



# Macrofaunal succession and community structure in *Salicornia* marshes of southern California

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Lack of basic understanding of ecosystem structure and function forms a major impediment to successful conservation of coastal ecosystems. This paper provides a description of the fauna and examines faunal succession in *Salicornia*-vegetated sediments of southern California. Environmental attributes (vegetation and sediment properties) and macrofaunal (animals  $\geq 0.3$  mm) community structure were examined in sediments of five natural, southern California *Salicornia* spp. marshes (Tijuana Estuary, San Diego Bay, Mission Bay, Upper Newport Bay and Anaheim Bay) and in created *Salicornia* marshes 16 months to 10 years in age, located within four of the bays. Oligochaetes and insects were the dominant taxa in both natural (71 to 98% of total fauna) and created (91 to 97%) marshes. In San Diego, Newport and Anaheim Bays, macrofaunal densities were generally higher in the created marshes (88 000 to 290 000 ind  $m^{-2}$ ) than in their natural counterparts (26 000 to 50 000 ind  $m^{-2}$ ). In the youngest system, Mission Bay, the reverse was true (natural: 113 000 vs created: 28 000 ind  $m^{-2}$ ). Similar species numbers were recorded from the created and adjacent natural marshes. Insects, especially chironomids, dolichopodids, and heleids, as well as the naidid oligochaete, *Paranais litoralis*, characterize early successional stages. Enchytraeid and tubificid oligochaetes reflect later succession evident in natural and older created marshes. Sediment organic matter (both combustible and below-ground plant biomass) was the environmental variable most commonly associated with densities of various macrofaunal taxa. These relationships were generally negative in the natural marshes and positive in the created marshes. Within-bay comparisons of macrofauna from natural *Salicornia*- vs *Spartina*-vegetated habitat in San Diego and Mission Bays revealed lower macrofaunal density (San Diego Bay only), proportionally fewer oligochaetes and more insects, and no differences in species richness in the *Salicornia* habitat. The oldest created *Salicornia* marsh (San Diego Bay) exhibited an assemblage intermediate in composition between those of the natural *Salicornia*- and *Spartina*-vegetated marshes. These results suggest: (a) faunal recovery following *Salicornia* marsh creation can require 10 or more years, (b) high macrofaunal variability among bays requires marsh creation reference site selection from within the same bay, and (c) *Spartina*-based research should not be used for *Salicornia* marsh management decisions.

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## Introduction

Salt marshes in arid climates around the world, such as the Mediterranean, South Africa and Australasia, are often dominated by succulents from the family Chenopodiaceae (Adam, 1990; pp. 154–179) and southern California is no exception. Two species of *Salicornia* (pickleweed), the perennial *S. virginica* and the annual *S. bigelovii*, are dominant vascular plants in many southern California salt marshes. These *Salicornia* species often co-occur with *Spartina foliosa* (Pacific cordgrass) at lower tidal elevations, and with other succulents and herbaceous plants at higher tidal levels (MacDonald, 1977; Zedler, 1982). On the Pacific coast of North America, in bays where tidal flushing is insufficient to support stands of *S. foliosa*, *S. virginica* may become a dominant (Ibarra-Obando & Poumian-Tapia 1991; Zedler 1996a); occasionally, dense monospecific stands of *S. virginica* may cover a marsh

(Zedler, 1996a). In addition to natural wetlands, *Salicornia* spp. often are found in created marshes in southern California. *Salicornia virginica* may be planted intentionally (Zedler, 1984, 1996a; Callaway *et al.*, 1997), but both *Salicornia* species colonize well on their own (Josselyn, 1982; Zedler, 1984). This is particularly true of *S. bigelovii*, which appears rapidly in unvegetated intertidal flats (Chapman, 1940; Neuenschwander *et al.*, 1979).

An understanding of *Salicornia*-dominated ecosystems is particularly important in the context of wetland conservation, biodiversity maintenance, management and restoration. Loss of coastal wetlands in California has been extensive and continues at an alarming rate (Schoenherr, 1992; Murray & Bray, 1993; Zedler 1996b). *Salicornia virginica* habitat in southern California marshes now support one endangered plant species (salt marsh birds beak, *Cordylanthus maritimus*) and two endangered birds, Belding's

Savannah sparrow (*Passerculus sandwichensis beldingi*) and, in some areas that lack suitable *Spartina* habitat, the light-footed clapper rail (*Rallus longirostris levipes*) (Massey *et al.*, 1984). Conservation of these habitats begins with a thorough knowledge of the plant and animal species that occur there. Species inventories or checklists are relatively simple and can be important for detecting shifts in community structures (Droege *et al.*, 1998), especially in southern California coastal areas where both baseline (pre-human impact) and benchmark (post-human impact point of reference) data, and truly pristine reference sites are commonly absent (Murray & Bray, 1993; Tegner & Dayton, 1997; Dayton *et al.*, 1998; Talley *et al.*, 1998a).

Scientific emphasis in California and elsewhere in the country has generally been on *Spartina* rather than *Salicornia* marshes (Matthews & Minello, 1994; Levin & Talley, in press). Investigations that have been conducted in *Salicornia* habitats of southern California marshes have focused on the plants themselves, including responses to salinity variation (Zedler, 1983; Callaway *et al.*, 1997), nitrogen additions (Covin & Zedler, 1988), groundwater inputs (Page, 1995), varying hydrologic regimes (Callaway *et al.*, 1997) and interactions with an exotic annual grass (Callaway & Zedler, 1998). There is limited information about the fauna associated with *Salicornia* spp. stands, about plant-animal interactions or the faunal differences between *S. bigelovii* and *S. virginica*, and *S. virginica* and *Spartina* habitats. An exception is De Szalay *et al.* (1996), who observed that the surface sediments of *S. virginica*-vegetated areas in northern California contained mostly dipteran and hemipteran insects which were affected by the presence or absence of vegetation.

In a review of vegetation influences on marsh macrofauna, Levin and Talley (in press) reported general differences between *Salicornia*- and *Spartina*-associated macrofauna ( $\geq 0.3$  mm) in Tijuana Estuary and Mission Bay that they attributed to tidal height. Within the higher-elevation *Salicornia* habitat, macrofaunal density and species richness were found to be related to the cover of *S. virginica*, *S. bigelovii* and amount of open space within marshes of three southern California bays (Levin & Talley, in press). Descriptions of fauna inhabiting southern California *Salicornia* marshes include the faunal communities found in the channels of Los Peñasquitos Lagoon (animals  $\geq 1$  mm; Nordby & Zedler, 1991). To date there has been no formal description of the macroinfauna ( $\geq 0.3$  mm) inhabiting *Salicornia*-vegetated sediments of southern California.

The present paper examines the macrofauna associated with naturally occurring *Salicornia* stands in five

southern California bays and draws comparisons with four created *Salicornia* habitats within these bays. The objectives of the research were to (a) characterize the infaunal assemblages of mature southern California *Salicornia* marshes, (b) delineate faunal succession and recovery rates in *Salicornia* systems through evaluation of 16-month, 5-yr, 6-yr, and 10-yr old created *Salicornia* marshes, (c) examine abiotic and vegetation controls on the marsh macrofaunal assemblages, and (d) compare macrofaunal community structure and successional sequences in *Salicornia* and adjacent *Spartina* habitats in southern California.

## Methods

### *Sample collection and processing*

Naturally occurring *Salicornia* spp. marshes were studied in five Pacific coast embayments located along a 170-km stretch of coastline in southern California (Figure 1). The marshes were in Tijuana Estuary (TJE: 32°34'N, 117°7'W), San Diego Bay (Paradise Creek Marsh, 32°38'N, 117°6'W), Mission Bay (Northern Wildlife Preserve, 32°47'N, 117°14'W), Upper Newport Bay (33°37'N, 117°53'W) and Anaheim Bay (33°44'N, 118°5'W). Each embayment except Tijuana Estuary contained created *Salicornia* marsh. In Tijuana Estuary we examined macrofauna from two *Salicornia* habitats, McCoy Tidal Pond and Ream Field, which differed markedly in soil characteristics. These differences provided a natural analogy to soil differences observed in created- vs natural-marsh comparisons. All of these embayments were flushed daily by ocean water.

Features of the created marshes are described in Table 1. The youngest site, in Mission Bay, was restored in fall 1995 by grading a former wetland buried with fill to tidal elevations and linking the habitat with a connecting channel to an existing marsh. The 5-year old created marsh in Anaheim Bay was one of three islands created in March and April 1990. The created marsh islands were located in a 21 ha salt water pond which was connected to the existing natural marsh creek by a channel leading under the surrounding berm. Some pre-existing patches of *S. virginica* were located on the western side of the pond, about 300 m from the sampling site (MEC, 1995). The 6-year old Newport Bay marsh was created from fill (T. Kelly, pers. comm.) and is bordered by the main creek of the estuary, a small side creek and natural *Spartina* habitat. The 10-year old San Diego Bay marsh (Connector marsh) was created in fall 1984 by grading a disturbed area to tidal elevations. Eight marsh islands were created, bordered

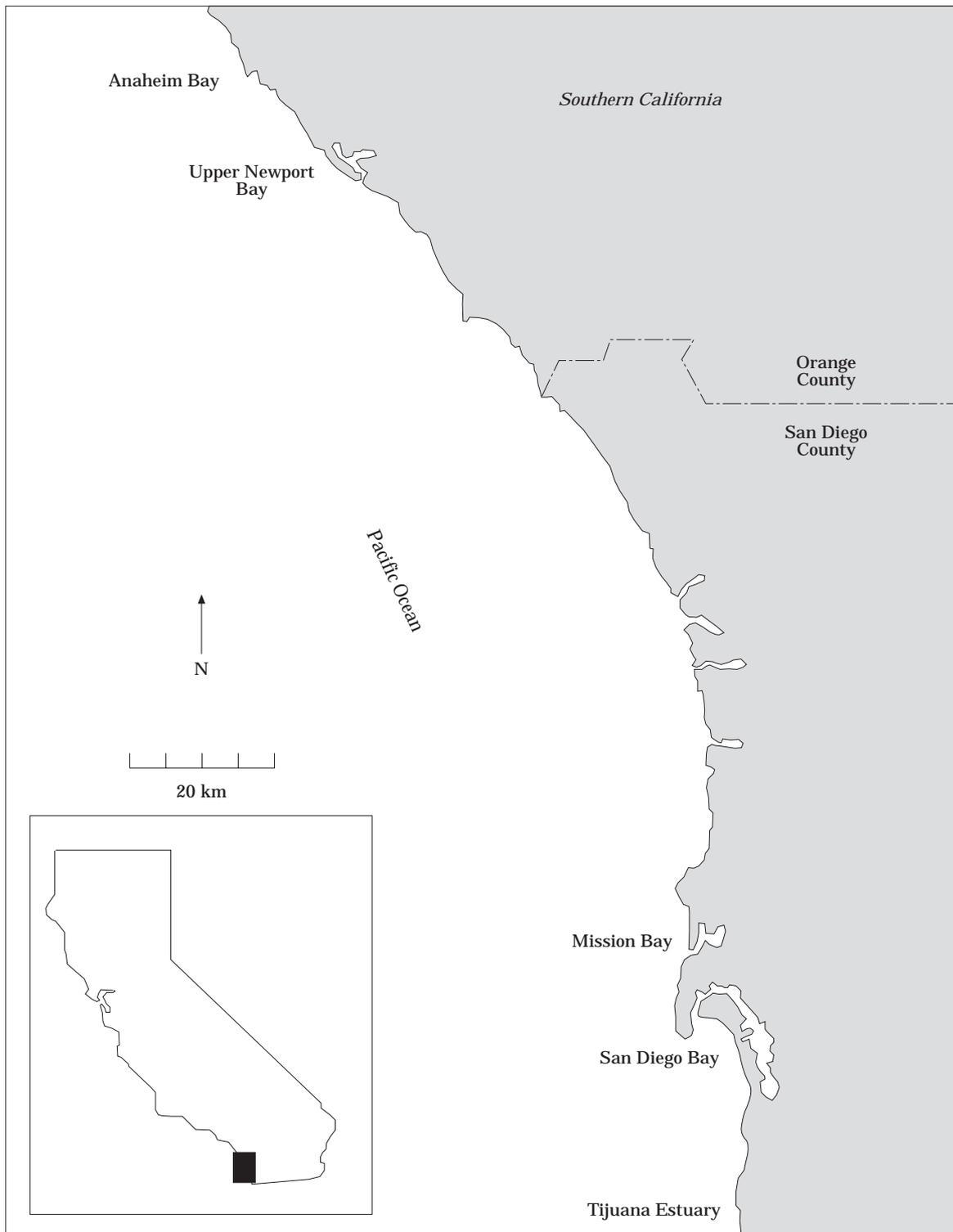


FIGURE 1. Location of study sites in southern California.

on each side by a creek that connects adjacent natural marsh habitat located both upstream and downstream (Langis *et al.*, 1991).

Sediments, vegetation and macrofauna were sampled in the natural and created *Salicornia* marshes

of San Diego, Mission, Upper Newport, and Anaheim Bays. In addition, *Spartina* habitat was sampled in San Diego and Mission Bays. All sampling in these bays took place during February 1995. Natural *Salicornia* habitat in Tijuana Estuary was sampled in August

TABLE 1. Information about the created *Salicornia* spp. marsh sites studied in southern California

	San Diego Bay	Mission Bay	Upper Newport Bay	Anaheim Bay
Creation date	Fall 1984	December 1995	Spring 1989	March/April 1990
Age at time of sampling	10 years	16 months	6 years	5 years
Transplants in mid to high marsh	None	None	None	None
Transplants in low marsh	<i>Spartina foliosa</i> Planted January to March 1985	<i>Spartina foliosa</i> Few succulents introduced with plugs $\geq 15$ m away, March 1996 & January 1997	None	None
Restored marsh area (all vegetation zones)	4.9 ha	2.8 ha	0.1 ha	0.3 ha
Distance of transect from nearest salt marsh	200 m	90 m	5 m	150 m
General location	One of eight islands located in a creek that connects to natural habitats to the north and south (area includes all islands)	Surrounded by berms and directly connected by a creek to the natural habitat	Downstream along a mutual creek and immediately adjacent to natural habitat	One of three 0.3 ha islands in a 21 ha pond. Connected by creek to natural habitat
Elevation sampled (m above MLLW)				
Created marsh	1.25–1.5	1.6–1.8	1.25–1.4	1.5–1.7
Natural marsh	1.4–1.6	1.75–1.8	1.25–1.5	1.4–1.6

MLLW=Mean lower low water.

TABLE 2. Macrofaunal sampling dates (month/year)

Site	<i>Salicornia</i> spp.		<i>Spartina foliosa</i>
	Natural	Created	Natural
Tijuana Estuary	8/96	—	—
San Diego Bay	2/95	2/95	2/95
Mission Bay	2/95, 4/97	4/97	2/95
Upper Newport Bay	2/95	2/95	—
Anaheim Bay	2/95	2/95	—

1996 (Table 2). Additionally, created- and natural-*Salicornia* marsh samples were collected from Mission Bay during April 1997 (Table 2). One 50-m transect was established parallel to the water line in each *Salicornia* marsh (1.3 to 1.8 m above mean lower low water (MLLW) or *Spartina* marsh (1.0 to 1.75 m above MLLW). Samples were taken at 5–10 m intervals along the transect line: 10 from Anaheim, Upper Newport, Mission and San Diego Bays (February 1995); six from Mission Bay in April 1997, and five per transect from each of the two sites in Tijuana Estuary (Table 3). The data collected from the natu-

ral *Salicornia* habitat in Mission Bay during February 1995 were used for comparisons with the adjacent *Spartina* habitat and the natural *Salicornia* and *Spartina* habitats in San Diego Bay, also sampled in February 1995. The April 1997 Mission Bay data were used for comparisons between the created and natural *Salicornia* marshes within the bay. Quadrats (0.25 m<sup>2</sup>) were randomly positioned within 5 m to the right or left of the transect line. In the field, subjective estimates of percent cover of open space, *Salicornia* spp. and other vascular plants within each quadrat were made by the first author. Cores were collected within each quadrat for analyses of sediment properties (particle size and organic matter content), macrofauna and below-ground plant biomass (1 core each). Sediment salinities were measured using the Practical Salinity Scale by extruding porewater from the upper 2 cm of sediment with a syringe through a Whatman filter No. 2 on to a Leica hand-held salinity refractometer.

Infauna were sampled to a depth of 6 cm using a 4.8-cm diameter corer. Animals in sediment cores were preserved in 10% buffered formalin, and stained with Rose Bengal prior to sieving. In the laboratory, samples were washed through a 0.3-mm mesh.

Animals retained on the sieve were sorted under a dissecting microscope and identified (with the aid of a compound scope if needed) to the species level, except for enchytraeid oligochaetes, insects and amphipods, which were identified to family or order. This identification procedure provided minimum estimates of species richness (hereafter referred to as species richness). Species richness was examined as a function of area (no. species per  $18 \text{ cm}^2 \times 6 \text{ cm}$  deep core) and as the total number of species collected from a single site on one date. All sorted infauna were stored in 70% ethanol. Below-ground detritus and plant biomass ( $\geq 0.3 \text{ mm}$ ) were separated from infaunal cores, dried and weighed. Sediment cores (4.8 cm diameter, 6 cm deep), collected within 10 cm of each infaunal sample, were analysed for sediment particle size and percent combustible organic matter. All sediments were homogenized and wet sieved through a 2 mm sieve to remove shells and roots prior to analysis. Sediment particle-size samples were then digested using hydrogen peroxide and wet sieved through a 63- $\mu\text{m}$  mesh. Both portions of the sample ( $\geq 63 \mu\text{m}$  and  $< 63 \mu\text{m}$ ) were dried and weighed to determine percent sand. Organic matter content of sediments ( $< 2 \text{ mm}$ ) was determined by weight loss of dried sediments after combustion overnight at  $550^\circ\text{C}$ .

One standard error about the mean is presented with mean data unless otherwise indicated. Proportion data were arcsin square-root transformed and numeric data were  $\log(x+1)$  transformed prior to all statistical analyses. One-way analysis of variance and *a posteriori* Student's *t*-tests (using JMP<sup>TM</sup> statistical software) were used to evaluate significant differences in macrofaunal, sediment and vegetation characteristics among marshes. Student's *t*-tests (using JMP<sup>TM</sup> statistical software) were used to evaluate significant differences in sediment and macrofaunal properties between the created and natural marshes within each bay, and between the *Salicornia* spp. and *Spartina foliosa* habitats within bays.

Multivariate approaches were used to examine macrofaunal assemblages, composition and density. Analyses were carried out using Primer Statistical software (Clarke & Warwick, 1994). Non-metric multidimensional scaling (MDS) was used to explore community similarities and differences for macrofaunal assemblages of (a) natural and created marsh pairs within each of 4 bays; (b) natural *Spartina foliosa* and *Salicornia* spp. habitat in San Diego and Mission Bays; and (c) natural *Salicornia*, restored *Salicornia* and natural *Spartina foliosa* habitat in San Diego Bay (see Field *et al.*, 1982; Clarke & Greene, 1988; Clarke, 1993). These analyses were based on Bray-Curtis similarity indices of  $\log(x+1)$  transformed,

unstandardized data. Macrofaunal variables were species lists with counts. Stress is a measure of how well the solution (in this case the two-dimensional MDS plots) represents the distances between the data. Clarke (1993) suggests values  $< 0.1$  are good and  $< 0.2$  are useful. Significance testing for differences in faunal communities between sites was done using an analysis of similarity (ANOSIM) procedure. This is a randomization permutation test based on rank similarities of samples (Clarke & Green, 1988; Clarke, 1993). The significance levels of the resulting pairwise comparisons were adjusted by the Bonferroni correction for the number of comparisons made. Analyses of macrofaunal dissimilarities between habitats, and the particular taxa contributing to the dissimilarity, were carried out using SIMPER (Clarke, 1993). Multivariate comparisons were only made between habitats that had equal number of replicates (Clarke & Warwick, 1994) and that were sampled on the same date (Table 2).

Forward linear stepwise multiple regressions (using Statistica statistical software) were run to examine relationships between macrofaunal and environmental or vegetation variables within the created and the natural marshes. Created marsh data collected from the three bays sampled in February 1995 (Table 2) were pooled, as were natural marsh data, in order to utilize the natural range in conditions between bays. Macrofaunal (dependent) variables included number of macrofaunal species per sample, densities of total macrofauna and the densities of major taxonomic groups. Environmental (independent) variables included percent sediment organic matter, percent sand, soil salinity, below-ground plant biomass (g dry weight), and percent of open space (absence of plants). Additional multiple regressions were employed to explore the relationships between vascular plant species (independent variables) and macrofauna (dependent variables) within the created and natural *Salicornia* marshes.

## Results

### *Naturally occurring Salicornia marshes*

The perennial *S. virginica* was a common plant at all sites (12 to 76% cover), whereas the annual *S. bigelovii* was found only in the natural marsh in Mission Bay, where it covered about 50% of the upper marsh. Other perennial succulents, *Batis maritima* and *Jaumea carnosa*, were present at all sites except Anaheim Bay, where the perennial herb, *Frankenia grandifolia* was abundant (23% cover) (Figure 2).

TABLE 3. Mean densities of macrofauna ( $\geq 0.3$  mm) in southern California natural and created *Salicornia* spp. marshes. Data are number per  $18 \text{ cm}^2 \times 6 \text{ cm}$  deep core ( $\pm 1\text{SE}$ ). t-tests compare natural and restored systems within each bay. Samples were collected August 1996 (Tijuana Estuary), February 1995 (San Diego, Mission, Upper Newport and Anaheim Bays), and April 1997 (Mission Bay)

	Tijuana Estuary		San Diego Bay		Upper Newport Bay		Anaheim Bay		Mission Bay		
	McCoy Tidal Pond Natural	Beam Field Natural	Natural	Created (10 years)	Natural	Created (6 years)	Natural	Created (5 years)	February 1995		April 1997
									Natural	Natural	Created (16 months)
<b>Mollusca</b>											
<i>Musculista senhousia</i>	0	0	0	0.6 $\pm$ 0.3†	0	0	0	0	0	0	0
<i>Acteocina inculta</i>	2.2 $\pm$ 2.2	0	0	0	0.2 $\pm$ 0.2	0	0	0	0	0	0
<i>Nassarius tegula</i>	1.4 $\pm$ 1.4	0	0	0	0	0	3.6 $\pm$ 1.9	0.4 $\pm$ 0.2	0	0	0
<i>Cerithidea californica</i>	0	0	0.4 $\pm$ 0.2	0.6 $\pm$ 0.3	0.1 $\pm$ 0.1	0.2 $\pm$ 0.2	0	0.1 $\pm$ 0.1	0	0	0
<i>Melampus olivaceus</i>	1.0 $\pm$ 1.0	1.0 $\pm$ 0.4	0	0	1.5 $\pm$ 0.9	0.1 $\pm$ 0.1	0	0.5 $\pm$ 0.4	0	0	0
<i>Assiminea californica</i>	3.2 $\pm$ 2.5	5.4 $\pm$ 2.3	2.8 $\pm$ 0.5	1.5 $\pm$ 0.9*	9.9 $\pm$ 2.7	4.1 $\pm$ 2.4*	2.9 $\pm$ 1.5	0.3 $\pm$ 0.2†	0.1 $\pm$ 0.1	0.3 $\pm$ 0.3	6.7 $\pm$ 6.5
<i>Alderia modesta</i>	0	0	0	0	0	0	0	0.1 $\pm$ 0.1	0	0	0
Haminae	0	0	0.1 $\pm$ 0.1	0	0	0	0	0	0	0	0
Opisthobranch	0	0	0	0	0	0.1 $\pm$ 0.1	0	0	0	0	0
<b>Polychaeta</b>											
Capitellidae	2.4 $\pm$ 2.4	0.2 $\pm$ 0.2	0	2.3 $\pm$ 1.7†	0	0	0.2 $\pm$ 0.1	0.8 $\pm$ 0.7	5.2 $\pm$ 2.5	0.5 $\pm$ 0.2	0*
<i>Exogone cf. lourei</i>	0	0	0	0.2 $\pm$ 0.2	0	0	0	0	0	0	0
<i>Namaneis quadraticeps</i>	0	0	1.1 $\pm$ 0.6	0*	1.2 $\pm$ 0.6	0†	0	0	0	0	0
Dorvilleidae	0	0	0	0	0.1 $\pm$ 0.1	0	0	0	0	0	0
<i>Streblospio benedicti</i>	1.0 $\pm$ 1.0	0.2 $\pm$ 0.2	0	1.7 $\pm$ 1.5	0	0	0	0.1 $\pm$ 0.1	0	0	0
<i>Polydora nuchalis</i>	6.2 $\pm$ 3.7	0	1.3 $\pm$ 0.5	2.0 $\pm$ 1.1	0.5 $\pm$ 0.4	0.7 $\pm$ 0.5	0.3 $\pm$ 0.2	2.0 $\pm$ 0.8*	0.2 $\pm$ 0.2	0.2 $\pm$ 0.2	0
<b>Oligochaeta</b>											
<i>Tubificoides fraseri</i>	2.4 $\pm$ 2.4	0.2 $\pm$ 0.2	2.1 $\pm$ 0.8	1.1 $\pm$ 0.8	0.2 $\pm$ 0.1	14.9 $\pm$ 4.2***	1.7 $\pm$ 1.2	0.1 $\pm$ 0.1	0	1.7 $\pm$ 1.3	0
<i>Monopylephorus rubroniveus</i>	13.4 $\pm$ 13.2	0	5.2 $\pm$ 3.3	20.4 $\pm$ 16.4	0.1 $\pm$ 0.1	3.6 $\pm$ 2.1†	32.2 $\pm$ 30.9	0.1 $\pm$ 0.1	0.8 $\pm$ 0.8	20.5 $\pm$ 20.5	0
<i>Paranais litoralis</i>	7.2 $\pm$ 3.7	0	17.4 $\pm$ 3.8	89.6 $\pm$ 29.8	3.5 $\pm$ 1.3	284.6 $\pm$ 112***	23.6 $\pm$ 16.1	142.9 $\pm$ 63.8	213.7 $\pm$ 40.6	0.2 $\pm$ 0.2	0
Enchytraeidae	25.8 $\pm$ 9.3	19.0 $\pm$ 5.9	10.6 $\pm$ 3.4	29.3 $\pm$ 10.5†	41.3 $\pm$ 9.0	181.8 $\pm$ 72.6**	14.5 $\pm$ 7.6	0**	86.7 $\pm$ 21.4	160.5 $\pm$ 25.0	0***
<b>Peracarid crustacea</b>											
<i>Corophium</i> spp.	0.8 $\pm$ 0.5	0	0	0	0	0	0.1 $\pm$ 0.1	0	0	0	0
<i>Orchestia traskiana</i>	0	0	0.3 $\pm$ 0.2	0	0	0	0.5 $\pm$ 0.3	0.2 $\pm$ 0.2	1.1 $\pm$ 0.4	1.0 $\pm$ 1.0	0
<i>Ligia occidentalis</i>	0	0	0	0.1 $\pm$ 0.1	0	0	0	0	0	0	0
Cirolanidae	0	0	0.1 $\pm$ 0.1	0	0	0	0	0	0	0	0
<i>Excrolana</i> spp.	1.6 $\pm$ 1.0	5.4 $\pm$ 4.9	0	0	0.1 $\pm$ 0.1	0	0	0	0	0	0
Oniscidae	0	0	0	0	0	0	0.3 $\pm$ 0.2	0	0.1 $\pm$ 0.1	0	0
Turbellaria	1.2 $\pm$ 1.0	0.6 $\pm$ 0.6	0	0.2 $\pm$ 0.1	0.6 $\pm$ 0.4	2.9 $\pm$ 1.5†	0.2 $\pm$ 0.2	0.9 $\pm$ 0.6	4.0 $\pm$ 1.0	2.0 $\pm$ 1.4	0
Nemertea	1.4 $\pm$ 1.0	0	0.5 $\pm$ 0.3	0.3 $\pm$ 0.2	1.0 $\pm$ 0.6	0.9 $\pm$ 0.4	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0.3 $\pm$ 0.3	0
<b>Insecta &amp; Arachnida</b>											
<b>Arachnida</b>											
Spider	0	0.2 $\pm$ 0.2	0	0.1 $\pm$ 0.1	0	0.2 $\pm$ 0.2	0.1 $\pm$ 0.1	0	0.1 $\pm$ 0.1	0	0
Acari (mite)	0.4 $\pm$ 0.2	0.2 $\pm$ 0.2	0.4 $\pm$ 0.2	0.3 $\pm$ 0.2	0.3 $\pm$ 0.2	9.5 $\pm$ 5.1*	0.3 $\pm$ 0.2	0	1.6 $\pm$ 1.3	1.0 $\pm$ 0.5	0.5 $\pm$ 0.2

TABLE 3. Continued

	Tijuana Estuary		San Diego Bay		Upper Newport Bay		Anaheim Bay		Mission Bay		
	McCoy Tidal Pond Natural	Beam Field Natural	Natural	Created (10 years)	Natural	Created (6 years)	Natural	Created (5 years)	February 1995		April 1997
									Natural	Natural	Created (16 months)
Coleoptera											
<i>Bledius</i> spp.	1.0 ± 1.0	0	0	0	0	0.5 ± 0.3	0	0.4 ± 0.8	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2
<i>Bledius</i> spp. (larvae)	0	3.2 ± 2.5	0.1 ± 0.1	0	0.1 ± 0.1	0.8 ± 0.5	0.3 ± 0.2	0.5 ± 0.3	0	0.2 ± 0.2	2.0 ± 0.9*
Carabidae	0	0.4 ± 0.4	0.2 ± 0.2	0.2 ± 0.2	0	0	0	0.1 ± 0.1	0	0	0.2 ± 0.2
Cicindelidae	0	0	0	0	0	0	0	0	0	0	0.2 ± 0.2
Coleoptera larvae	0	0	0	0	0	0	0	0	0	0.2 ± 0.2	0
Collembola									0		
Poduridae	0.4 ± 0.4	0.2 ± 0.2	4.8 ± 4.2	6.8 ± 4.2	0.7 ± 0.4	0.2 ± 0.1	0	0	0	0	0.2 ± 0.2
Smythuridae	0	0	0	0	0.1 ± 0.1	0	0.1 ± 0.1	0	0	0	0
Diptera											
Chironomidae larvae	0	0	0	0.2 ± 0.2	1.8 ± 0.7	8.9 ± 2.1*	7.0 ± 2.9	42.3 ± 12***	33.3 ± 7.9	12.5 ± 5.6	7.5 ± 2.4
Chironomidae adult	0	0	0	0.1 ± 0.1	0	0	0	0	0	0	0
Diptera	0	0	0	0.1 ± 0.1	0	0	0.1 ± 0.1	0	0	0.3 ± 0.3	0.2 ± 0.2
Dipteran pupae	0.2 ± 0.2	0	0.1 ± 0.1	0.1 ± 0.1	0	0	0	1.0 ± 0.5*	0	0	0
Dipteran larvae (cf. Phoridae)	0	0	0	0	0	0	0	0.1 ± 0.1	0	0	0
Dolichopodidae larvae	0.8 ± 0.4	0	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	2.5 ± 0.7***	0.6 ± 0.2	2.4 ± 0.7*	1.4 ± 0.6	1.3 ± 0.6	2.8 ± 1.1
Dolichopodidae cocoon	0	0	0	0	0	0	0	0	0	0	0.2 ± 0.2
Dolichopodidae pupae	0	0	0	0	0	0	0	0.1 ± 0.1	0	0	0
Dolichopodidae adult	0	0	0	0	0	0	0.1 ± 0.1	0	0	0	0
Heleidae	0.2 ± 0.2	0	0.1 ± 0.1	0.2 ± 0.2	0	7.1 ± 1.9***	0.9 ± 0.5	15.4 ± 3.8***	6.1 ± 4.3	1.0 ± 0.4	0.3 ± 0.2
Muscidae	0.4 ± 0.4	0.2 ± 0.2	1.9 ± 1.9	0.1 ± 0.1*	0.1 ± 0.1	0.1 ± 0.1	0	0	1.2 ± 0.4	0.7 ± 0.3	0.2 ± 0.2
Psychodidae	0.2 ± 0.2	0	0.1 ± 0.1	0.6 ± 0.4	0.3 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	0	0	0	0
Stratiomyidae A	0	0.6 ± 0.4	0.1 ± 0.1	0	0.1 ± 0.1	0	0	0.1 ± 0.1	0	0	0
Stratiomyidae B	0.4 ± 0.2	0	0	0	0	0.3 ± 0.3	0	0	0	0	2.5 ± 2.5
Hemiptera									0		
Hemiptera (ant)	0	0	0.2 ± 0.1	0	0	0	0.1 ± 0.1	0	0	0	0
Hemiptera B	0	0	0	0	0	0	0	0	0	0.5 ± 0.3	0
Saldidae	0	0	0	0.2 ± 0.1	0	0	0	0	0	0.2 ± 0.2	0.2 ± 0.2
Homoptera									0		
Aphidae	0	0	0	0	0	0	0.1 ± 0.1	0	0	0	0
Coccinidae	9.4 ± 9.4	1.4 ± 1.2	0.1 ± 0.1	0.1 ± 0.1	0.5 ± 0.2	0.8 ± 0.4	0.1 ± 0.1	0	0.1 ± 0.1	0	0.2 ± 0.2
Unknowns											
Insect A	0	0	0	0	0.1 ± 0.1	0	0	0	0	0	0
Insect B	0	0	0	0	0.1 ± 0.1	0	0	0	0	0	0
Cnidaria											
Sea anemone	0	0	0	0.1 ± 0.1	0	0	0	0	0	0	0
Urochordata	0	0	0	0	0.1 ± 0.1	0	0	0	0	0	0
No. macrofauna 18 cm <sup>-2</sup>	85 ± 28	38 ± 10	47 ± 10	159 ± 52	65 ± 12	525 ± 123***	90 ± 40	211 ± 69*	357 ± 38	205 ± 9	51 ± 26**
No. macrofauna m <sup>-2</sup>	46 783 ± 15 536	21 235 ± 5532	26 101 ± 5530	88 037 ± 28 977	35 779 ± 6470	290 103 ± 68 074	49 825 ± 22 175	116 904 ± 38 544	197 421 ± 20 848	113 475 ± 5088	28 037 ± 14 433
No. species 18 cm <sup>-2</sup>	8.6 ± 2.5	6.0 ± 1.3	9.0 ± 0.8	8.1 ± 1.0	7.7 ± 1.0	10.0 ± 0.5*	7.5 ± 0.8	7.7 ± 0.7	7.6 ± 0.3	7.7 ± 0.6	5.8 ± 1.2
No. species site <sup>-1</sup>	25	16	24	29	27	23	26	24	18	21	16
Number of 18 cm <sup>2</sup> cores	5	5	10	10	10	10	10	10	10	6	6

† = 0.05 ≤ P &lt; 0.1 \* = 0.01 ≤ P &lt; 0.05 \*\* = 0.001 ≤ P &lt; 0.01 \*\*\* = P &lt; 0.001

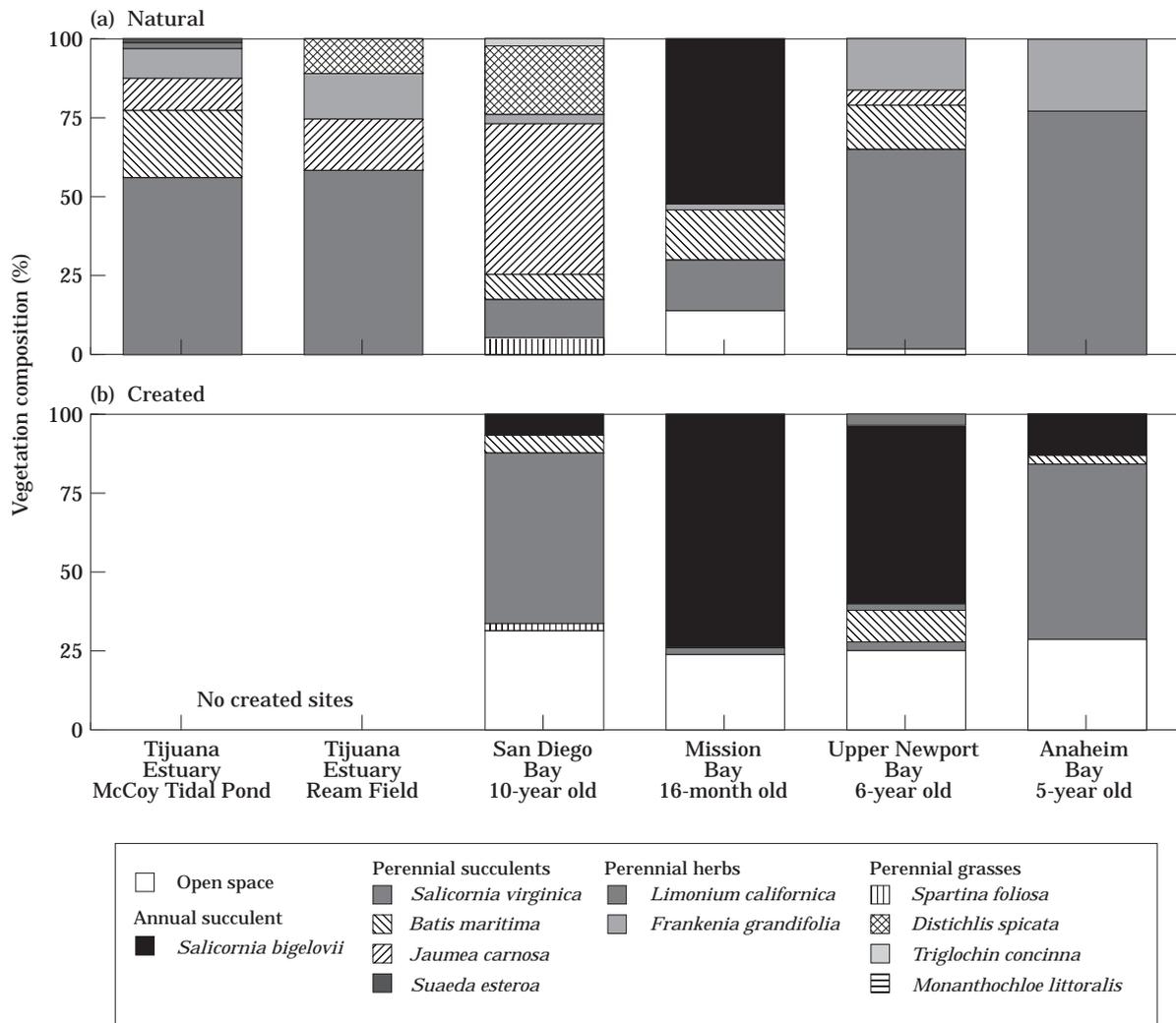


FIGURE 2. Vegetation composition (percent cover) of (a) natural and (b) created *Salicornia* spp. marshes in southern California. Ages of the created sites at the time of sampling are shown. San Diego, Upper Newport and Anaheim Bays were sampled in February 1995, Tijuana Estuary in August 1996, and Mission Bay in April 1997.

Sediment properties varied among bays and sites (Figure 3). Mission Bay marsh sediments had the highest (43%) and McCoy Tidal Pond in Tijuana Estuary had the second highest (26%) organic matter content. Percent organic matter varied from 3 to 18% at the other sites. Percent sand was greatest at Ream Field (Tijuana Estuary) (68%), and ranged from 17 to 21% at the other sites (Figure 3). Variation within Tijuana Estuary was as great as among the bays. McCoy Tidal Pond had low sand content, high organic matter content and high below-ground biomass; Ream Field exhibited the opposite characteristics (Figure 3). In the natural marshes during February 1995, sediment salinities averaged 15 in Upper Newport Bay, 30 and 32 in Anaheim and San Diego Bays, respectively, and 37

in Mission Bay. Salinity was 44 to 50 in Tijuana Estuary during August 1996 and 71 in Mission Bay in April 1997 (Figure 3).

Macrofaunal densities ranged from a low of 21 235 (Ream Field, Tijuana Estuary) to a high value of 113 475 ind  $m^{-2}$  (Mission Bay) (Table 3). From 16 to 27 species were identified from each site (Table 3). The macrofauna at all sites consisted mainly of oligochaetes (52 to 89%), insects (7 to 31%), and molluscs (0 to 19%). Peracarid crustaceans (amphipods and isopods, (1 to 8%), polychaetes (0 to 13%), and nemerteans and turbellarians (0 to 2%) were present but usually rare. Among the oligochaetes, enchytraeids and the nauid *Paranais littoralis* were the most abundant taxa. Tubificid oligochaetes (*Tubificoides fraseri* and *Monopylephorus rubroniveus*) were common

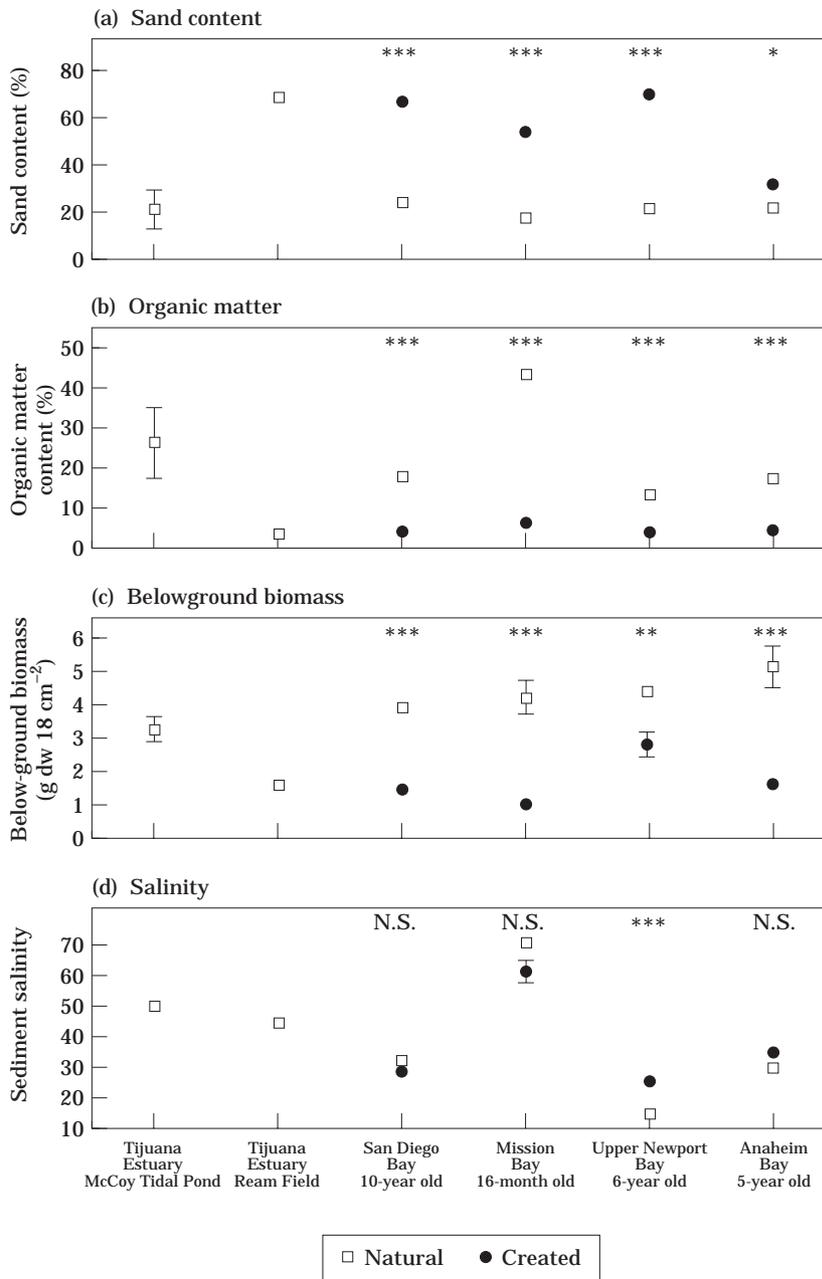


FIGURE 3. Mean ( $\pm$  1SE) (a) sand content, (b) organic matter content, (c) below-ground plant biomass, and (d) sediment salinity of natural and created *Salicornia* spp. marshes in southern California. Asterisks indicate significance between restored and natural sites within each bay; \*\*\* =  $P < 0.001$ ; \*\* =  $0.001 \leq P < 0.01$ ; \* =  $0.01 \leq P < 0.05$ , NS = Not significant. San Diego, Upper Newport and Anaheim Bays were sampled in February 1995, Tijuana Estuary in August 1996, and Mission Bay in April 1997.

but less abundant [Figure 4(a), Table 3]. Insects were the most speciose group present (Table 3). Dominant insect taxa included dolichopodids, chironomids, heleids, and staphylinids (*Bledius* spp.). The molluscs consisted mainly of the gastropods *Assiminea californica*, *Melampus olivaceus* and *Cerithidea californica*.

*Created Salicornia marshes*

*Salicornia virginica* was the dominant vascular plant in the created marshes of Anaheim Bay (53% cover) and San Diego Bay (54% cover). *Salicornia bigelovii* was the prevalent plant in created marshes of Newport Bay (57% cover) and Mission Bay (73% cover). Except for

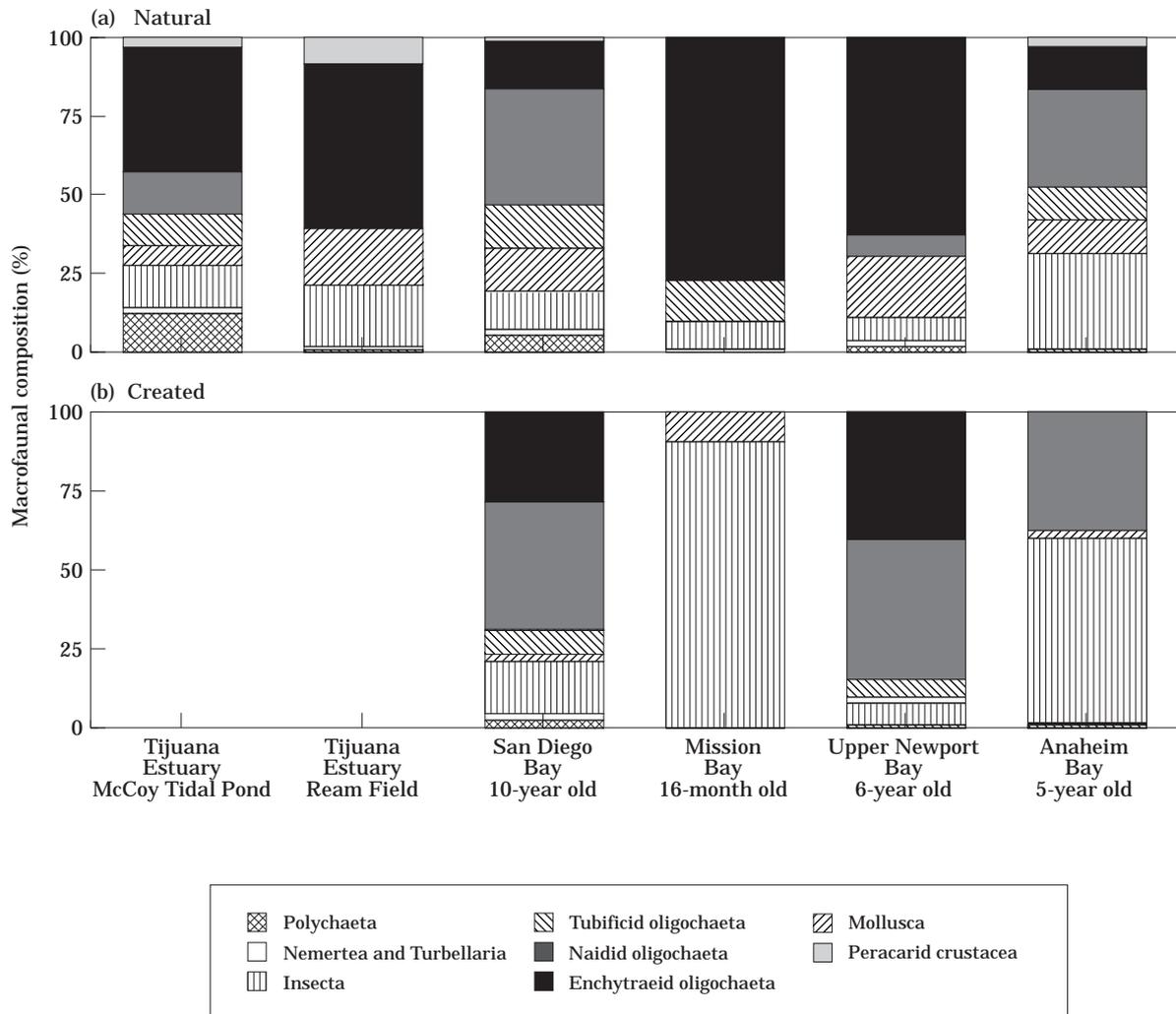


FIGURE 4. Macrofaunal composition of (a) natural and (b) created *Salicornia* spp. marshes in southern California. Ages of the created sites at the time of sampling are shown. San Diego, Upper Newport and Anaheim Bays were sampled in February 1995, Tijuana Estuary in August 1996, and Mission Bay in April 1997.

*B. maritima*, few other vascular plant species were present in the created marshes, in marked contrast to the natural systems (Figure 2). Open space ( $t_{18} \geq 4.3$ ;  $P \leq 0.0005$ ) and percent cover of *S. bigelovii* ( $t_{18} \geq 2.1$ ;  $P \leq 0.05$ ) were significantly higher in the created than natural marshes, except in Mission Bay, where *S. bigelovii* was dominant in the natural marsh as well ( $t_{10} = 2.0$ ;  $P = 0.070$ ; Figure 2). The created habitats exhibited 25 to 32% open (unvegetated) space, compared to <2% in the natural systems (except in Mission Bay, 14%). Sediment sand content was significantly greater and organic matter content and below-ground biomass were significantly lower in the created marshes than in their natural counterparts (Figure 3). There were generally no differences in sediment salinity between the created and natural marshes (Figure 3). Salinities in the created marsh

sediments sampled in February 1995 averaged 26 in Upper Newport Bay, 29 in San Diego Bay and 36 in Anaheim Bay. Salinity was 62 in the created marsh of Mission Bay during April 1997.

With the exception of the youngest marsh (Mission Bay), macrofaunal densities were 2 to 8 times higher in all of the created marshes (88 000 to 290 000 ind  $m^{-2}$ ) than in their natural counterparts [Figure 5(a)]. In the 16-month old created marsh, densities were only one-quarter those of the natural system. However, species richness was similar in all created and natural sites, except in Newport Bay, where created-marsh richness was higher [Figure 5(b)].

Taxonomic composition of the macrofauna varied between created and natural *Salicornia* marshes. Insects and oligochaetes together comprised most of the created-marsh macrofauna (91 to 97%), as in the

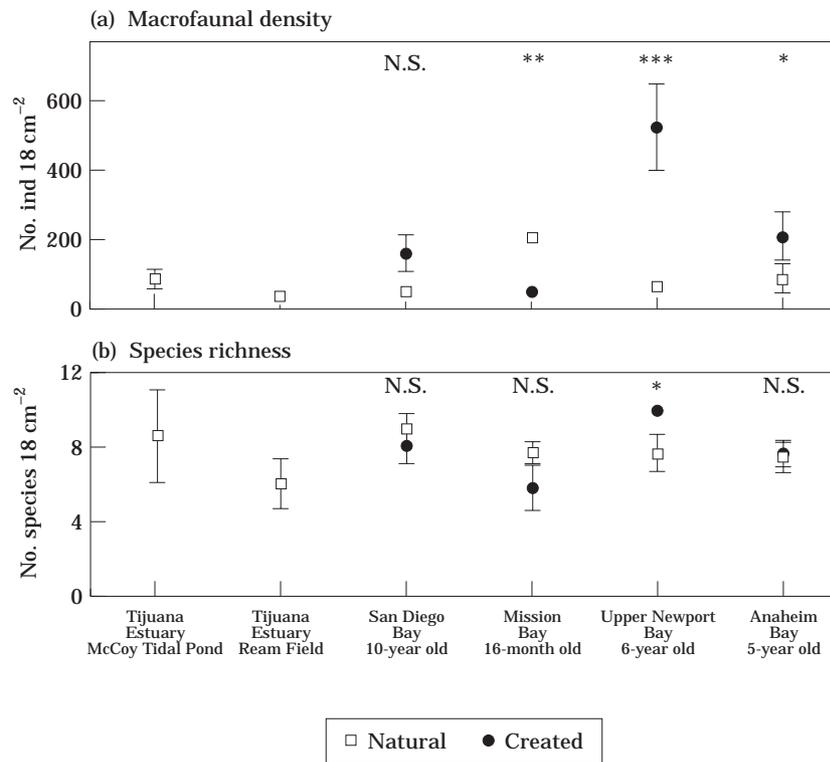


FIGURE 5. Mean ( $\pm$  1SE) (a) macrofaunal density (number of ind  $18\text{ cm}^{-2}$  core) and (b) species richness per  $18\text{ cm}^{-2}$  core in the created and natural *Salicornia* spp. marshes of southern California. Asterisks indicate significance between created and natural sites within each bay; \*\*\*= $P < 0.001$ ; \*\*= $0.001 \leq P < 0.01$ ; \*= $0.01 \leq P < 0.05$ , N.S.=Not significant. San Diego, Upper Newport and Anaheim Bays were sampled in February 1995, Tijuana Estuary in August 1996, and Mission Bay in April 1997.

natural *Salicornia* marshes (71 to 98%). However, the created marshes generally exhibited higher proportional representation of insects and the naidid oligochaete, *P. littoralis*, and lower proportions of tubificid and enchytraeid oligochaetes than in the natural marshes (Figure 4). Absolute density differences between species in created and natural marshes within the same bay were observed infrequently, except in Newport Bay (Table 3). The only taxa to exhibit significantly higher densities in the natural marshes were the gastropod *A. californica* (San Diego, Upper Newport and Anaheim Bays), the nereid polychaete *Namaneris quadraticeps* (San Diego and Upper Newport Bays), enchytraeid oligochaetes (Anaheim and Mission Bays), and muscid insects (San Diego Bay) (Table 3). Chironomid, dolichopodid, and heleid insects exhibited higher densities in the created than natural marshes of both Newport and Anaheim Bays (Table 3). Upper Newport Bay also exhibited significantly greater numbers of tubificid, enchytraeid and naidid oligochaetes in the created than natural marsh (Table 3).

The differences between natural and created marshes were mirrored to some extent by differences

among the created systems. By viewing the different-aged created sites as a temporal sequence, it is possible to seek evidence of succession in development of the *Salicornia*-marsh macrofauna. MDS plots indicate increasing similarity between created and natural-marsh assemblages over time (Figure 6). The 16-month old system exhibited the greatest differences (76% dissimilarity; SIMPER) between created- and natural-marsh community composition, the 5–6-year old system exhibited intermediate separation (68% dissimilarity), and the 6- and 10-year old systems exhibited greatest similarities with their natural counterparts (60% and 61% dissimilarity) (Figure 6). Significant community differences between natural and created marsh pairs were observed for all embayments ( $P < 0.001$ ; ANOSIM) except San Diego Bay ( $P = 0.006$ , ANOSIM) ( $\alpha = 0.002$ , based on Bonferroni adjustment). During created-marsh development there appears to be a decrease in the proportional representation of insects (from  $91 \pm 8$  in the youngest to  $16 \pm 7\%$  of total composition in the oldest marsh) and an increase in the representation (and densities) of enchytraeid and tubificid oligochaetes with marsh age (from no oligochaetes in the youngest to  $27 \pm 6\%$

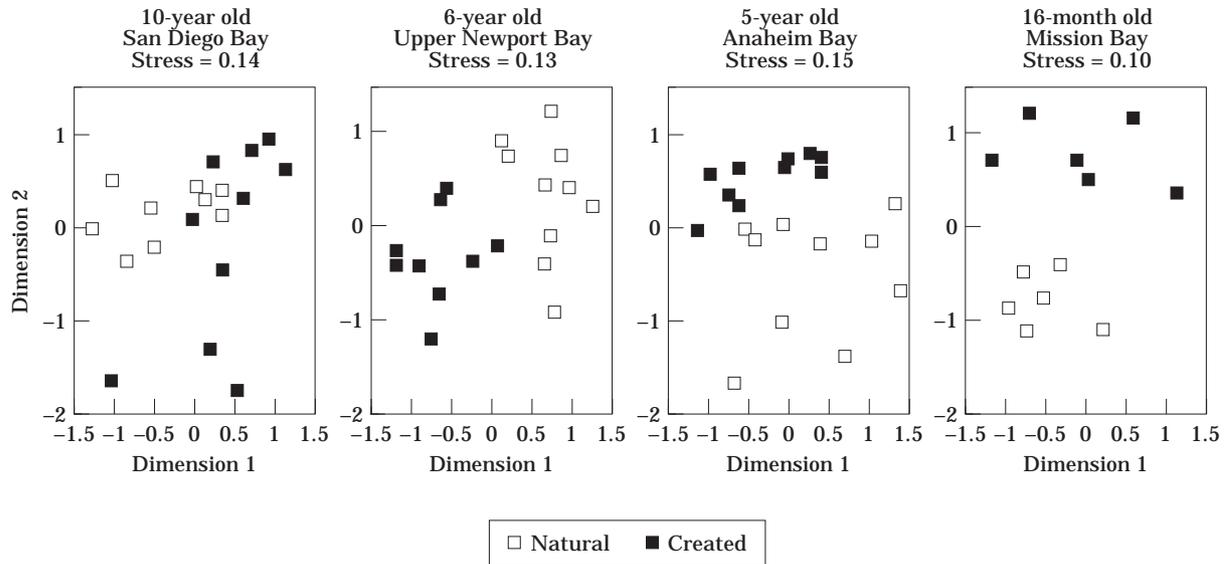


FIGURE 6. Two-dimensional multidimensional scaling plot of macrofaunal samples ( $\geq 0.3$  mm) from four created and four natural *Salicornia* spp. marshes in southern California. Each point represents a single  $18\text{ cm}^2$  core taken in February 1995.

enchytraeid and  $7 \pm 3\%$  tubificid oligochaetes in the oldest marsh). In the oldest created system (San Diego Bay), proportional representation of major taxa was similar in the created and natural marsh (Figure 4); assemblage differences (evident in Figure 6) were driven largely by higher created-marsh densities (Table 3).

#### Comparisons between *Salicornia* spp. and *Spartina foliosa* habitats

**Natural systems.** *Salicornia*-vegetated habitats of San Diego and Mission Bay differed from adjacent *Spartina*-vegetated habitats in exhibiting higher sediment organic matter content and salinity, higher below-ground biomass (similar in Mission Bay) and lower sand content (similar in San Diego Bay) ( $t$ -tests, all  $P \leq 0.04$ ).

No habitat-related differences in macrofaunal species richness per core were observed in either bay (Table 4). In San Diego Bay, macrofaunal density was higher in the *Spartina* ( $166\,453 \pm 48\,489\text{ ind m}^{-2}$ ) than *Salicornia* ( $26\,102 \pm 5\,546\text{ ind m}^{-2}$ ) habitat ( $t_{18}=5.0$ ;  $P \leq 0.001$ ), but no comparable differences were observed in Mission Bay (*Salicornia*:  $199\,411 \pm 20\,115$ ; *Spartina*:  $152\,462 \pm 20\,248\text{ ind m}^{-2}$ ) (Table 4). Together, 38 species were found in the *Spartina* habitats and 32 species were found in the *Salicornia* habitats of San Diego and Mission Bays. Of those, 19 species were found in both areas leaving 40 to 50% of the infauna exclusive to each habitat.

Macrofaunal composition, interpreted as proportional representation, differed between plant habitats.

*Salicornia* habitat in both bays supported a greater proportion of insects (San Diego Bay:  $t_{18}=3.4$ ,  $P=0.003$ ; Mission Bay:  $t_{18}=3.7$ ,  $P=0.002$ ) and lower proportion of oligochaetes (San Diego Bay:  $t_{18}=3.4$ ,  $P=0.030$ ; Mission Bay:  $t_{18}=2.2$ ,  $P=0.040$ ) than in *Spartina* habitat (Table 4). In particular, *Salicornia* sites supported more naids, and fewer tubificids and enchytraeid oligochaetes, as well as more peracarids (Mission Bay) and molluscs (San Diego Bay) than *Spartina*-vegetated areas (Table 4).

The distinction between the macrofaunal assemblages of the *Spartina* and *Salicornia* habitats within San Diego (50% dissimilarity,  $P < 0.001$ , ANOSIM) and Mission Bays (64% dissimilarity;  $P < 0.001$ , ANOSIM) (Bonferroni adjusted  $\alpha = 0.008$ ) is evident in the 2-D multidimensional scaling plots [Figure 7(a)]. In San Diego Bay, the macrofaunal assemblage differences are due to higher densities of the three oligochaete families and polychaetes (*Capitella* spp. and the spionid, *Streblospio benedicti*) in the *Spartina* than *Salicornia* habitats. In Mission Bay, there were lower densities of the naidid oligochaete *P. littoralis* and chironomid insect larvae, and higher densities of tubificid and enchytraeid oligochaetes in the *Spartina* relative to *Salicornia* habitat.

**Natural vs created systems.** In order to examine the hypothesis that early successional *Salicornia* marshes resembled *Spartina* habitat with respect to macrofauna, we examined assemblage similarities among the created *Salicornia*, natural *Salicornia*, and natural *Spartina* habitats in San Diego Bay [Figure 7(b)]. Due to the high number of comparisons made, a

TABLE 4. Mean ( $\pm$  1SE) of environmental variables, species richness, total macrofauna  $m^{-2}$ , and proportional macrofaunal abundances from the *Spartina foliosa* and *Salicornia* spp. habitats in San Diego and Mission Bays. Data are from February 1995,  $n=10$   $18\text{ cm}^2 \times 6\text{ cm}$  depth cores. Results of Student's *t*-test shown,  $\alpha=0.05$

Variable	San Diego Bay				Mission Bay			
	<i>Spartina</i>	<i>Salicornia</i>	$t_{18}$	P	<i>Spartina</i>	<i>Salicornia</i>	$t_{18}$	P
Organic matter (%)	13.3 $\pm$ 0.7	17.8 $\pm$ 1.0	3.7	0.002	18.0 $\pm$ 1.3	44.0 $\pm$ 1.0	14.6	<0.001
Sand content (%)	23.5 $\pm$ 2.6	23.8 $\pm$ 1.6		N.S.	39.6 $\pm$ 3.0	24.1 $\pm$ 3.6	3.5	0.003
Salinity	30.8 $\pm$ 0.4	32.2 $\pm$ 0.5	2.2	0.040	24.7 $\pm$ 1.4	36.6 $\pm$ 1.7	5.2	<0.001
Below-ground biomass (g dw)	2.4 $\pm$ 0.3	3.9 $\pm$ 0.3	3.8	0.001	5.5 $\pm$ 0.5	5.5 $\pm$ 0.4		N.S.
Species richness (no. per core)	10.4 $\pm$ 0.6	9.0 $\pm$ 0.8		N.S.	7.0 $\pm$ 0.5	7.6 $\pm$ 0.3		N.S.
Macrofauna (no. $\times$ 1000 $m^{-2}$ )	166 $\pm$ 48	26 $\pm$ 5	5.0	<0.001	152 $\pm$ 20	199 $\pm$ 20		N.S.
Mollusca (%)	0.9 $\pm$ 0.1	11.8 $\pm$ 0.3	4.1	<0.001	0.1 $\pm$ 0	0.0 $\pm$ 0		N.S.
Polychaeta (%)	8.8 $\pm$ 0.4	3.7 $\pm$ 0.3		N.S.	2.4 $\pm$ 0.1	0.8 $\pm$ 0.1		N.S.
Peracarida (%)	1.1 $\pm$ 0.2	0.3 $\pm$ 0.1		N.S.	0.0 $\pm$ 0	0.4 $\pm$ 0	3.7	0.002
Insecta and Arachnida (%)	2.8 $\pm$ 0	11.3 $\pm$ 0.2	3.4	0.003	1.6 $\pm$ 0.02	12.1 $\pm$ 0.2	3.6	0.002
Oligochaeta (%)	82.7 $\pm$ 0.3	66.2 $\pm$ 0.4	2.3	0.030	92.2 $\pm$ 0.2	83.5 $\pm$ 0.2	2.2	0.040
Tubificidae (%)	26.2 $\pm$ 0.5	10.6 $\pm$ 0.3	2.2	0.040	13.6 $\pm$ 0.6	0.0 $\pm$ 0	4.5	<0.001
Naididae (%)	25.9 $\pm$ 0.4	36.8 $\pm$ 0.2		N.S.	8.6 $\pm$ 0.2	58.2 $\pm$ 0.7	6.3	<0.001
Enchytraeidae (%)	20.9 $\pm$ 0.7	11.0 $\pm$ 0.5		N.S.	64.9 $\pm$ 0.8	22.4 $\pm$ 0.5	3.9	0.001
Nemertea and Turbellaria (%)	0.1 $\pm$ 0	0.2 $\pm$ 0.1		N.S.	0.5 $\pm$ 0.1	0.9 $\pm$ 0		N.S.

N.S. = not significant.

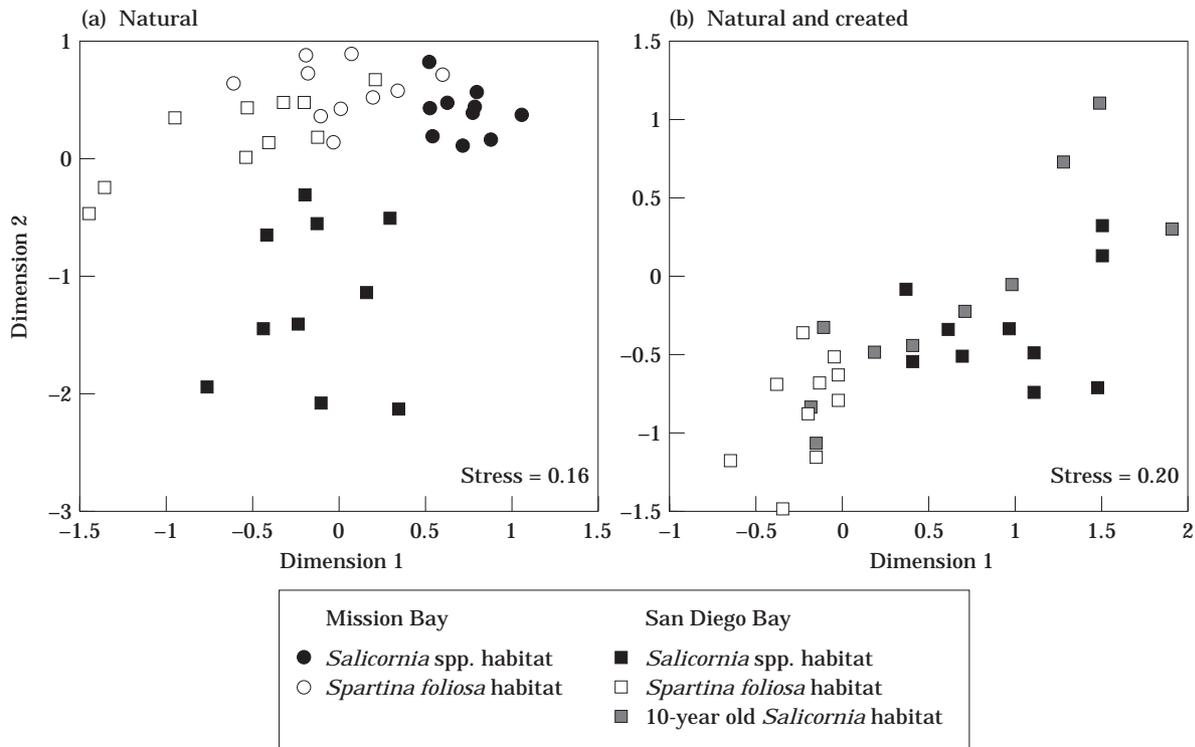


FIGURE 7. Multidimensional scaling of macrofauna from (a) the *Spartina foliosa* and *Salicornia* spp. habitats of San Diego and Mission Bays, and (b) the natural *Spartina foliosa*, natural *Salicornia* spp. and created *Salicornia* spp. habitats of San Diego Bay in southern California. Each point represents a single  $18\text{ cm}^2$  core taken in February 1995.

Bonferroni-adjusted alpha was used ( $\alpha=0.017$ ). The macrofaunal assemblage of the 10-year old created *Salicornia* site in San Diego Bay was slightly less

similar to the natural *Salicornia* spp. site (Dissimilarity 63%,  $P=0.001$ , ANOSIM) than to the adjacent natural *Spartina* site (Dissimilarity 59%,  $P=0.002$ ,

ANOSIM) [Figure 7(b)]. Members of the three oligochaete families (the naidid, *P. littoralis*, Enchytraeidae, and the tubificid, *M. rubroniveus*) explained about 30% of the variability among the macrofaunal assemblages of the three habitats.

There were 29 macrofaunal species found in the created *Salicornia* marsh of San Diego Bay. Of those species, 55% were also found in the natural *Salicornia* marsh and 69% were found in the *Spartina* marsh. Five taxa (the mussel *Musculista senhousia*, capitellid polychaetes, *Streblospio benedicti*, turbellarians and chironomid insect larvae) were found only in the created *Salicornia* and *Spartina* marshes, while three taxa (terrestrial isopods, dipteran pupae and carabid beetles) were found only in the natural and created *Salicornia* marshes. The community [Figure 7(b)] and species overlap analyses support the hypothesis that created *Salicornia* marsh faunas represent a transitional stage, intermediate between natural *Spartina* and *Salicornia* marsh faunas.

#### *Environmental controls on marsh macrofauna*

**Sediment effects.** Sediment organic matter availability appears to be a primary influence on macrofauna in both natural and created systems. In natural marsh sediments, combustible organic matter or below-ground biomass was negatively associated with densities of molluscs, polychaetes and naidid oligochaetes (Table 5). In created marsh sediments, where combustible organic matter was low and differed little among sites (Figure 3), below-ground plant biomass, which is largely a measure of live and detrital plant buildup in soils, was the most influential parameter. Below-ground biomass was positively related to total macrofaunal densities, and densities of total oligochaetes, enchytraeid oligochaetes, and turbellarians and nemerteans in created *Salicornia* marshes (Table 5). Measures of particle size (% sand) also appeared to influence the dominant macrofaunal taxa, although not all responded in a similar manner (Table 5). For example, in the created systems, insects were most abundant in finer-grained sediments, while tubificid and enchytraeid oligochaetes were associated with sandier sediments (Table 5). Salinity was an important factor only in the natural marsh where enchytraeid oligochaetes were more abundant and tubificid oligochaetes were less abundant at lower salinities (Table 5).

**Vegetation effects.** In the natural marshes, macrofaunal abundances usually were negatively associated with the percent cover of plant species. Species richness, total macrofaunal density, densities of polychaetes,

insects and arachnids, and naidid and enchytraeid oligochaetes were reduced with increasing cover of: *S. virginica*, *Batis maritima*, *Distichlis spicata* or *Frankenia grandifolia* [Table 5(b)]. However, the percent cover of *S. foliosa* was positively associated with abundances of tubificid oligochaetes ( $R^2=0.15$ ;  $P=0.030$ ), and molluscs were positively associated with percent cover of both *F. grandifolia* and *B. maritima* [ $R^2=0.42$ ;  $P<0.001$ ; Table 5(b)].

In the created marsh, macrofaunal densities tended to be negatively associated with cover of the perennial, *S. virginica* [abundances of tubificid oligochaetes, enchytraeid oligochaetes, nemerteans and turbellarians; Table 5(b)] and positively associated with percent cover of the annual, *S. bigelovii* [species richness, total macrofaunal densities, insects and arachnids and tubificid oligochaetes; Table 5(b)].

## Discussion

### *Natural Salicornia marshes*

In this paper we have demonstrated the variability of macrofauna inhabiting sediments of natural *Salicornia* habitats among five different embayments. As the first full community description of macro-infauna inhabiting *Salicornia*-vegetated sediments in California, these data represent an important step in establishing a benchmark against which future changes can be compared. However, wetlands in all of the embayments studied have been modified to some extent by urban development and other human activities. It is unlikely that the existing faunas represent those of the wetlands in their pristine state. Invasion of exotic species and local loss of some large taxa have been documented for bivalves in Mission Bay (Crooks, 1998a,b), and are likely to have occurred among other taxa in the bays studied. The problem of shifting baselines (Tegner & Dayton, 1997; Dayton *et al.*, 1998) is a serious one that plagues all coastal environments that are subject to over-fishing, habitat fragmentation, pollution or other sources of change.

### *Salicornia marsh recovery*

**Successional stages.** Clear evidence was observed of temporal macrofaunal succession among the 16-month, 5-year, 6-year and 10-year old *Salicornia* marshes (Figure 6). Early habitation was primarily by the naidid oligochaete, *P. littoralis*, and three insect taxa (Figure 4, Table 3). *Paranais littoralis* lives near the sediment surface and reproduces asexually. This species can swim as an adult under high-density conditions (Levinton *et al.*, 1995) or may be easily

TABLE 5. Multiple regressions examining relationships between sediment variables (a) or plant species (b), and the macrofaunal densities within three created and natural *Salicornia* spp. marshes of southern California. Independent variables included (a) sediment salinity, organic matter content, sand content, below-ground plant biomass and % open space (absence of plants); (b) percent cover of all plant species found within each area (see Figure 2). Marshes were located in San Diego Bay, Upper Newport Bay, and Anaheim Bay. All were sampled in February 1995. Ages of created marshes at time of sampling were 5 years (Anaheim Bay), 6 years (Upper Newport Bay) and 10 years (San Diego Bay). Criteria for inclusion of independent variables into the analysis were  $F \geq 3.6$  or  $P \leq 0.06$

Dependent variable	Natural marshes						Created marshes					
	Independent variable	R <sup>2</sup>	+/-	df	F	P	Independent variable	R <sup>2</sup>	+/-	df	F	P
(a) Sediment variables												
Species richness						NS						NS
Macrofauna						NS	Below-ground biomass	0.20	+	1,28	6.7	0.02
Mollusca	Organic matter content	0.15	-	1,28	4.8	0.040	Organic matter content	0.14	+	1,28	4.6	0.04
Polychaeta	Below-ground biomass	0.22	-	1,28	8.1	0.008						NS
Peracarida	Sand content	0.13	+	1,28	4.0	0.050	% open space	0.24	-	2,27	4.3	0.020
							Below-ground biomass		-			
Insecta and Arachnida						NS	Sand content	0.30	-	1,28	11.8	0.002
Oligochaeta						NS	Below-ground biomass	0.17	+	1,28	5.6	0.020
Tubificidae	Salinity	0.21	+	1,28	7.6	0.010	Sand content	0.25	+	1,28	9.3	0.005
Naididae	Organic matter content	0.61	+	4,25	9.9	<0.001	Below-ground biomass	0.15	+	1,28	4.8	0.040
	Below-ground biomass		-									
	Salinity		+									
	Sand content		+									
Enchytraeidae	Salinity	0.34	-	1,28	14.6	<0.001	Sand content	0.51	+	1,28	29.1	<0.001
Turbellaria and Nemertea						NS	Below-ground biomass	0.12	+	1,28	3.8	0.060
(b) Plant species												
Species richness	<i>Salicornia virginica</i>	0.27	-	2,27	5.1	0.010	<i>Salicornia bigelovii</i>	0.16	+	1,28	5.2	0.030
	<i>Distichlis spicata</i>		-									
Macrofauna	<i>Distichlis spicata</i>	0.25	-	2,27	4.6	0.020	<i>Salicornia bigelovii</i>	0.53	+	2,27	15.6	<0.001
	<i>Salicornia virginica</i>		-				<i>Batis maritima</i>		-			NS
Mollusca	<i>Frankenia grandifolia</i>	0.42	+	2,27	9.9	<0.001						
	<i>Batis maritima</i>		+									
Polychaeta	<i>Frankenia grandifolia</i>	0.26	-	1,28	10.1	0.004	<i>Batis maritima</i>	0.18	-	1,28	6.2	0.020
Peracarida						NS	<i>Salicornia virginica</i>	0.16	+	1,28	5.4	0.030
Insecta and Arachnida	<i>Distichlis spicata</i>	0.12	-	1,28	3.7	0.060	<i>Salicornia bigelovii</i>	0.14	+	1,28	4.4	0.050
Oligochaeta						NS	<i>Salicornia virginica</i>	0.36	-	1,28	15.8	<0.001
Tubificidae	<i>Spartina foliosa</i>	0.15	+	1,28	5.0	0.030	<i>Salicornia virginica</i>	0.14	-	1,28	4.5	0.040
Naididae	<i>Frankenia grandifolia</i>	0.36	-	3,26	4.8	0.009	<i>Salicornia bigelovii</i>	0.34	+	2,27	6.7	0.004
	<i>Batis maritima</i>		-				<i>Spartina foliosa</i>		+			
	<i>Salicornia virginica</i>		-									
Enchytraeidae	<i>Distichlis spicata</i>	0.27	-	2,27	5.0	0.010	<i>Salicornia virginica</i>	0.33	-	1,28	13.8	<0.001
	<i>Salicornia virginica</i>		-									
Turbellaria and Nemertea						NS	<i>Salicornia virginica</i>	0.40	-	1,28	19.1	<0.001

+ = positive and - = negative relationships. NS = not significant. df = degrees of freedom.

transported with bedload movement (R. Diaz, pers. comm.). Either case would facilitate short-distance colonization over m to km scales. The chironomid, heleid and dolichopodid insects that initially colonized the created sites all have winged adults capable of aerial dispersal. Batzer *et al.* (1997) reported unexpected opportunistic colonization of seasonally flooded *S. virginica* wetlands in central California by the chironomid, *Chironomus stigmaterus*.

The early successional events reported here for *Salicornia* marshes differ from those observed in young *Spartina alterniflora* marshes on the Atlantic coast. In the *S. alterniflora* systems, opportunistic polychaetes with dispersive planktonic larvae, such as *Streblospio benedicti*, *Capitella* spp. and *Polydora cornuta*, are the early colonizers (La Salle *et al.*, 1991; Moy & Levin, 1991; Minello *et al.*, 1994; Sacco *et al.*, 1994; Levin *et al.*, 1996; Posey *et al.*, 1997). Polychaete taxa were absent or rare from *Salicornia* marsh sediments in southern California (Table 2), although they were common genera in nearby mudflats (Levin *et al.*, 1998; Talley *et al.*, in press). Naidid oligochaetes and insects appear to replace these polychaetes as early colonizers in young *Salicornia* marshes.

The older *Salicornia* marshes we studied (natural and created) exhibited increased proportions of enchytraeid and tubificid oligochaetes (Figure 4). This increase probably is related to increased time for colonization by slow dispersers (Levin *et al.*, 1996) and to an accumulation of sediment organic matter with concomitant moisture retention. Tubificid oligochaetes were notably slow to recolonize young *S. alterniflora* marshes on the Atlantic coast (La Salle *et al.*, 1991; Levin *et al.*, 1996). However, Posey *et al.* (1997) observed similar numbers of the tubificid oligochaetes, *Monopylephorus parvus* and *M. rubroniveus* in 4- 11- and 15-year old created marshes, all in close proximity to one another. Both tubificid and enchytraeid oligochaetes have direct development and produce offspring in cocoons, with no obvious means of planktonic dispersal (Giere & Pfannkuche, 1982). Their greater representation in Upper Newport than Anaheim Bay marshes (Figure 4), which are both fairly similar in age, may result from different proximity to source populations. The created marsh in Upper Newport Bay is directly connected to and only 5 m from the natural *Salicornia* marsh, whereas the created Anaheim Bay marsh is on an island 150 m from the natural marsh (Table 1).

Enchytraeid oligochaetes, which have terrestrial affinities, are frequently associated with marsh vegetation (Healy & Walters, 1994) or below-ground detritus (Giere & Pfannkuche, 1982; Levin *et al.*,

1997; Levin & Talley, in press; this study). Among the created marshes, enchytraeids were most abundant at Newport Bay (Table 3), where below-ground biomass was greatest (Figure 3). Limited access to created-marsh sediments, combined with a need for detritus or fine-grained sediments not present in very young *Salicornia* marshes, may be responsible for slow recovery of tubificid and enchytraeid oligochaetes.

Increased availability of incident light may enhance benthic micro- and macro-algal production. These conditions should favour early successional species such as *P. litoralis*, which is recorded as feeding on diatoms and detritus at the sediment surface (Giere & Pfannkuche, 1982; Levinton & Stewart, 1988) and chironomid insects which can live within benthic filamentous algal mats (unpub. obs.; Levin *et al.*, 1997). Our estimates of percent open space were not a suitable proxy for the amount of light reaching the sediment surface due to the varying densities of the *Salicornia* spp. and *Spartina foliosa* plant canopies. Measurements of light attenuation and benthic micro- and macro-algal production, which were not made in this study, would be required to assess the relationships between macrofauna and benthic algae.

*Recovery rates.* After 5 to 10 years, the sediments, vegetation, and macrofauna of created *Salicornia* marshes still did not completely resemble the nearby natural marshes. In a study of 1 to 17-year old *S. alterniflora* marshes, Sacco *et al.* (1994) reported that macrofaunal similarities between natural and created marsh pairs in North Carolina were less related to marsh age than to physical disturbance. Sediment and faunal differences found between our highest energy natural marsh (Ream Field) and the nearby, low-energy McCoy Tidal Pond natural marsh in Tijuana Estuary were often similar to the differences found between the restored and natural marsh pairs in other bays. For example, Ream Field had 88% lower organic matter content, 52% lower below-ground biomass and 69% higher sand content than McCoy Tidal Pond (Figure 3). The restored marshes contained 72 to 86% lower organic matter content, 36 to 76% lower below-ground biomass and 64 to 68% higher sand content (except for Anaheim Bay) than most of their natural marsh counterparts (Figure 3). Differences in macrofauna at the two natural sites in Tijuana Estuary resembled the relationship between the youngest restored marsh and its natural counterpart. There were lower macrofauna densities and species richness, a greater proportion of insects, and a smaller proportion of tubificid oligochaetes in the sandy, organic-poor sediments (i.e. the 16-month old restored marsh and Ream Field) (Figures 4, 5).

High soil organic matter and fine particle size have been linked to higher macrofaunal abundances in *Spartina* marshes where tubificid oligochaetes, capitellid and spionid polychaetes are common (Lana & Guiss, 1991; Moy & Levin, 1991; Sacco *et al.*, 1994; Levin *et al.*, 1996; Craft, in press). Significant positive relationships between combustible organic matter or below-ground biomass and numerous created marsh taxa were also observed in this study (Table 5). Plant detritus and live roots beneath the sediment surface may provide food for deposit feeders (Lopez & Levinton, 1978), retain soils moisture at low tide and provide refuge from predators (e.g. Orth *et al.*, 1984; Moss & Timms, 1989; Lee & Kneib, 1994). It is likely however, that at the very high concentrations found in natural marshes (Figure 3), excess below-ground biomass can inhibit macro-infaunal development (e.g. Brenchley, 1982; Capehart & Hackney, 1989) [Table 5(a,b)]. Also, organic rich, moist soils of older marshes may enhance vascular plant production, which may shade sediments, or may promote reducing conditions, either of which can reduce benthic algal growth and hinder infaunal success.

Our observations of macrofaunal succession in *Salicornia* marshes of southern California agree with findings for *Spartina* marshes which indicate that 4 to 5 years is insufficient for development of a natural fauna (Levin *et al.*, 1996; Scatolini & Zedler, 1996), but that similarities between natural and created marsh faunas may be evident in eight to 10 years (La Salle *et al.*, 1991; this study). However, we caution that even when there are similarities in macrofaunal densities or assemblage composition between created and natural systems, functional characteristics such as food web support, nutrient cycling, population size structure or parasite loads may remain different (Levin *et al.*, 1996; Talley *et al.*, 1998b; Levin *et al.*, 1999; Talley, in press; C. Currin, L. Levin, D. Talley & T. Talley, unpubl. data).

#### Comparisons with natural *Spartina foliosa* habitats

Because the majority of salt marsh faunal research has been conducted in *Spartina* habitats (Levin & Talley, in press), it is important to ascertain the degree to which *Spartina* faunas resemble *Salicornia* faunas, and thus the extent to which research results from one vegetation zone might be applied to another. Results presented here suggest *Spartina* and *Salicornia* marshes are not interchangeable with respect to their infauna [Figure 7(a)].

Differences between *Salicornia* and *Spartina* habitats can provide insight into the temporal succession of these marsh systems. When both genera co-occur in

salt marshes, *Spartina* occupies lower tide levels (Zedler, 1977; Mitsch & Gosselink, 1993, pp. 239–243). *Spartina* marsh is an early developmental stage that will accrete sediments and organic material and eventually become *Salicornia* (or mid-marsh) habitat (Chapman, 1940; Redfield, 1972). Accordingly, this study revealed higher densities of animals with terrestrial affinities (e.g. insects and terrestrial isopods) naturally occurring in the *Salicornia* zone (Table 3) and those with aquatic affinities (e.g. polychaetes) in the *Spartina foliosa* zone (this study; Levin *et al.*, 1998). Observed differences between faunas in *Spartina* and *Salicornia* marshes are hypothesized to result from diminished inundation time as well as variations in soil or plant properties (e.g. shading, below-ground structure). Three of the five species shared between the *Spartina* and created *Salicornia* marsh in San Diego Bay, that were absent in the natural *Salicornia* marsh, were marine taxa (the mussel *M. senhousia*, capitellid polychaetes and the spionid polychaete, *S. benedicti*). These observations suggest that the macrofauna of created *Salicornia* marshes share some early successional properties with *S. foliosa* marshes [Figure 7(b)].

#### Lessons for conservation and restoration

The high colonization potential of *Salicornia* spp. in disturbed areas, and their success in southern California (Zedler, 1982), make *Salicornia* a natural choice for marsh-creation projects. Faunal recovery of newly planted *Salicornia* habitats may take at least 10 years, thus any program monitoring restoration effectiveness might require a decade or more. During this period, total density overshoots might occur, but these do not necessarily indicate recovery of assemblage function. Extensive among-bay variation observed for macrofaunal assemblages in *Salicornia* and *Spartina* marshes of southern California (Figure 4, Table 3; Levin *et al.*, 1998) suggests that reference sites for evaluation of created-marsh recovery should be located within the same bay whenever possible.

Knowledge of faunal differences between *Salicornia* and *Spartina* habitats should influence conservation efforts and the design of created systems in environments like southern California where both types of vegetation are vanishing rapidly. The loss of *Spartina foliosa* from southern California wetlands due to altered hydrography, and the frequent replacement with *Salicornia* spp. (Zedler *et al.*, 1980; Ibarra-Obando & Poumian-Tapia, 1991) could have serious consequences for maintenance of faunal diversity. A more complete understanding of *Salicornia* marsh structure and function is needed. This will require additional

information about the ecology and natural history of the resident infaunal taxa, especially insects and oligochaetes.

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