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Long-Term Effects of Tidal Exclusion on Salt Marsh Plain Species at Estero de Punta Banda, Baja California

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Abstract Disturbance is an important factor influencing plant species composition and diversity. We addressed changes in plant composition and soil characteristics in Estero de Punta Banda, Baja California, Mexico following 22 years of disturbance by tidal exclusion. Currently, sediments in the non-tidal site are dry, 26±1% moisture, and hypersaline, 143±12; while those at the tidal marsh are wet, 36.2±1% moisture, with 40.3±2.6 salinity. The non-tidal site has lost seven species including annuals, short- and long-lived perennials, ephemerals, and parasites. Current dominants are the perennials *Batis maritima* and *Sarcocornia pacifica*. Average species richness at the non-tidal site is 4.4±0.32 vs.10±0.18 species per square meter at the tidal site. Average species diversity index is lower at the diked area. The general biodiversity loss that results from tidal exclusion in arid estuaries, contrasts with the species-rich communities that develop in diked humid-climate estuaries.

Keywords *Batis maritima* · Tidal restriction · Anthropogenic disturbance · Hypersaline soils · Arid estuaries

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Introduction

Disturbance is an important factor affecting the community structure and dynamics of coastal marshes (Brewer and Bertness 1996; Bhattacharjee et al. 2007). A variety of factors can act as agents of natural disturbance (i.e., wrack deposition; Valiela and Rietsma 1995) or of introduced disturbance (i.e., eutrophication; Sánchez-Carrillo and Álvarez-Cobelas 2001). Community response to a disturbance will be driven by the resulting abiotic changes and determined by the attributes of the component species (Bonin and Zedler 2008); the life history attributes of the plant species available for recruitment or invasion can be used to predict this response (Hobbs and Huenneke 1992).

Depending on the magnitude of the disturbance organisms may be killed or displaced, consumable resources may be depleted, or habitat structure may be degraded or destroyed (Lake 2000). Given their temporal patterns, disturbances can be characterized as pulses, presses and ramps; pulses are short and sharply delineated disturbances, presses may arise sharply and then reach a constant level that is maintained, and ramps may steadily increase in time without an endpoint, or reach an asymptote after an extended period (Lake 2000). The population, community or ecosystem has a pulse, press, or ramp response (Glasby and Underwood 1996; Lake 2000). The characterization of the response is linked with the qualities of resistance, a measure of the capacity of a system to withstand a disturbance, and resilience, a measure of the capacity of the system to recover from disturbance (Lake and Barmuta 1986).

Changes in hydrologic and hydrographic processes, resulting from water control structures such as berms, dikes, and tide gates are a common type of disturbance in salt marshes (Roman et al. 1984; Kennish 2002). These

structures facilitate the drainage and canalization of wetlands, to increase the area for industrial activities, agriculture and forestry (Kennish 2001; Hansson et al. 2005). Water control structures in coastal marshes can reduce (Beeftink 1975; Alexander and Dunton 2002) or increase freshwater input into salt marshes (Adams and Bate 1994; Davis and Froend 1999; Álvarez-Rogel et al. 2007), alter water levels (Beeftink 1987), or restrict tidal inundation (Joenje 1974; van Noordwijk-Puijk et al. 1979; Joenje and Verhoeven 1993; Leeuw de et al. 1994; Ritter et al. 2008). The resulting hydrologic changes not only have an immediate compositional impact on wetland vegetation but also affect ecosystem-level processes, such as primary production and biomass accumulation (Roman et al. 1984; Barrett and Niering 1993; St. Omer 1994; Brockmeyer et al. 1997; Burdick et al. 1997; Zedler et al. 2001; Ritter et al. 2008).

Management and restoration of salt marsh vegetation requires understanding the plant community response to hydrologic disturbance and the trajectories following a disturbance event (Keddy 1992); however, long-term vegetation monitoring data sets are not common (Bhattacharjee et al. 2007). In this paper, we present data on the long-term response of salt-marsh vegetation to tidal restriction in Estero de Punta Banda, in Baja California, Mexico. A dike that impeded tidal flow was constructed in 1984, and the area suffered no further modification after 1986. Ibarra-Obando and Poumian-Tapia (1991) documented the short term vegetation response to the construction of the dike at Estero de Punta Banda represented by the loss of annual and short-lived salt-marsh species, and the persistence of perennials. The current study focuses on the response of perennials to more than 20 years of tidal exclusion.

Estero de Punta Banda is an arid estuary, part of the Californian marshes that extend between Point Conception (California, USA) to Bahía de San Quintín (Baja California, Mexico; Zedler et al. 2001). Estero de Punta Banda has experienced habitat and biodiversity loss from hydrological modifications in a small section of the estuary (Ibarra-Obando and Escofet, 1987; Ibarra-Obando and Poumian-Tapia 1991; Zedler et al. 2001). The Californian biogeographic region is characterized by its low, seasonal precipitation, low runoff, and frequent droughts. As a consequence, tidal circulation is extremely important to coastal marshes, as seawater provides most of the soil moisture for intertidal wetlands (Zedler 1982).

Historical records of eight halophyte distributions in 23 coastal marshes in Southern California indicate that species richness is greatest in wetlands with long histories of good tidal flow, and lowest in wetlands that have been closed to tidal flow for one or more lengthy periods (Zedler et al. 2001). In Tijuana Estuary (California, USA), 130 km north of Estero de Punta Banda, a tidal exclusion event resulted in impaired tidal flow, and reduced biodiversity (Zedler et al. 2001). Studies in this site suggest that salt marsh plant species' traits (O'Brien and Zedler 2006; Bonin and Zedler 2008) and species identity or functional groups (Callaway et al. 2003; Sullivan et al. 2007) can help explain the disappearance or persistence of salt marsh plain species in response to disturbance, *sensu* Underwood (1996).

Given the hypersaline soil conditions at the non-tidal marsh, we hypothesized that existing gaps would be occupied by salt-tolerant, deep rooted clonal perennials. We also hypothesized that a significant reduction in species' richness and diversity would characterize this site. We used structural characteristics of salt marsh plain species and apparent soil loss as indices of habitat deterioration. We compared the disturbed area with a nearby non-modified marsh plain outside the dike using soil salinity, percent soil humidity, percent cover, and percent frequency of occurrence as response variables. We assess changes in species composition, based on richness and diversity, and changes in species dominance (species dominance index (SDI); Frieswyk et al. 2007).

Materials and Methods

Study Site

Estero de Punta Banda (31.666°−31.80° N; −116.566° −116.666° W, hereafter EPB) is located 120 km south of the Mexico–USA border. It is "L"-shaped with a 3-km portion extending inland in a southeasterly direction and a 7.5-km long channel connected by an inlet to a semi-protected coastal system, Bahía de Todos Santos (Fig. 1). The estuary covers 16.40 km^2, of which 4.60 km^2 are navigable waters, 8.95 km^2 are salt marshes, and 2.85 km^2 are mudflats (Ibarra-Obando and Escofet 1987). Depth decreases along the main channel from 6 to 1 m (mean low water) from the mouth of the estuary to the head. Maintenance of the tidal circulation regime is facilitated by the mouth's position relative to other sites on the lagoon (Pritchard et al. 1978).

The region is characterized by a "Mediterranean climate" (cool, wet winters and hot, dry summers), and by frequent and sometimes persistent years of drought. Evaporation from the estuary's surface exceeds precipitation over an annual cycle, and salinity increases from the mouth to the inland portion of the estuary (Acosta-Ruíz and Álvarez-Borrego 1974; Celis-Ceseña and Álvarez-Borrego 1975).

EPB is in the Californian biogeographic region (Zedler et al. 2001). These marshes are characterized by: (1) a small number of dominant plant species in the marsh plain; (2) naturally occurring assemblages that range from one to

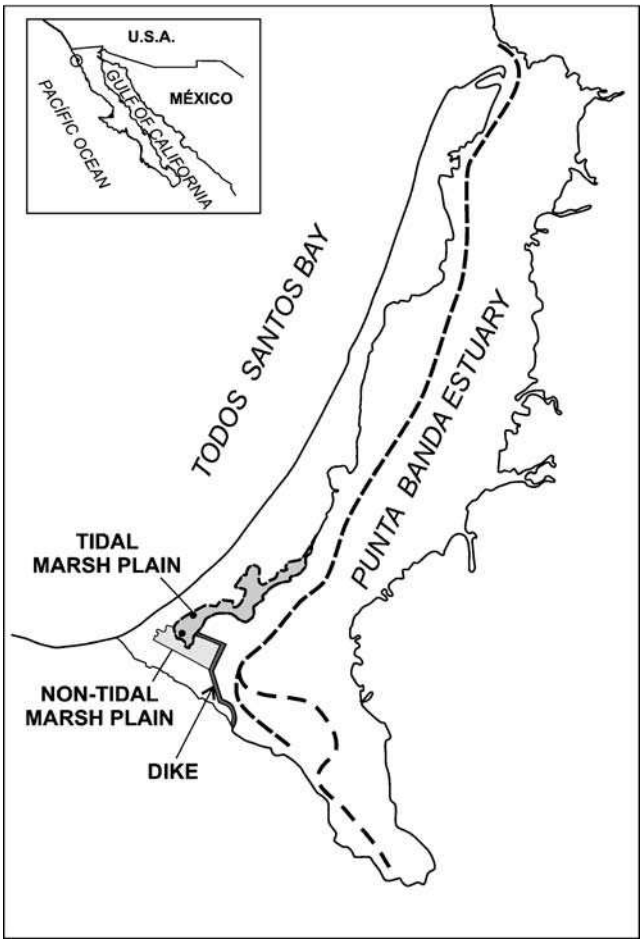

Fig. 1 Geographic location of the Estero de Punta Banda (EPB). The EPB is located about 120 km south of the USA–Mexico border and about 10 km south of the city of Ensenada. It has a characteristic "L" shape. The *dotted line* represents the navigation channel. The dike on the south-west corner of the estuary is indicated. *Dots* indicate the location of the tidal and non-tidal marsh, respectively

many species; (3) various growth forms within species; and (4) the presence of species that are readily grown from seed, and become reproductive in their first or second year (Zedler et al. 2001; Callaway et al. 2003). There are three distinct habitat types: (1) High marsh: 30 to 70 cm elevation range which includes seven species. *Arthrocnemum subterminale* (*Salicornia subterminalis*) (Parish) Standl. is the visual indicator of the lower and upper boundaries of the high marsh because of its conspicuousness and compact distribution. (2) Marsh plain: 30-cm elevation range with heterogeneous topography due to the presence of tidal channels and creeks. *Sarcocornia pacifica* (*Salicornia virginica*) (Standley) AJ Scott is the dominant marsh plain species. Seven additional species are present, *Batis maritima* L., *Frankenia salina* (Molina) I.M. Johnst., *Jaumea carnosa* (Less.) A. Gray. *Limonium californicum* (Boiss.) A. Heller, *Salicornia bigelovii* Torr., *Suaeda esteroa* Ferren and Whitmore and *Triglochin maritima* L. (*Triglochin concinna*). And (3) Cordgrass habitat—the bayward portion of the marsh plain and lower elevations are occupied by *Spartina foliosa* Trin (Zedler et al. 1999).

In November 1983, construction was started in the southwestern corner of EPB to establish a plant for the assembly of oil-drilling platforms. As part of the project, a dike was built to delimit the industrial patio, enclosing a 0.45 km^2 area (Fig. 1). The plan was to assemble the platforms on the patio and ship them to Alaska through the Pacific Ocean. Although the development plans included opening a second inlet in the estuary at the southernmost part of the sandbar close to the diked area, the inlet was never constructed. A year after the construction started, salt marsh vegetation inside the dike had either been buried by the dredging material or was decaying due to the effects of tidal exclusion (Ibarra-Obando and Escofet 1987). Between 1984 and 1986 industrial activity slowed, giving us time to monitor the changes in the salt marsh vegetation. During this period, the loss of annual and short-lived species was evident (Ibarra-Obando and Poumian-Tapia 1991). As a consequence of a drop in international oil prices, the project was canceled at the end of 1986. Mexican authorities never required any mitigation actions, so the perturbed area remained isolated from tidal exchange.

Field Work

We visited EPB each February and September between 2001 and 2007 (except for February 2006). We collected vegetation and soil samples as in 1984-1986 (Ibarra-Obando and Poumian-Tapia 1991). During each visit to the field, we placed twenty 0.25 m^2 circular quadrats randomly in the marsh plain of both the tidal and non-tidal sites. In each quadrat we measured: (1) Interstitial soil water salinity with a refractometer, using samples collected in a plastic core at 2–3 cm depth; (2) percent soil moisture in the top 5 cm collected with a scoop, using the gravimetric method; (3) percent cover in seven classes (0, 1, 2–5, 6–25, 26–50, 51–75, 76–100). Average percent cover was calculated from midpoints of the cover classes; (4) percent frequency of occurrence of specific species, calculated relative to the total number of quadrats sampled during the study period.

In 2005, we also measured the topographic profiles of transects that had been established in 1985 in both the tidal and non-tidal marsh plains for comparison between these two dates. For this, a Top Con topographic station model GTS-226 was used. The topographic profiles in the tidal and non-tidal marsh were compared by analyzing the elevation difference and transect length, considering a transect 1-m wide. The differential leveling technique was used, and elevation control points referred to mean low low water (MLLW) were established at the beginning of each transect.

Data Processing

We analyzed differences in soil salinity, soil moisture, perennials percent cover and percent frequency of occurrence between the tidal and non-tidal sites and across sampling dates. Since the data was not homoscedastic, we used non-parametric statistics. Differences between areas (tidal and non-tidal) were analyzed with a Mann–Whitney U test. Differences between sampling dates used a Kruskall–Wallis test (Zar 1974).

We identified dominant species and used the change in the species dominance index (SDI; Frieswyk et al. 2007) as an indicator of the change in community condition through time. This index measures three attributes of dominance: cover, species suppression and tendency towards high cover. These three attributes represent functional (species suppression) and structural (cover and tendency toward high cover) aspects of abundance. SDI is defined as:

$$\mathrm{SDI} = (\mathrm{THC} + \mathrm{MSS} + \mathrm{MC})/3$$

where

$$\begin{aligned}\mathrm{THC} &= \text{tendency towards high cover}\\ &= (\text{the number of times a species has the highest cover})\\ &\quad / (\text{total occurrences});\\ \mathrm{MSS} &= \text{Mean species suppression} = \text{inverse of plot richness}\\ &= 1/(\text{number of species in a plot});\\ \mathrm{MC} &= \text{mean cover}\\ &= \text{average of midpoints of percent cover classes}\end{aligned}$$

Species were considered dominant when the SDI value was above the mean for that transect at that sampling date. We also assigned a dominance form to each occurrence of a dominant species using the individual values for THC, MSS, and MC, as monotype, ubiquitous, matrix, diffuse, compressed, aberrant, and patchy (Frieswyk et al. 2007). These dominance forms are defined as: monotype, which has high values for MC, MSS and THC; ubiquitous has high MC and MSS; matrix is characterized by high MC and THC; diffuse has high MC; compressed, high MSS and THC; aberrant, high MSS, and patchy, high THC. We present SDI dominance forms aggregated through time in the period 1985–2007 and by time period a given species was dominant, regardless of the form.

We used percent cover data to analyze community structure. We applied univariate and multivariate methods from the PRIMER package (Clarke and Warwick 1997). Univariate diversity indices were:

$$N_o = \text{species richness} = \text{total number of species present}$$

$$N_1 = \exp(\mathrm{H}'), \text{ where } \mathrm{H}' = \text{Shannon} - \text{Wiener diversity index}$$

Multivariate analyses included a one-way analysis of similarities (ANOSIM) between sites using a dissimilarity matrix with standardized and fourth root transformed data, as this transformation takes into account the occurrence of rare species (Clarke and Warwick 1997). We plotted dissimilarities in a non-metric multidimensional scaling (MDS) graph. We employed hierarchical cluster analysis to identify groups and a Similarity Percentages (SIMPER) to assess species contributions to within-groups similarity, and between groups dissimilarity.

Results

Interstitial soil salinity in the non-tidal area was usually above the range of that measurable with the refractometer (up to 160). We used this maximum value to characterize the samples with the highest salinity, recognizing that it represents an underestimation of the actual salinity. For the whole study period, the mean interstitial soil salinity at the non-tidal area was 143±12, versus 40.3±2.6 at the tidal area ($p<0.01$), indicating interstitial soil salinity in the non-tidal area was at least 3.5 times the salinity of soil in the tidal area. Interstitial soil salinity was reduced to 99.3±10.1 in February 2003 ($p<0.01$) and to 36.7±4.6 in February 2005 ($p<0.05$) in the non-tidal area. Statistically significant reductions in interstitial soil salinity were observed at the tidal area in the same years ($p<0.001$ Fig. 2a).

Soil moisture was higher in the tidal area (36.2±1% humidity) than in the non-tidal area, (26±1% humidity; $p<0.001$), with 2003 showing the highest values in both sites ($p=0.003$). Comparison of data measurements performed in February with those from September indicate lower soil moisture values in September, which is consistent with the Mediterranean climate of the region ($p=0.008$; Fig. 2b).

Between November 1984 and November 1986, the short-term response of salt marsh vegetation to tidal restriction was the disappearance of *Salicornia bigelovii*, *Suaeda esteroa*, and *Jaumea carnosa* from the non-tidal marsh (Ibarra-Obando and Poumian-Tapia 1991). Between 1986 and September 2001, when we began the current study, four additional salt marsh plain species disappeared: the obligate parasite *Cuscuta salina* Engelm.; the long-lived perennial, *Distichlis spicata* (L.) Greene; *Triglochin maritima,* a perennial with ephemeral shoots and perennial

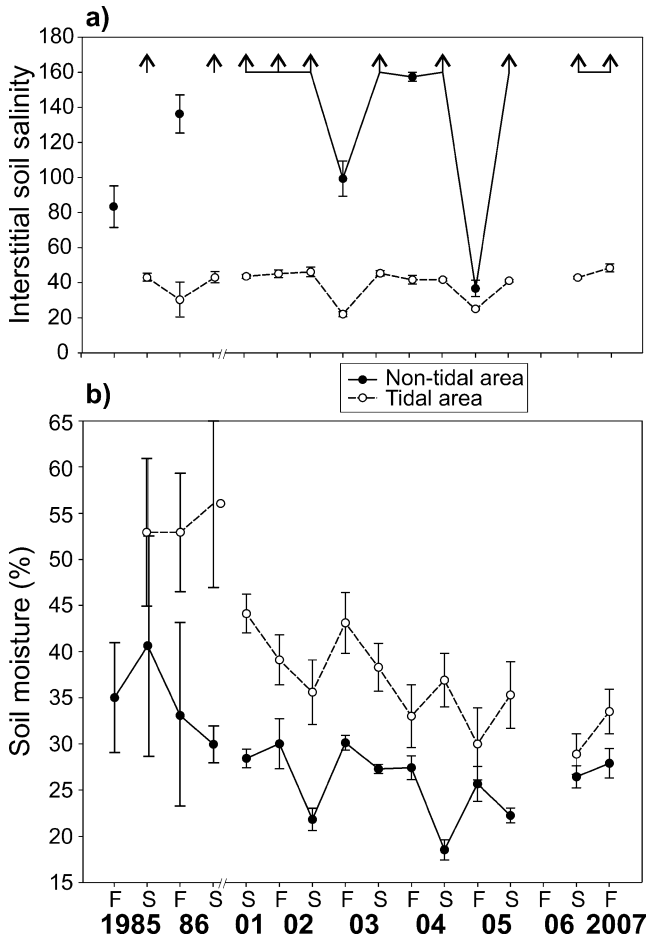

Fig. 2 Sediment characteristics during 1985–1986 and 2001 to 2007 at the tidal (*white circles*) and non-tidal areas (*black circles*). **a** Interstitial soil salinity. *Arrows* represent values that exceed the refractometer's scale, and **b** Percent soil moisture. *Dots* represent means and *bars* represent ± 1 SE. February 2006 was not sampled

roots, and *Limonium californicum*, a long-lived perennial. Data on percent cover and percent frequency of occurrence for each species *can be consulted as electronic supplementary material* (Appendix 1). We will focus in results at the community level, with species in figures arranged following their zonation pattern as described in Zedler (1982). It is worth noting that although a total of eight species were dominant at one point or another, not all eight were concurrently dominant.

The SDI showed changes in the dominant species and in dominance through time (1985–1986; 2001–2007) in both the tidal and non-tidal marsh. In the tidal marsh, we found that a larger number of species (eight) were dominant between 1985 and 2007, as compared with the non-tidal site (Fig. 3). At the tidal marsh, *J. carnosa* was consistently dominant every year sampled. The eight species dominant in the tidal marsh were most often the monotype and diffuse forms (Fig. 4). In the non-tidal marsh, we found that following the construction of the dike, mean SDI indicated that *B. maritima* rapidly became a monotypic dominant and remained so through 2007. *S. pacifica* and *J. carnosa* were also dominant for a few years (Fig. 3) and presented different types of dominance through the period sampled, most often the monotype form (Fig. 4). The dominance of *B. maritima* at the non-tidal marsh allowed us to accept our first hypothesis, which stated that gaps would be occupied by salt-tolerant, deep rooted clonal perennials.

Between September 1985 and February 2007 tidal exclusion promoted a reduction in species richness and diversity. For species richness, N_o, we found an average value of 10±0.18 species per 0.25 m^2 at the tidal area, versus 4.4±0.32 species per square meter at the non-tidal area (p=0.000). The average species diversity index, N_1, in the tidal area was 5.87±0.24, and 3.01±0.14 index at the non-tidal area (p=0.000) (Table 1). As a consequence, we accepted our second hypothesis, which stated that a significant reduction in species richness and diversity would characterize the non-tidal site.

One year after tidal exclusion, in 1985, a significant difference between tidal and non-tidal areas had been established. Since that date, two different salt marsh floras have developed, as indicated by the ANOSIM test (p= 0.001). This figure shows the tidal group to the right, and the non-tidal group to the left, with February and September 1985 at the non-tidal site as the transition between groups. The tidal group shows a seasonal separation that is no longer present in the non-tidal group. The stress value of 0.05 indicates that this is a good

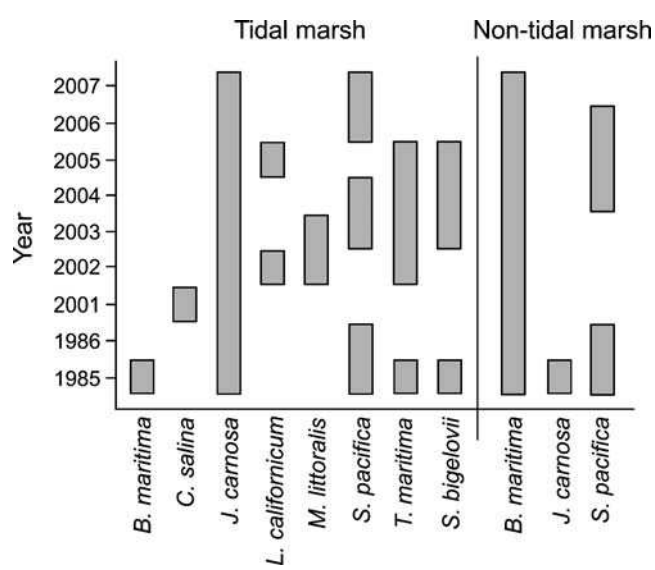

Fig. 3 Species dominance through time (1985–2007) for the tidal and non-tidal sites. Dominance was calculated with the Species Dominance Index (Frieswyk et al. 2007), that measures three attributes of dominance: cover, species suppression, and tendency towards high cover. *Gray bars* indicate which years the species was dominant

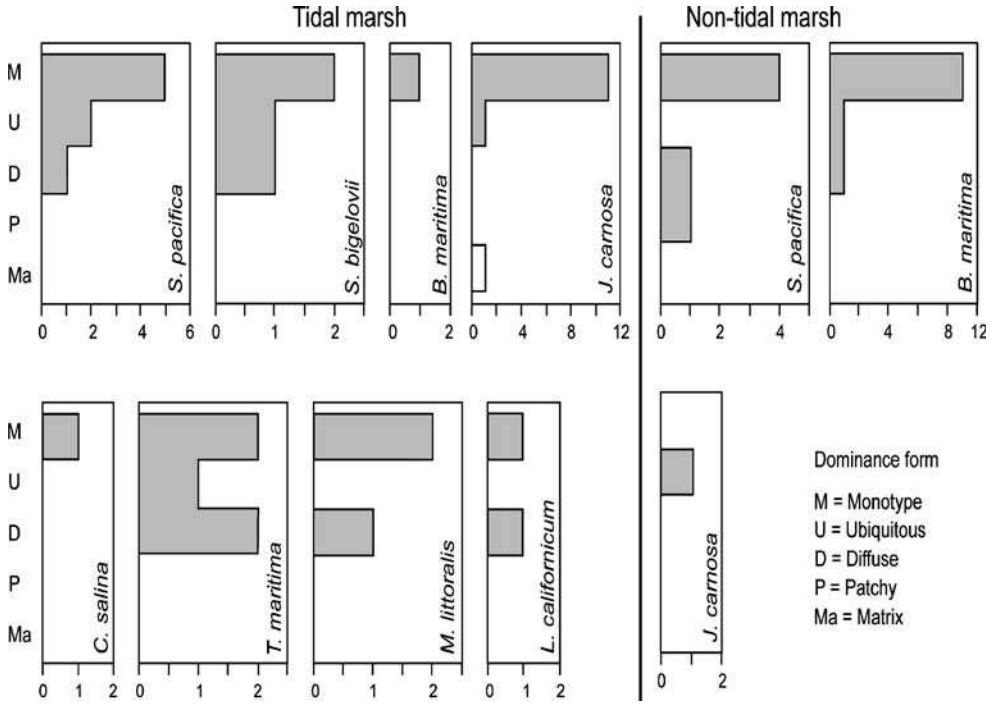

Fig. 4 Number of times a species showed the five types of dominance in the tidal and non-tidal marshes in the period 1985–2007. Two additional types of dominance, compressed, and aberrant, were never present in our samples

representation of how the sites have differentiated from each other (Fig. 5).

When we compared the consistency of species composition over time, we noticed that it was fairly similar between tidal, 82.54%, and non-tidal sites, 78.80%. Major contributors at the tidal site were: *J. carnosa*, 18.24; *S. pacifica,* 13.86; and *L. californicum*, 12.82%, meaning that these species were always present. Considering these three species, the cumulative similarity is 44.92%. At the non-tidal site, *B. maritima* and *S. pacifica* contributed with 35.89% and 30.73% respectively, for a cumulative similarity of 66.6%. The high percentage contributed by these two species between 1985 and 2007 indicates that perturbed conditions which allowed them to become so abundant

Table 1 Species richness (N_0), and Shannon–Wiener diversity index (N_1) at EPB for the two study periods: 85–86 and 01–07

		Tidal area		Non-tidal area	
Year	Month	N_0	N_1	N_0	N_1
1985	F	NM	NM	6	3.939
	S	11	6.778	8	3.626
1986	F	9	4.547	5	3.002
	S	9	5.803	3	2.674
2001	F	NM	NM	NM	NM
	S	10	4.369	3	2.076
2002	F	10	6.722	4	2.307
	S	10	6.159	4	3.150
2003	F	10	4.891	4	2.362
	S	10	5.731	4	2.521
2004	F	9	4.798	4	3.509
	S	11	6.769	4	3.055
2005	F	10	6.263	4	3.759
	S	11	6.498	4	2.873
2006	F	NM	NM	NM	NM
	S	10	7.191	5	3.158
2007	F	10	5.768	4	3.177
	Mean±1 SE	10±0.181	5.87±0.244	4.4±0.320	3.01±0.142

F February, *S* September, *NM* Not measured.

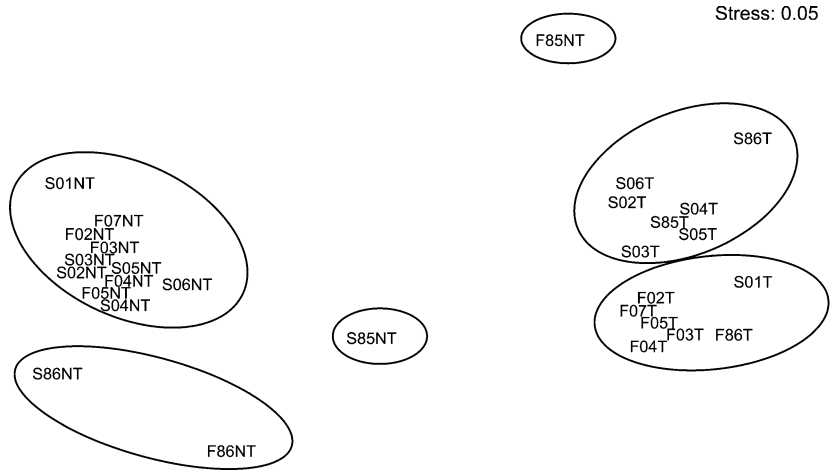

Fig. 5 MDS plot for the February (*F*) and September (*S*) data, collected at the tidal (*T*) and non-tidal (*NT*) areas during 1985–1986 and 2001–2007. Two different groups are clearly shown, distinguishing the tidal and non-tidal groups, with September and February 1985 as the transition between them

have persisted all these years. The average dissimilarity between the tidal and non-tidal sites is 51.29%. The two species that had the most contribution to this dissimilarity were *J. carnosa*, 16.90%, and *L. californicum*, 12.79%, both of which were present at the non-tidal site in 1985, but no detected since then (Appendix 1).

Changes in the topographic profiles between 1985 and 2005 are shown in Fig. 6, using two types of representations. For tidal and non-tidal areas, the top figure shows the area between the two profiles, making the difference between sediment gain and loss. The bottom figure shows these changes as histograms, with bars every meter along the transect. In the histograms, sediment gains are above zero and sediment losses below zero. The topographic profile in the non-tidal marsh plain is 150 m long, with an elevation range between 1.64 and 0.58 m with respect to MLLW. No natural channels are present. Besides percolation and runoff, vehicles driving on the surface also cause disturbance to the marsh plain. By 2005 this transect showed an elevation loss along essentially its entire length (Fig. 6). A very short portion, near 120 m, did not lose elevation and actually had a slight gain. So, with this exception, the average elevation loss was −44.6 cm. The tidal marsh showed modest elevation losses, 10–20 cm, at either end, substantial elevation gain, about 30 cm near 100 m, and essentially no change between 40 and 90 m. The average change in this transect was −3.4 cm (Fig. 6).

Discussion

The dike construction at EPB represents a press disturbance with a ramp response (Lake 2000), as after the initial species loss, subsequent losses have taken place. In total, seven species have been lost in 22 years, including all life forms: annuals, short and long-lived perennials, ephemerals, and parasites. The disappearance of these species translates into the loss of wetland ecosystem functions and services, for example the community engineering function performed by *T. maritima* (Fogel et al. 2004; Morzaria-Luna 2005), and the community's ability to recover from disturbance provided by *S. bigelovii* and *S. esteroa* seedlings, which can fill canopy gaps (Zedler et al. 2001).

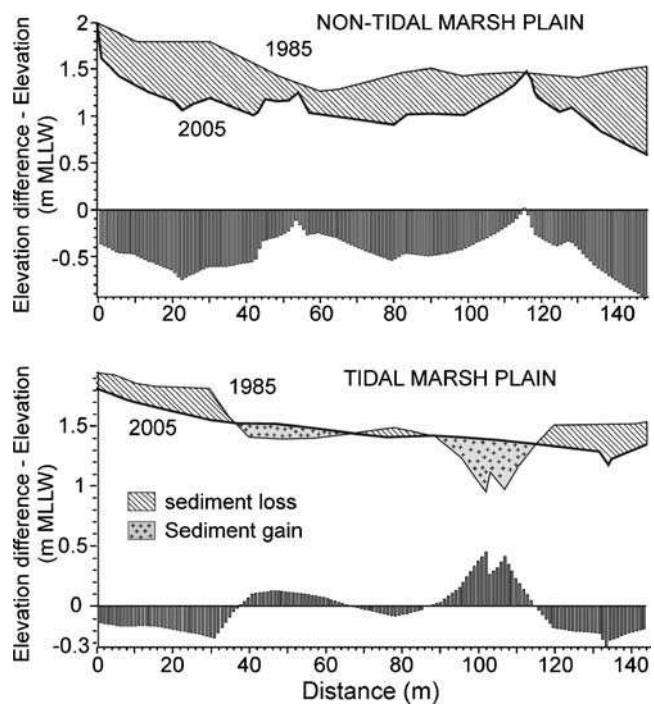

Fig. 6 Topographic profiles at the tidal and non-tidal marsh plain for 1985 and 2005. For tidal and non-tidal areas, the top figure shows the area between the two profiles, making the difference between sediment gain and loss. The *bottom figure* shows these changes as histograms, with *bars* every meter along the transect. In the histograms, sediment gains are above zero and sediment losses below zero

Soil Conditions

Shortly after dike construction, sediments became dry, and hypersaline. This condition persists until present, and is only temporarily ameliorated during rainy winters (Fig. 2). Similar short term salinity reductions due to rainfall have been reported for Tijuana Estuary in southern California (Zedler 1983), and in the Nueces Marsh in south Texas (Alexander and Dunton 2002).

Hypersaline soil conditions can develop in bare patches of salt marsh soil; in a New England estuarine marsh Bertness et al. (1992) found that soil surface salinity in bare patches was 2–3 times higher than in vegetation, with a seasonal increase during summer. The absence of plant shading was identified as the mechanism responsible for the elevated salinities, as soils are exposed to radiation and evaporation (Zedler 1982; Bertness 1991). The role of salinity in structuring wetlands is widely recognized. Not only do dominant species shift along an estuarine salinity gradient (e.g., Latham et al. 1994; Piernik 2003; Crain et al. 2004), but species diversity is reduced as salinity increases (Crain et al. 2004). Salinity effects have been found to be greater under disturbance conditions (Baldwin and Mendelssohn 1998). Bare patches are colonized by fugitive species, which are displaced to disturbed habitats where they can find refuge from superior competitors (Bertness et al. 1992). Fugitive species, like *Distichlis*, can rapidly colonize hypersaline gaps vegetatively, depending on physiological integration with ramets rooted outside gaps (Brewer and Bertness 1996).

The tidal restriction at EPB likely resulted in further changes in soil chemistry that can affect plant community structure, including higher sulfide concentration (Baldwin and Mendelssohn 1998) and lower soil carbon accumulation (Chmura et al. 2003). Soil chemistry needs to be included in future monitoring of the study area.

Species Dominance

SDI allowed us to characterize both which species dominate and how they dominate, as indicators of community condition. In the tidal marsh, we found species such as *T. maritima*, *S. pacifica*, and *Mönanthochloe littoralis* with different dominance forms in the period sampled. The most common types of dominance forms, in addition to monotype, were ubiquitous and diffuse both indicative of marsh plain vegetation with many associated species, as found in diverse salt marshes in Baja California (Morzaria-Luna et al. 2004). Several factors might contribute to the presence of different dominance forms, including small-scale spatial differences in abiotic attributes, such as nutrient availability and sedimentation levels (Frieswyk et al. 2007) and anthropogenic stress, such as vehicles driving over the marsh plain.

J. carnosa was dominant in the tidal marsh, most frequently of monotypic form (Fig. 4) and was only dominant in the non-tidal marsh in 1985 (Fig. 3). This species is frequently colonized by arbuscular mycorrhizas, which enhance survival by increasing nutrient acquisition and soil particle aggregation (Brown and Bledsoe 1996), leading it to thrive on the marsh plain.

SDI identified three dominant marsh plain species in the non-tidal marsh during the period studied 1985–2007. *B. maritima* was consistently a dominant of monotype form, indicating widespread high cover and few associated species (Frieswyk et al. 2007). In addition to producing more roots in water logged soils (Sullivan et al. 2007), *B. maritima* is a clonal species and clonality has been found to be particularly important for species invading hypersaline soils, as it helps buffer the plant's stress response (Brewer and Bertness 1996; Pennings and Callaway 2000). The structure and development of root systems of fugitive plants reflect, in part, patterns of resource utilization, with root systems of species inhabiting dry disturbances being more extensive than the root systems of species inhabiting more moist sites (Platt and Weis 1977).

In their study on the effects of freshwater inundation on the coastal marshlands of the Nueces estuary, Texas, Alexander and Dunton (2002) confirmed their hypothesis that succulent halophytes highly adapted to hypersaline and dry conditions, like *B. maritima*, are relatively intolerant of continuously waterlogged soils. Alexander and Dunton (2002) found that prolonged soil saturation following flooding acted as a disturbance and resulted in reduced cover of *B. maritima*.

Community Structure

Tidal exclusion resulted in a reduction in species richness and diversity (Table 1), as has been reported in both arid and humid-climate salt marshes. For example, 26 years after drainage of a fen meadow in the Netherlands 45% of the species had been lost (Grootjans et al. 2005). At Tijuana Estuary, 10 years after an 8 months mouth-closure episode, species richness and diversity were still low (Zedler and West 2008). While Ritter et al. (2008) found the lowest site-level total species richness under minimal tidal exchange in the Elkhorn Slough watershed of central California. In the case of the EPB, tidal exclusion represented a press disturbance, to which some of the highly diverse salt marsh plain species could not recover,

leading to the present dominance of the salt-tolerant, *B. maritima.* Salinity can have additive effects with other variables to reduce species richness. For example, in two Louisiana marshes, salinity and water level had significant effects on species richness only following disturbance (Baldwin and Mendelssohn 1998). In this study, gaps created after disturbances were colonized by more stress-tolerant species, which were more salt- or flood-tolerant communities, depending on the water level and salinity at the time of disturbance.

The observed decrease in species richness likely translates into the loss of ecosystem functions. *T. maritima* which was originally found at the non-tidal site, sequesters a large amount of *N* as indicated by the high concentration of *N* in its roots (Morzaria-Luna 2005) and ameliorates waterlogging stress through root production (Fogel et al. 2004). The two other species lost from the non-tidal site, *S. bigelovii* and *S. esteroa,* play important roles in filling canopy gaps and their loss could impair the plant community's ability to recover from disturbance. Not only that, but given its rapid height growth *S. esteroa* seems to be the first perch for the endangered Belding's Savannah sparrow, *Passerculus sandwichensis beldingi* (Zedler et al. 2001). In California (USA) this species is endangered (Massey 1977; Unitt 1984), while in Baja California (Mexico) it is considered a threatened species (SEMARNAT 2002). When the full complement of marsh plain species is present, the community presumably has maximum variety of interspecific interactions and feedback mechanisms (Zedler et al. 2001). This is exemplified by *T. maritima*, which can act as a keystone species by contributing to spatial variability in *N* availability (Morzaria-Luna 2005), and thus prevent overdominance by *S. pacifica*, *F. salina*, or *J. carnosa*, and opening space for seedling recruitment of *S. bigelovii* and *S. esteroa* (Zedler et al. 2001). For these regional marshes, it has been found that diversity levels predict 32% of the variability in *N* retention (Callaway et al. 2003). Although none of these functions has been measured at EPB, we assume that the loss is at least as large as that observed by Callaway et al. (2003).

At EPB, tidal and non-tidal marshes now represent two different groups as indicated by the ANOSIM and SIMPER analyses: 51.3% dissimilarity (Fig. 5). The fact that *S. pacifica* is present in both groups is consistent with its wide distribution in Californian marshes, including those that have experienced tidal exclusion (Zedler et al. 2001). *B. maritima* and *J. carnosa* were also present in both groups, although they were both rare in one group or the other.

In contrast with the salination process that results from tidal restriction in arid estuaries (e.g., Alexander and Dunton 2002; Zedler and West 2008; Ritter et al 2008; this study), in humid climate estuaries embankment generally results in a desalination process, as wetlands receive fresh water input mainly from precipitation and drainage (Joenje 1974; Joenje and Verhoeven 1993). In quickly desalinating areas, a rapid increase of biomass and the appearance of many species have been reported. For example, in the Lauwerszee-polder, The Netherlands, in a single year the number of species increased from 30 to over 150 (Joenje 1974); clay sediments become better aerated, and percolating precipitation water washes the salt downwards allowing the development of vegetation (Joenje and Verhoeven 1993).

Final Remarks

This study is the first to document the loss of salt marsh vegetation through a reduction in soil moisture and an increase in soil salinity levels in the coastal zone of Mexico. Our findings illustrate how anthropogenic impacts can lead to hypersaline conditions that promote a shift in species dominance and reductions in salt marsh species richness and diversity. These trends confirm, once more, the fragility of estuaries in general and of salt marsh vegetation in particular.

Baja California is in the process of establishing a "Plan for Ecological Regulation" for its coastal areas. The Estero de Punta Banda (EPB) should be included as part of the Todos Santos Bay system and activities in the estuary must be regulated. In February 2006, the EPB was designated for inclusion in the Ramsar List of Wetlands of International Importance, acknowledging "its relevance for the conservation of global biological diversity and for sustaining human life through the ecological and hydrological functions it performs" (Ramsar Convention on Wetlands, 1971; http://www.ramsar.org/). We hope this designation establishes the protection status this site requires, and as part of it, tidal regime can be reestablished.

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Appendix 1

Percent cover and percent frequency of occurrence for salt marsh plain species at Estero de Punta Banda, Baja California, Mexico, between February 1985 and February 2007. F = February; S = September. NT = Non tidal marsh; T = Tidal marsh; NM = Not measured.

PERCENT COVER

Sampling date	*Sarcocornia pacifica*		*Salicornia bigelovii*		*Limonium californicum*	
	NT	T	NT	T	NT	T
F85	20	NM	0	NM	0	NM
S85	42	15	3	14	0.6	6
F86	18	18	0	0	0	8
S86	29	4	0	26	0	8
Mean	27.3	12	0.75	13	0.15	7.3
Standard error	5.5	4.3	0.75	7.5	0.15	0.7
Maximum	42	18	3	26	0.6	8
Minimum	18	4	0	0	0	6

PERCENT COVER

Sampling date	*Sarcocornia pacifica*		*Salicornia bigelovii*		*Limonium californicum*	
	NT	T	NT	T	NT	T
S01	9.5	11.6	0	0.0	0	13.4
F02	6.6	24.3	0	0.0	0	13.8
S02	4.4	13.4	0	4.8	0	6.3
F03	7.6	14.5	0	0.0	0	8.1
S03	6.4	12.4	0	11.7	0	5.2
F04	11.9	15.6	0	0.0	0	7.9
S04	16.2	4.1	0	18.5	0	7.4
F05	11.7	11.5	0	0.0	0	12.7
S05	6.4	9.5	0	16.9	0	4.9
S06	20.9	13.5	0	10.8	0.8	6.8
F07	8.8	20.4	0	0.0	0	10.5
Mean	10.0	13.7	0.0	5.7	0.1	8.8
Standard error	1.5	1.6	0.0	2.2	0.1	1.0
Maximum	20.9	24.3	0.0	18.5	0.8	13.8
Minimum	4.4	4.1	0.0	0.0	0.0	4.9

PERCENT COVER

Sampling date	*Suaeda esteroa*		*Monanthochloe littoralis*		*Jaumea carnosa*	
	NT	T	NT	T	NT	T
F85	0.8	NM	2	NM	17	NM
S85	0.03	4	1	3	5	38
F86	0	2	0	0	3	57
S86	0	8	0	0.8	0	46
Mean	0.21	4.7	0.8	1.3	6.25	47
Standard error	0.2	1.8	0.5	0.9	3.73	5.5
Maximum	0.8	8	2	3	17	57
Minimum	0	2	0	0	0	38

PERCENT COVER

Sampling date	*Suaeda esteroa*		*Monanthochloe littoralis*		*Jaumea carnosa*	
	NT	T	NT	T	NT	T
S01	0	2.3	3.2	2.8	0	50.8
F02	0	9.2	4.4	14.5	0	20.3
S02	0	6.5	10.7	19.6	0	25.1
F03	0	2.0	4.4	3.9	0	36.6
S03	0	0.9	8.3	3.6	0	35.1
F04	0	2.6	12.0	3.6	0	41.2
S04	0	6.7	3.2	12.3	0	20.9
F05	0	2.8	6.3	4.1	0	34.0
S05	0	2.1	5.2	5.2	0	23.6
S06	0	10.3	5.7	11.4	0	23.2
F07	0	0.4	11.7	5.8	0	29.4
Mean	0.0	4.2	6.8	7.9	0.0	30.9
Standard error	0.0	1.0	1.0	1.7	0.0	2.9
Maximum	0.0	10.3	12.0	19.6	0.0	50.8
Minimum	0.0	0.4	3.2	2.8	0.0	20.3

PERCENT COVER

Sampling date	*Cuscuta salina*		*Frankenia salina*		*Batis maritima*	
	NT	T	NT	NT	NT	T
F85	0	NM	0	NM	2	NM
S85	0	5	6	1	26	12
F86	0	4	3	1	22	4
S86	0	13	13	0	47	15
Mean	0	7.3	5.5	0.7	24.3	10.3
Standard error	0	2.8	2.8	0.3	9.2	3.3
Maximum	0	13	13	1	47	15
Minimum	0	4	0	0	2	4

PERCENT COVER

Sampling date	*Cuscuta salina*		*Frankenia salina*		*Batis maritima*	
	NT	T	NT	T	NT	T
S01	0	35.9	0.0	0.5	34.9	0.2
F02	0	1.4	0.3	1.5	26.6	2.3
S02	0	0.4	4.1	2.7	22.5	1.6
F03	0	1.9	0.6	2.1	29.1	0.6
S03	0	0.4	5.4	0.8	48.2	5.7
F04	0	0.0	5.1	2.9	24.0	0.6
S04	0	4.0	2.7	0.4	16.9	2.2
F05	0	3.9	6.9	5.4	14.8	3.3
S05	0	4.8	2.1	0.3	21.9	1.8
S06	0	1.0	1.8	0.3	23.2	10.3
F07	0	3.6	0.5	2.0	10.2	2.0
Mean	0.0	5.2	2.7	1.7	24.7	2.8
Standard error	0.0	3.1	0.7	0.5	3.1	0.9
Maximum	0.0	35.9	6.9	5.4	48.2	10.3
Minimum	0.0	0.0	0.0	0.3	10.2	0.2

PERCENT COVER

Sampling date	*Distichlis spicata*		*Triglochin maritima*	
	NT	T	NT	T
F85	11	NM	0	NM
S85	0	3	0.2	1
F86	0	1	0.2	20
S86	0	2	0	0
Mean	2.8	2	0.1	7
Standard error	2.8	0.6	0.06	6.5
Maximum	11	3	0.2	20
Minimum	0	1	0	0

PERCENT COVER

Sampling date	*Distichlis spicata*		*Triglochin maritima*	
	NT	T	NT	T
S01	0	0.5	0	1.6
F02	0	0.8	0	29.2
S02	0	0.4	0	0.0
F03	0	0.1	0	35.6
S03	0	0.0	0	6.8
F04	0	0.2	0	16.7
S04	0	0.3	0	0.4
F05	0	0.1	0	25.3
S05	0	0.4	0	1.7
S06	0	0.9	0	0.0
F07	0	0.1	0	9.7
Mean	0.0	0.3	0.0	11.5
Standard error	0.0	0.1	0.0	4.0
Maximum	0.0	0.9	0.0	35.6
Minimum	0.0	0.0	0.0	0.0

PERCENT FREQUENCY OF OCCURRENCE

Sampling date	*Sarcocornia pacifica*		*Salicornia bigelovii*		*Limonium californicum*	
	NT	T	NT	T	NT	T
F85	95	NM	0	NM	0	NM
S85	95	95	25	95	25	55
F86	90	95	0	0	0	70
S86	85	95	0	95	0	70
Mean	91.3	95	6.3	63	6.3	65
Standard error	2.4	0	6.3	31.7	6.3	5
Maximum	95	95	25	95	25	70
Minimum	85	95	0	0	0	55

PERCENT FREQUENCY OF OCCURRENCE

Sampling date	*Sarcocornia pacifica*		*Salicornia bigelovii*		*Limonium californicum*	
	NT	T	NT	T	NT	T
S01	30	90	0	0	0	100
F02	20	95	0	0	0	90
S02	25	85	0	45	0	90
F03	35	82	0	0	0	94
S03	30	70	0	88	0	53
F04	35	75	0	0	0	70
S04	35	50	0	70	0	60
F05	50	80	0	0	0	75
S05	30	70	0	80	0	55
S06	55	85	0	70	5	60
F07	60	80	0	0	0	60
Mean	36.8	78.4	0.0	32.1	0.5	73.4
Standard error	3.8	3.7	0.0	11.5	0.5	5.2
Maximum	60.0	95.0	0.0	88.2	5.0	100.0
Minimum	20.0	50.0	0.0	0.0	0.0	52.9

PERCENT FREQUENCY OF OCCURRENCE

Sampling date	*Suaeda esteroa*		*Monanthochloe littoralis*		*Jaumea carnosa*	
	NT	T	NT	T	NT	T
F85	5	NM	45	NM	100	NM
S85	5	45	25	20	65	100
F86	0	35	0	5	40	100
S86	0	35	0	5	0	100
Mean	2.5	38	17.5	10	51.3	100
Standard error	1.4	3.3	10.9	5	21.1	0
Maximum	5	45	45	20	100	100
Minimum	0	35	0	5	0	100

PERCENT FREQUENCY OF OCCURRENCE

Sampling date	*Suaeda esteroa*		*Monanthochloe littoralis*		*Jaumea carnosa*	
	NT	T	NT	T	NT	T
S01	0	40	5	70	0	100
F02	0	50	5	70	0	85
S02	0	45	20	75	0	65
F03	0	47	5	65	0	100
S03	0	59	15	53	0	82
F04	0	45	15	55	0	65
S04	0	50	5	60	0	75
F05	0	45	10	70	0	80
S05	0	30	10	50	0	60
S06	0	60	15	55	0	55
F07	0	10	10	35	0	60
Mean	0.0	43.7	10.5	59.8	0.0	75.2
Standard error	0.0	4.2	1.6	3.5	0.0	4.7
Maximum	0.0	60.0	20.0	75.0	0.0	100.0
Minimum	0.0	10.0	5.0	35.0	0.0	55.0

PERCENT FREQUENCY OF OCCURRENCE

Sampling date	*Cuscuta salina*		*Frankenia salina*		*Batis maritima*	
	NT	T	NT	T	NT	T
F85	0	NM	0	NM	65	NM
S85	0	50	35	40	60	65
F86	0	40	40	15	100	40
S86	0	40	75	0	100	40
Mean	0	43	37.5	18	81.3	48.3
Standard error	0	3.3	15.3	11.7	10.9	8.3
Maximum	0	50	75	40	100	65
Minimum	0	40	0	0	60	40

PERCENT FREQUENCY OF OCCURRENCE

Sampling date	*Cuscuta salina*		*Frankenia salina*		*Batis maritima*	
	NT	T	NT	T	NT	T
S01	0	70	0	30	55	40
F02	0	70	20	50	70	60
S02	0	20	35	45	75	25
F03	0	12	50	41	95	35
S03	0	18	35	35	100	35
F04	0	0	40	45	95	20
S04	0	45	30	25	70	25
F05	0	35	65	70	100	30
S05	0	25	25	30	75	20
S06	0	10	35	20	95	60
F07	0	20	15	35	65	35
Mean	0.0	29.5	31.8	38.8	81.4	35.1
Standard error	0.0	7.0	5.2	4.2	4.8	4.2
Maximum	0.0	70.0	65.0	70.0	100.0	60.0
Minimum	0.0	0.0	0.0	20.0	55.0	20.0

PERCENT FREQUENCY OF OCCURRENCE

Sampling date	*Distichlis spicata*		*Triglochin maritima*	
	NT	T	NT	T
F85	100	NM	0	NM
S85	0	50	10	20
F86	0	35	5	100
S86	0	35	0	0
Mean	25	40	3.8	40
Standard error	25	5	2.4	30.6
Maximum	100	50	10	100
Minimum	0	35	0	0

PERCENT FREQUENCY OF OCCURRENCE

Sampling date	*Distichlis spicata*		*Triglochin maritima*	
	NT	T	NT	T
S01	0	30	0	10
F02	0	35	0	80
S02	0	20	0	0
F03	0	18	0	82
S03	0	0	0	35
F04	0	10	0	70
S04	0	0	0	50
F05	0	10	0	80
S05	0	25	0	40
S06	0	25	0	0
F07	0	10	0	45
Mean	0.0	16.6	0.0	44.8
Standard error	0.0	3.5	0.0	9.5
Maximum	0.0	35.0	0.0	82.4
Minimum	0.0	0.0	0.0	0.0

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