Bright purple bracts distinguish the variety, which is endemic to Humboldt Bay salt marshes. In early to middle spring, patches of Orthocarpus appear in brilliant bursts of color. The flowers, about 2 cm. long, are typically pink, with yellow on the tip of the lower lip. A white form is reported in this study occurring in the Jacoby Creek salt marsh, and by Newton

(1986b) occurring in Second Slough, Eureka.

COMPOSITAE

Grindelia stricta ssp. blakei (Humboldt Bay gumplant): a woody perennial, 3-5 dm., with reddish-brown stems and alternate, clasping leaves. The subspecies is endemic to Humboldt Bay and is listed by the California Native Plant Society as rare and endangered. The profuse yellow flowers, to 5 cm. across, bloom in late summer and are surrounded by green, recurved bracts. Leaves and bracts are resinous, hence the name "gumplant."

Jaumea carnosa (jaumea): a succulent perennial, 1-3 dm., decumbent or ascending, with linear, opposite leaves. The terminal, solitary flowers are yellow and about one cm. across.

JUNCAGINACEAE

Triglochin: the genus is characterized by a distinctive inflorescence: a spikelike raceme of minute, greenish flowers at the top of a naked scape, blooming in early spring. The basal leaves are narrow and somewhat fleshy.

T. concinnum (slender arrowgrass): a delicate plant, 0.5-3 dm., with deep-green leaves that are well-spaced. Ligules are two-lobed. Scapes are often slightly shorter than the leaves.

T. maritimum (common arrowgrass): a taller, more robust plant, 1-10 dm., with lime-green leaves tending to grow in dense tufts. The species can further be distinguished from T. concinnum by having entire ligules and scapes always taller than the leaf blades.

JUNCACEAE

Juncus lesueurii (salt rush): a rush, 3-9 dm., found in sand dune habitats as well as tidal marshes. In dunes, salt rush has arching stems and a compact inflorescence, but where it grows bordering salt marsh, stems are erect and the inflorescence an open panicle. These two growth forms may represent two subspecies (Shapiro and Ass. 1980).

CYPERACEAE

Carex lyngbyei (Lyngby's sedge): a monoecious sedge, 2-9 dm., with erect staminate spikes located above the drooping, purplish pistillate spikes.

Scirpus cernuus ssp. californicus (slender club-rush): a small annual, 0.5-2 dm., with green, filiform culms, generally growing in tufts. The solitary brown spikelets are each subtended by a single involucre leaf appearing as a continuation of the culm.

Scirpus maritimus (saltmarsh bulrush): a 5-10 dm. bulrush with sharply triangular stems and a capitate inflorescence subtended by several elongated bracts.

GRAMINEAE

Deschampsia caespitosa (tufted hairgrass): densely tufted perennial grass, 6-12 dm., with leaves mostly basal and with an open panicle.

Distichlis spicata (saltgrass): a bluish-green perennial grass, 2-3 dm., with wiry stems arising from horizontal, creeping rootstocks. The stiff, two-ranked leaf blades characteristically ascend from the stem at 45-degree angles. Green spikes appear in early summer, soon drying to straw-brown. Saltgrass is dioecious, with the male spike taller than the blades and the thicker female spike shorter than or equal to the height of the blades. Saltgrass is dormant through the winter.

Parapholis incurva (curved sea hard-grass): a yellowish-green annual grass native to Europe, with culms mostly decumbent, but with erect, slender spikes that resemble culms. Spikelets are embedded in cavities of the cylindrical, articulate rachis, falling attached to the rachis joints. Anthers are 0.5-1 mm. long.

Parapholis strigosa (sea hard-grass): similar to P. incurva, also native to Europe, and only recently discovered in Humboldt Bay as the first record of the species in North America (T.P. Worley pers. comm. 1986). P. strigosa is distinguished from P. incurva primarily by having larger anthers, 1.5-4 mm. long.

Spartina densiflora (cordgrass): a coarse grass, 3-10 dm., native to Chile, introduced to Humboldt Bay in the mid-1800s. In Humboldt Bay this species was once considered a northern ecotype of Spartina foliosa

(Pacific cordgrass). The tussocky habit of Spartina densiflora is the most striking feature distinguishing the species from S. foliosa, which grows in evenly-spaced culms. In addition, S. densiflora has narrower leaves, narrower indurate culms, smaller spikelets and often some purplish coloration in its stems and spikelets. In Humboldt Bay the cordgrass blooms around June and continues some degree of vegetative growth year-round. S. foliosa flowers later and is dormant over winter (Spicher and Josselyn 1985).