

# Biogeographical Distribution of Salt Marsh Halophytes on the Coasts of the Sonoran Desert

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## Abstract:

Twenty-four species of intertidal halophytes were recorded from 15 coastal salt marshes of the Sonoran desert. The Pacific salt marshes were found to be the most diverse, with 14.4 species per marsh, while the western Gulf of California had 8.9, and the eastern Gulf, 13.7. A low species diversity was found in the northwestern Gulf due to the absence of mid- and high-zoned halophytes. High-zoned species were geographically patchier on all coasts.

The species formed three elevational groups within the intertidal zone: LOW: *Spartina foliosa* Trin, *Distichlis palmeri* (Vasey), *Rhizophora mangle* L., *Laguncularia racemosa* (L.), *Avicennia germinans* (L.), *Salicornia bigelovii* Torr., *S. europaea* L., and *Batis maritima* L.; MID: *Salicornia virginica* L., *Suaeda californica* S. Wats., *Jaumea carnosa* (Less.), *Sesuvium verrucosum* Raf., *Limonium californicum* (Boiss.) and *Cressa truxillensis* H.B.K.; HIGH: *Salicornia subterminalis* Parish, *Allenrolfea occidentalis* (S. Wats.), *Frankenia grandifolia* Cham. and Schlect, *F. palmeri* S. Wats., *Monanthochloe littoralis* Engelm., *Distichlis spicata* (L.), *Suaeda fruticosa* (L.), *Atriplex barclayana* (Benth.), *A. canescens* (Pursh) and *Sporobolus virginicus* (L.). Thirty additional species were recorded in the supralittoral zone.

## Introduction

The Sonoran desert has over 3400 km of coastline. This includes the outer Baja peninsular coast (1250 km), the inner Baja peninsular coast (1300 km) and the Sonora mainland coast (900 km) (Figure 1). While the total salt marsh acreage is unknown, the Sonoran desert coast is frequently indented by salt marshes. These salt marshes are typically hypersaline "negative estuaries" since they receive little or no fresh water influx (Thompson et al., 1979). Negative estuaries are characterized by high salinities at their heads due to evaporation. (Water Resources Study Team, 1979). The extremes of salinity and temperature in the Gulf Coast of the Sonora desert salt marshes are comparable to those found in the Red Sea. The Pacific coast salt marshes however, tend to have similar salinities from head to mouth due to the moderated climate produced by the cool waters of the California current.

The salt marsh flora of Baja California has been described from Ensenada south to Puerto Chale (24°30'N) (Dawson 1962; Phleger and Ewing, 1962; Macdonald, 1967 and 1969; Neuenschwander, 1972; Thorsted, 1972; Macdonald and Barbour, 1974). The occurrences of some Gulf of California salt marsh plants has been mentioned (Kniffen, 1932; Nicols, 1965; Felger, 1966; Foster, 1975; Felger and Lowe, 1976); but no detailed study has been made to date. This report compares distributions of salt marsh halophytes from 14 negative estuaries along the Pacific and Gulf coasts, and one positive river estuary near Mulege, Baja California, where the Rio Santa Rosalia enters the Gulf of California.

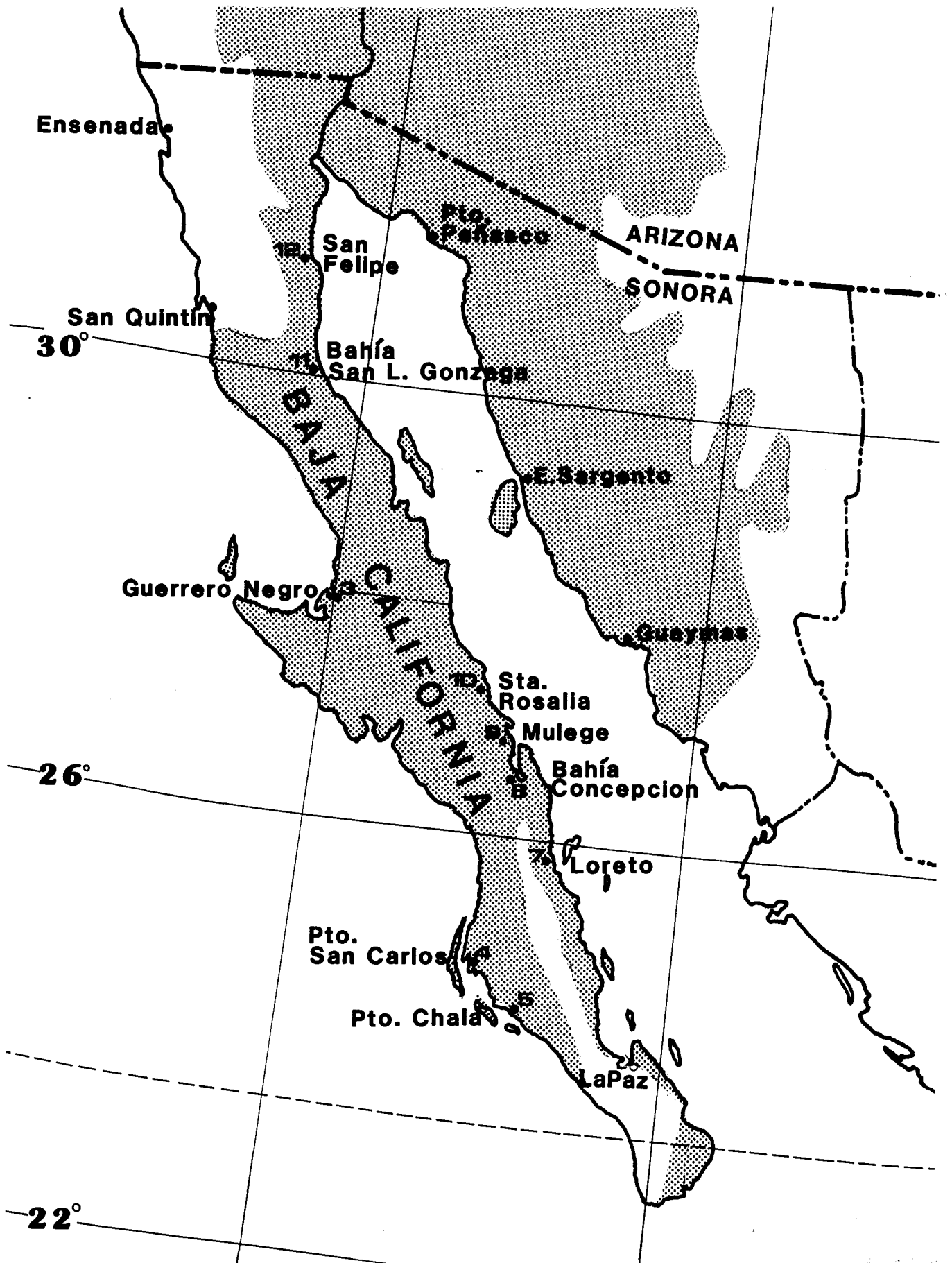
## Survey Method

Fifteen salt marshes (Figure 1) were surveyed for halophytes during August of 1979. These primary data were supplemented by earlier visits to six additional sites on the Sonoran coast during the previous 4 years. We consider a halophyte as any phanerogam capable of growing in sea water (34 to 40 ppt), i.e., within the intertidal zone. The sea grasses, *Zostera marina* L., *Phyllospadix torreyi* Wats. and *Ruppia maritima* L., which occur in subtidal zones of Sonoran desert coasts were not surveyed. Percent of coverage by the halophytes was estimated from the area covered by the foliage of a species projected on the ground (Smith, 1966) and then converted to the following coverage classes derived from Braun-Blanquet (1951). Plants were considered: a) RARE, if less than 1%; b) UNCOMMON, 1-5%; c) COMMON, 6-25%; and d) ABUNDANT 26-100%. Vertical ranges of the intertidal distributions were based on natural halophyte zones: low, mid, high and supralittoral [see Macdonald and Barbour 1974]. We found, however, that the mid to high vegetation change was not always apparent. Taxonomic designations follow Shreve and Wiggins (1964), Munz (1974) and Wiggins (1980).

## Results

No overall correlation between number of species per marsh and latitude was evident along any coastline, even though species composition varied with latitude. Species diversity was significantly lower in the western gulf (8.9 per marsh) than in the Pacific (14.4 per marsh) or the Sonoran coast (13.7 per marsh) (Table 1). The marshes of San Felipe (30°10'N) and Bahia San Luis Gonzaga (29°45'N) had only six species, each, and are largely responsible for the lowered diversity.

In total, 24 species were recorded from the intertidal zone: 15 of which were found on all coastlines. Twenty-one species



**Figure 1.** Map showing limits of the coastal Sonoran Desert and the salt marsh study sites.

were found on the Pacific coast of Baja California, 18 on the gulf coast of Baja California, and 19 on the gulf coast of Sonora (Figure 2). Four species were found only on the Pacific coast of Baja California, whereas 3 species were found only in the Gulf of California.

Species composition of each marsh was examined as a function of vegetation zones. The halophyte zones were distinguished as low, middle and high intertidal zones (Figure 3), and a supralittoral zone (Table 2) in accord with Macdonald and Barbour's zones (1974).

*Spartina foliosa* was the dominant plant in the low zone of salt marshes on the Pacific coast as far south as Guerrero Negro (28°N). Three degrees further south, in marshes surrounding Bahia Magdalena (25°N), mangrove species were the dominants in the low zone. *S. foliosa* was still present and occurred as far south as Puerto Chale (24°30'N) but does not penetrate into the mangroves' significantly attenuated sunlight. The northern gulf endemic *Distichlis palmeri*, was a dominant in the low zone. But, unlike *S. foliosa*, its range did not extend south of the mangroves. Also in the low zone, the annual succulents were found: *Salicornia bigelovii* on the Pacific coast and *S. europaea* on the gulf coasts. Although they were rarely dominant, they were found in almost all of the marshes. *Batis maritima* was found in all the marshes except San Felipe and Bahia San Luis Gonzaga, often as a subdominant.

In the middle zone, the perennial succulent, *Salicornia virginica* was typically the dominant species. The widely distributed *Sesuvium verrucosum* and *Cressa truxillensis* were found along all three coastlines and *Cressa* became a subdominant in the depauperate salt marshes of the north-

western gulf. The well distributed *Suaeda californica* did not occur below San Felipe on the gulf coast of Baja California. *Jaumea carnosa* and *Limonium californicum* were restricted to the northern Pacific coast of Baja California.

In the high zone the distributions were patchier than the low and middle zone. The short, bristly grass, *Monanthochloe littoralis*, for example, formed extensive mats in some salt marshes, but was absent from others. To the south it was more conspicuously absent. Also to the south on the Sonoran coast another high-zoned grass *Sporobolus virginicus*, ranged south from the mangrove-populated Estero Sargento (29°20'N). *Suaeda fruticosa* was present along the tide line at various locations on all three coastlines. The typically supralittoral halophytes, *Atriplex barclayana*, *A. canescens* and *Distichlis spicata*, appeared in the high zone of some estuaries.

The desert shrub, *Frankenia palmeri*, and the closely related alkali heath, *F. grandifolia*, were found along all three coastlines, although not below 28°N latitude. These two species appeared the most dissimilar along the Pacific coast and the most similar in the northern Gulf of California. The width-length ratio of *F. grandifolia* leaves differed significantly between specimens from the Pacific and gulf coasts (Table 3). Specimens from Guerrero Negro appeared to be transitional, in that leaf length was less than specimens from Ensenada or San Quintin, but greater than specimens from Puerto Penasco (Table 3). Leaf dimensions of *F. palmeri* were similar among specimens from all locations (data not shown). At San Felipe, where *F. grandifolia* was absent, *F. palmeri* seemed to move into the niche of *F. grandifolia*.

*Allenrolfea occidentalis* grew to two meters in height

**Table 1.** Number of intertidal halophyte species per marsh in Sonoran desert coastal salt marshes. Pacific Baja = Pacific coast of Baja California; Gulf Baja = Gulf of California coast of Baja California; Gulf Sonora = Gulf of California coast of Sonora.

Pacific Baja	
Ensenada (31°45'N)	13
San Quintin (30°30'N)	13
Guerrero Negro (28°N)	15
Pto. San Carlos (25°N)	15
Pto. Chale (24°30'N)	16
Average species/marsh	14.4
Gulf Baja	
San Felipe (31°10'N)	6
Bahia Luis Gonzaga (29°45'N)	6
Sta. Rosalia (27°N)	10
Mulege (27°N)	12
Bahia concepcion (20°35'N)	8
Loreto (26°N)	6
La Paz (24°10'N)	14
Average species/marsh	8.9
Gulf Sonora	
Pto. Penasco (31°15'N)	16
Estero Sargento (29°30'N)	13
Guaymas (28°N)	12
Average species/marsh	13.7

\*Significantly different from means for Pacific Baja and Gulf Sonora at 95% confidence interval by Duncan's multiple-range test (Steel and Torrie 1960:107-109).

**Table 2.** Sonoran desert halophytes from the supralittoral and adjacent desert saline habitats. Locations indicate areas (Figure 1) from which plants were recorded.

Species	Locations
Abronia maritima	2,4,6,7
Amaranthus cf. palmeri	6
Ambrosia dumosa	3,4,5,11,15
Atriplex barclayana	4,11
Atriplex canescens	13
Atriplex lentiformis	13
Atriplex semibaccata	2
Atriplex watsonii	1,2
Baccharis sp.	7,15
Carpobrotus aequilaterus	1,15
Carpobrotus edulis	1,15
Cuscuta salina	2
Dudleya spp.	2
Gasoul crystallinum	1,2,3,5,15
Gasoul nodiflorum	1,2,3,4
Heliotropium curassavicum	1,3,4,7,9,10
Hordeum vulgare	4
Juncus cf. acutus	9
Lycium sp. #1	1,2,4
Lycium sp. #2	2,6,7,9,10
Maytenus phyllanthoides	4,6,7,8,10
Opuntia fulgida	7
Opuntia bigelovii	15
Parapholis incurvata	1
Phoenix dactylifera	7,10
Plantago sp.	9
Prosopis juliflora	7,8,10
Simmondsia chinensis	15
Tamarix pentandra	2,3
Triglochin maritima	3

[Bahia San Luis Gonzaga] and was a dominant bush along the tide line in many of the marshes. The smaller *Salicornia subterminalis* occupied a similar habitat along the northern Pacific and gulf coasts of Baja California and along the Sonoran coast. In the Gulf of California, however, it was exclusively intertidal.

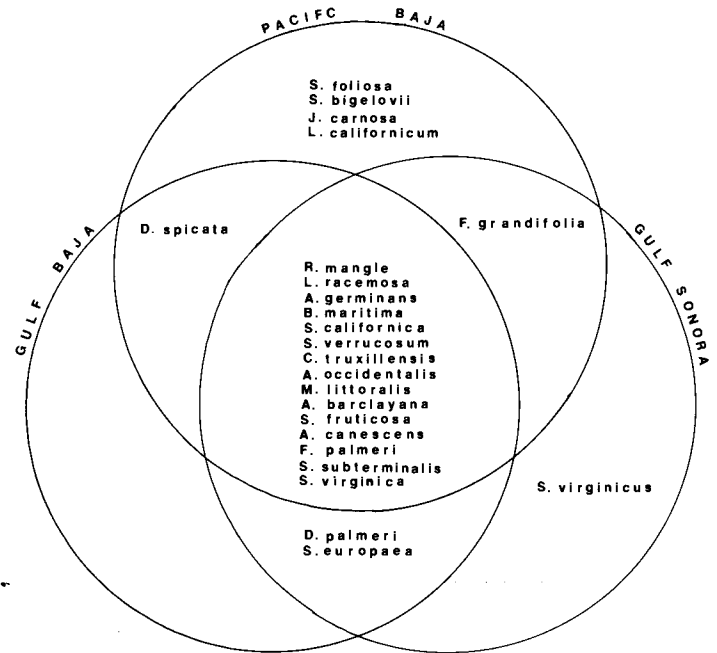
The supralittoral species were even patchier than the high-zoned species (Table 2). Many species were recorded from only one salt marsh, and the average representation was only 2.3 marshes per species. The most widely distributed supralittoral species was *Heliotropium curassavicum* L. (present in 6 marshes), followed by *Ambrosia dumosa* (A. Gray), *Lycium* sp. #2, and *Maytenus phyllanthoides* Benth. (present in 5 marshes each).

**Discussion**

The results support the conclusion that the three coasts of the Sonoran desert are of the same salt marsh phytogeographic region, in that 15 of 24 species are found on all three coasts. *Salicornia bigelovii* may be only a variant of *S. europaea* (Shreve and Wiggins, 1964; Munz, 1974). In this case, the number of shared species is 16, and the Pacific coast would have only 3 unique species. Two of these, *Jaumea carnosa* and *Limonium californicum*, are californian species that just enter the northern region of the Pacific coast of the Sonoran desert. The Pacific coast salt marshes have significantly more species per salt marsh than those of the gulf.

Despite the gulf's rigorous physical extremes and the seemingly severe selection pressure only a single species, the salt grass *D. palmeri*, is endemic. *D. palmeri* may be derived from *D. stricta* populations in the vicinity of the mouth of the Colorado River. The reproductive structures clearly indicate affinities with *D. stricta* (Shreve and Wiggins, 1964). In the Colorado River Delta area, the Cocopa indians cultivated and harvested the grain of *D. palmeri*. This human influence may have assisted in its differentiation.

Some of the species found in the estuaries represent inland desert and alkali flat halophytes, such as *Allenrolfea occidentalis*, *Atriplex barclayana* and *A. canescens*. These high-zoned species tolerate extreme salinities and temperatures. The low and middle zone species rarely occur inland, although the lower zoned species may extend north into the temperate Pacific



**Figure 2.** Venn diagram showing species distributions and overlaps with respect to the three Gulf of California coastlines.

coast salt marshes as far as San Francisco Bay (Macdonald and Barbour, 1974).

The dominant tropical species were the three species of mangroves. Temperature undoubtedly controls the northern limits of the mangroves along all three coastlines. Moser (unpublished) has described the freezing damage to mangroves in Estero Sargento, Sonora. This estuary is near the northern mangrove limit along the mainland gulf coast (29°N latitude). This is considerably north of the mangrove limits on the colder Pacific coast of Baja California (26°N). The mangrove limit on the gulf coast of Baja California (27°N) is between the other two limits. This mangrove distribution closely follows the mean sea surface of the coldest month, January. Robinson's (1973) 70°F (15.6°C) January isotherms coincide with the limits of the mangroves on all three Sonoran desert coastlines.

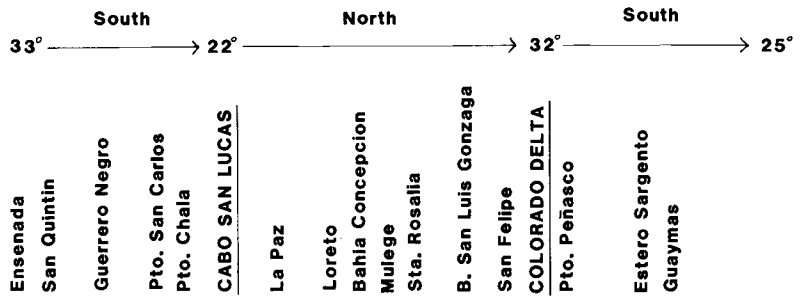
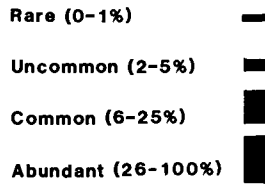
The southern limits of four species, *Frankenia grandifolia*, *F. palmeri*, *Jaumea carnosa*, and *Limonium californicum*, occur at approximately 28°N. The first two species are disjunctly distributed between the Pacific and gulf coasts. The latter two were only found on the Pacific coast. The factor(s) limiting these southern distributions may be related to temperature, such as cold stratification of seeds or predator survival.

A few exotic species are beginning to move into the relatively undisturbed Sonoran desert salt marshes. Macdonald and Barbour (1974) have noted that in Bahia San Quintin, "Fifteen species were encountered on the marsh, all but one of which [*Mesembryanthemum nodiflorum* L. [= *Gasoul nodiflorum* L.] were indigenous—a marked contrast to the many introduced species of the more disturbed American (U.S.A.) marshes..." The present study adds another species to the introduced list: the South African *G. crystallinum* (L.) in

**Table 3.** Length, width, and ratio of width to length of leaves of *Frankenia grandifolia* collected at four sites along the Pacific coast of Baja California and the eastern coast of the Gulf of California. Fully expanded basal leaves from secondary branches of herbarium specimens were measured with a caliper. Ten leaves were measured per datum point. Within a column, values followed by the same letter are not significantly different at the 95% confidence interval by Duncan's multiple-range test (Steel and Torrie 1960:107-109).

Geographical Region	Collection Site	Length (Millimeters)	Width (Millimeters)	Ratio Width : Length
Temperate Pacific Coast	Ensenada	13.1 a	6.7 a	1 : 1.98 a
	San Quintin	14.1 a	6.5 a	1 : 2.24 a
Desert Pacific Coast	Guerrero Negro	6.7 b	3.1 b	1 : 2.18 a
Desert Gulf Coast	Puerto Penasco	7.1 b	1.2 c	1 : 6.21 b

LEGEND



Low Zoned Halophytes

1. *Spartina foliosa*

2. *Distichlis palmeri*

3. *Rhizophora mangle*

4. *Laguncularia racemosa*

5. *Avicennia germinans*

6. *Salicornia bigelovii*

7. *Salicornia europaea*

8. *Batis maritima*

Mid Zoned Halophytes

9. *Salicornia virginica*

(= *Salicornia pacifica*)

10. *Suaeda californica*

11. *Jaumea carnosa*

12. *Sesuvium verrucosum*

13. *Limonium californicum*

14. *Cressa truxillensis*

High Zoned Halophytes

15. *Salicornia subterminalis*

16. *Allenrolfea occidentalis*

17. *Frankenia grandifolia*

18. *Frankenia palmeri*

19. *Monanthocloe littoralis*

20. *Distichlis spicata*

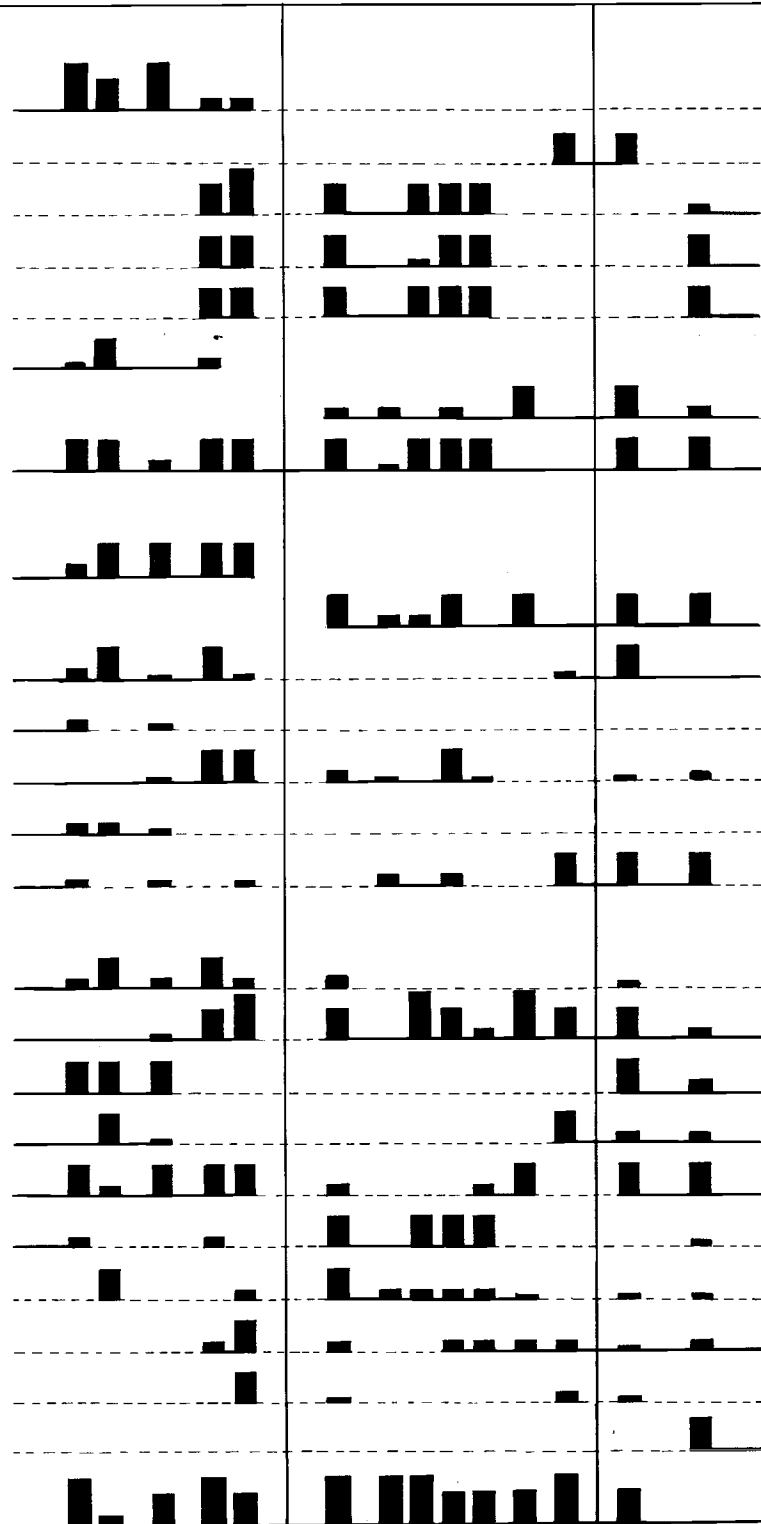
21. *Suaeda fruticosa*

22. *Atriplex barclayana*

23. *Atriplex canescens*

24. *Sporobolus virginicus*

Bare ground



the supralittoral of Bahia San Quintin. In 1978, this species also appeared at Station Beach, Puerto Penasco, Sonora, on the eastern coast of the northern Gulf of California. *G. crystallinum* has not been observed in Sonoran salt marshes.

The high proportion of indigenous species in the Sonora desert salt marshes as compared to the United States Pacific coast marshes may be due to the lesser influence of man (Macdonald and Barbour 1974). But it should not be overlooked that these desert marshes represent a harsh environment which may protect the native species against encroachment by exotic species.

In conclusion, the Sonoran desert salt marsh halophyte flora is a unique phytogeographical region undisturbed by invading species and man. Although the region has only one endemic species (possibly derived by man) there appears to be an excellent opportunity to study natural speciation processes in an undisturbed halophyte flora. The desert forms still have intact ranges, even with respect to the patchy upper zoned halophyte species. Future studies may reveal how the disjunct distributions arose and what mechanism[s] may be limiting the southern distributions. Our observations that the mangroves' northern limits (26°, 27°, and 29°N latitude) corresponding to the 70°F (15.6°C) isotherm supports the conclusion that the mangroves are temperature limited. The desert coastal estuaries north of the mangrove limit have extreme physical conditions, but have been the least studied. Hopefully, this note on desert halophytes will both stimulate and assist future studies in this interesting area.

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**Figure 3.** Distribution and estimated abundances of Sonoran Desert salt marsh halophytes and bare ground. Intertidal species are grouped according to their vertical distribution within the halophyte zone. Solid lines indicate inferred distributions.