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Colonization, succession, and nutrition of macrobenthic assemblages in a restored wetland at Tijuana Estuary, California

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Abstract

Modes of colonization, the successional trajectory, and trophic recovery of a macrofaunal community were analyzed over 19 months in the Friendship marsh, a 20-acre restored wetland in Tijuana Estuary, California. Traditional techniques for quantifying macrofaunal communities were combined with emerging stable isotopic approaches for evaluation of trophic recovery, making comparisons with a nearby natural *Spartina foliosa* habitat. Life history-based predictions successfully identified major colonization modes, although most taxa employed a variety of tactics for colonizing the restored marsh. The presence of *S. foliosa* did not seem to affect macrofaunal colonization or succession at the scale of this study. However, soil organic matter content in the restored marsh was positively correlated with insect densities, and high initial salinities may have limited the success of early colonists. Total macrofaunal densities recovered to natural marsh levels after 14 months and diversity, measured as species richness and the Shannon index (H'), was comparable to the natural marsh by 19 months. Some compositional disparities between the natural and created communities persisted after 19 months, including lower percentages of surface-feeding polychaetes (*Polydora* spp.) and higher percentages of dipteran insects and turbellarians in the Friendship marsh. As surficial structural similarity of infaunal communities between the Friendship and natural habitat was achieved, isotopic analyses revealed a simultaneous trajectory towards recovery of trophic structure. Enriched $\delta^{13}C$ signatures of benthic microalgae and infauna, observed in the restored marsh shortly after establishment compared to natural *Spartina* habitat, recovered after 19 months. However, the depletion in $\delta^{15}N$ signatures of macrofauna in the Friendship marsh indicated consumption of microalgae, particularly nitrogen-fixing cyanobacteria, while macroalgae and *Spartina* made a larger contribution to macrofaunal diets in the natural habitat. Future successional studies must continue to develop and employ novel combinations of techniques for evaluating structural and functional recovery of disturbed and created habitats.

Keywords: infauna; salt marsh; succession; colonization; isotope ratio; California coast; insecta; polychaeta

1. Introduction

Attempts to counter wetland losses due to coastal development commonly include salt marsh restoration and creation. In southern California, more than 75% of historic wetlands have been lost to development, and a number of endangered bird and plant species rely on the heavily disturbed remnants of coastal habitats (Zedler, 1991). Marsh restoration sites serve conservation goals while simultaneously providing the valuable opportunity to manipulate biotic and abiotic features and to evaluate factors that facilitate community recovery (Ewel et al., 2001; Craft and Sacco, 2003). While the attempt to construct salt marsh habitats is not new, the key ecological parameters vital to optimal ecosystem function continue to evade ecologists.

Scientific studies of salt marsh recovery initially targeted vascular plants and fishery organisms (Mathews and Minello, 1994). However, there has been increasing

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attention on cryptic infauna that provide trophic support for birds, nekton, and epifauna (Cammen, 1976; Sacco et al., 1994; Levin et al., 1996). Macroscopic infauna trap particles and transfer them from the water column to the sediment as feces or psuedofeces. With waving palps, crunching mandibles, and grinding radulas, these organisms initiate decomposition of organic material and bridge primary salt marsh production with higher consumers (Levin et al., 2001). Variation in the structure of infaunal communities among wetlands and potential absences of advanced successional groups in disturbed or restored habitats are likely to manifest as functional disparities at the ecosystem level.

Studies of infauna in created salt marsh habitats have documented structural disparities between communities in artificial and natural *Spartina alterniflora* marshes. Created *S. alterniflora* marshes in North Carolina, ranging in age from 1 to 28 years, differed from natural ones in terms of infaunal density and trophic structure (Moy and Levin, 1991; Sacco et al., 1994; Levin et al., 1996; Craft and Sacco, 2003). Oligochaetes were better represented in natural than created marshes and species composition and trophic roles remained distinct after 4 years (Levin et al., 1996). Recovery of oligochaete densities has been found to require as long as 25 years (Craft and Sacco, 2003). The implications of structural differences in infaunal communities have been addressed by studies comparing foraging patterns of fish in created marshes. Disparities between prey resources for *Fundulus* and *Oncorhyncus*, in natural and created marshes, persisted for at least 3 years (Moy and Levin, 1991; Simenstad and Thom, 1996).

On the western coast of the United States, infaunal studies have been conducted in natural and created *Salicornia* habitats in southern California (Talley and Levin, 1999; Levin and Talley, 2000). A comparison of five natural and four artificial marshes found similar species richness but higher infaunal densities in the created *Salicornia* marshes except for those in a 16-month-old marsh (Talley and Levin, 1999).

Studies addressing the influence of vegetation presence on infaunal communities, regardless of the type, have produced inconsistent results (reviewed in Levin and Talley, 2000). Most studies have focused on the influence of *S. alterniflora* on infaunal communities, finding variable results (da Cunha Lana and Guiss, 1991; Levin et al., 1996). In natural *Spartina foliosa* habitat (Northern Wildlife Preserve) in Mission Bay, California, densities and species richness were higher in a mudflat than in the adjacent salt marsh (Levin et al., 1998). However, no effects of *S. foliosa* transplants on species richness or total density of infaunal communities in a created marsh of Mission Bay were observed over 3 years, although shoot densities were weakly correlated both positively and negatively with densities of particular macrofaunal taxa (Levin and Talley, 2002).

Colonization abilities of taxa shape infaunal communities in salt marshes. Few studies have successfully unraveled the relative significance of distinct dispersal mechanisms for colonization (but see Levin et al., 1996). Life-history traits such as dispersal potential seem to constrain succession within a given site while their relative significance is subject to seasonality and hydrodynamics of the area (Hall et al., 1992). In North Carolina, where marshes are more extensive, taxa with planktonic larval stages recovered more rapidly than those without such dispersal mechanisms in *S. alterniflora* marshes (Craft and Sacco, 2003). However, on the west coast of the United States, a survey of infauna in Tijuana Estuary revealed that most taxa exhibited limited larval dispersal, which led to specific predictions about their relative colonization potential (Table 1).

In addition to infaunal community structure, a key element in the recovery of wetland function involves trophic support. Nutritional roles of salt marsh primary producers have been under scrutiny for decades (e.g. Haines, 1976; Fry and Sherr, 1984). Key roles for *Spartina* (Peterson et al., 1985; Peterson et al., 1986), and benthic microalgae (Currin et al., 2003) have been demonstrated using stable isotope analyses. In southern California wetlands, where algal production may account for over 50% of total primary production (Zedler, 1980; Sullivan and Currin, 2000), benthic microalgae are known to be a critical food source for many marsh invertebrates (Kwak and Zedler, 1997; Page, 1997). Stable isotopic techniques have only recently been used to assess trophic recovery of created marshes (Talley, 2000; Currin et al., 2003). The composition of animal diets may differ in newly restored and mature wetlands because algal development often proceeds more quickly than vascular plant development in created or restored marshes (Piehler et al., 1998; Currin et al., 2003). The consequences of these primary producer trends for the diets of co-occurring macrobenthos are just beginning to be explored (Currin et al., submitted).

In this study, we directly examine infaunal colonization modes and nutritional support in a restored *S. foliosa* and mudflat habitat, the Friendship marsh in Tijuana Estuary, California and draw comparisons with nearby natural habitats. We ask: (1) Do life-history characteristics (dispersal potential, development) affect colonization modes utilized by each taxon? (2) Do the observed patterns of infaunal recovery in the Friendship marsh reflect the recovery potential of taxa as predicted from observations in a nearby created marsh in Mission Bay, California? (3) What is the relative importance of abiotic environmental, life-history, and biotic factors (e.g. vegetation) in guiding infaunal succession? (4) How similar are sources of nutrition for infauna in the newly restored and natural marsh, and how do sources change with time? Lastly, we ask (5) did the marsh reconstruction successfully create, after 2 years, an infaunal

Table 1
Modes for colonizing the Friendship marsh at Tijuana Estuary as predicted by Levin et al. (1997) and observed modes from this study

Taxon		Predicted colonization mode	Predicted dispersal potential	Rafts	Larval collectors	Plankton
Corophium	A	Swimming adults and rafting	High (rafting), Low (swimming)	X	X	
Pachygrapsus crassipes	C	Planktonic larvae	High		X	
Paranais litoralis	O	Adult swimming and rafting	High (swimming adults), low (rafting)	X	X	X
Tubificoides fraseri	O	Poor colonization potential predicted	Low	X		
Polydora nuchalis[a]	P	Rafting	Moderate to low (rafting)	X	X	
Polydora cornuta[a]	P	Planktonic larvae, rafting	Moderate (plankton), Moderate to low (rafting)	X	X	X
Chironomidae	I[b]	Flying adults, rafting	High to moderate (rafting)	X	X	
Dolichopodidae	I[b]	Flying adults and rafting	High to moderate (rafting)	X	X	
Muscidae	I[b]	Flying adults, rafting	High to moderate (rafting)	X (pupa also)	X	
Hemiptera (adults only)	I[b]	No prediction	No prediction	X	X	
Turbellarians		Planktonic larvae and rafting	Moderate (plankton) larvae, low (rafting)	X	X	X

From Levin (1984) and Levin et al. (1997) and. X denotes that taxa were observed in the indicated sampling device. A, amphipod; C, crab, I, insect; O, oligochaete; P, polychaete.
[a] *Polydora* juveniles and larvae were not identified to species.
[b] Unless otherwise noted, insect families refer to larval forms.

community comparable in density, composition, and diversity to that of the adjacent natural habitat?

2. Materials and methods

2.1. Field site description

The Tijuana River National Estuarine Research Reserve is located immediately north of the U.S.–Mexico Border (32°34′ N, 117°7′ W). The reserve is enveloped by Tijuana to the south and Imperial Beach and San Diego to the north and includes salt marshes, mudflats, as well as riparian and dune habitats. The salt marshes are mainly vegetated by *Spartina foliosa* and *Salicornia* spp. Three quarters of the watershed for Tijuana Estuary lies in Mexico (Zedler, 1991).

The Friendship Marsh, located on the south arm of the Tijuana River Estuary (Fig. 1), was opened to flushing in February 2000 in the southwestern portion of the Tijuana River National Estuarine Research Reserve. The marsh occupies 20 acres of habitat that was restored by excavating 136 000 cubic yards of historic fill material. The Friendship marsh contains three elevation zones; a lower elevation mudflat, an intermediate zone (1.0–1.75 m above MLLW) containing *Spartina foliosa* transplants initially spaced at 2- and 4-m intervals in two density treatments, and an upper marsh elevation zone with naturally recruited vascular plants including *Batis maritima*.

The Friendship marsh has been divided into six blocks for study (Fig. 1). Each block contains lower (mudflat), middle (cordgrass-vegetated), and upper (now *Salicornia*-vegetated) elevations. Half of the vegetated treatments in each block were originally amended with powdered kelp while the rest were unamended (Fig. 1). This study focused only on the unamended *S. foliosa*-vegetated zones that were planted with 2 m spacing and adjacent (lower) mudflats.

The natural marsh habitat adjacent to the Friendship marsh was included in this study for comparative purposes. We sampled six mudflats and adjacent *S. foliosa* patches (about 10 m^2) along a main creek about 500 m from the Friendship marsh.

2.2. Sample collection and processing

Mechanisms utilized by infauna to colonize the Friendship marsh were studied by sampling algal and plant rafts, pumping plankton samples, and deploying larval collectors. Rafts provided information about animals that were interpreted to have arrived from outside of the marsh by a non-planktonic mechanism, plankton samples indicated animals able to enter via incoming tidal waters, and larval collectors identified macrofauna that may have colonized via incoming tidal waters or via sediment resuspension. Algal rafts, defined as clumps of algae observed to arrive on marsh sediment, were collected at low tide in February, April, and August 2000. Rafts were rinsed with filtered seawater and contents were sieved onto a 63-μm screen, then preserved in jars with 10% buffered formalin and stained with Rose Bengal. Algal rafts were dried and weighed on all dates except in February.

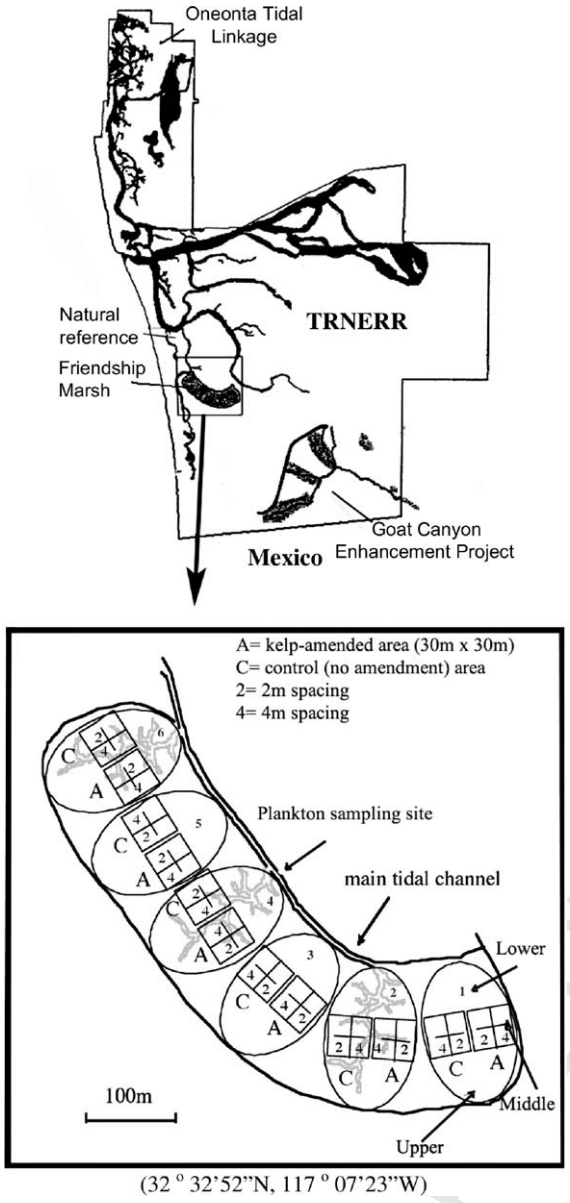

Fig. 1. The Tijuana River National Estuarine Research Reserve (TRNERR) in southern California including position of the Friendship Marsh, from the Model Marsh Research and Monitoring Review by the Southwest Wetlands Interpretative Association in May 2001; arrow points to enlargement of the Friendship Marsh. Samples for this study were taken in control treatments only, indicated by 'C,' with 2 m spacing. Secondary creek treatments were not examined. The lower marsh elevation is that nearest to the main tidal channel, *Spartina foliosa* vegetation comprises the elevation marked by rectangles, and upper marsh elevations are furthest from the channel.

Plankton samples were extracted by pumping 30 l of water through a 75-μm screen at three sites in April 2000 with an incoming tide. Sites were located at the mouth of a central creek and on either side of the main channel mouth in the Friendship marsh (Fig. 1). Pumped plankton samples were preserved in 4% buffered formalin.

Larval collectors were constructed from two 50-ml plastic centrifuge tubes by removing the bottom of one tube, and taping the cylinder to the top of another complete tube. The collectors were inserted into the Friendship marsh sediment so that they extended 4 cm above the surface. Each collector was filled with filtered sea water. Four collectors were deployed in each of the six blocks, with two in the vegetated zone and two in the adjacent mudflat. The larval collectors were uncapped over an 8-day period in April 2000 and 2 days in August 2000. Contents of the collectors were sieved thorough a 63-μm screen, stained, and preserved in 4% formalin and stored in water-tight plastic bags.

Samples for analysis of soil salinity, percent organic matter in sediment, vascular vegetation density and height, and sediment cores for infaunal analyses were collected in the Friendship marsh and the adjacent natural marsh in February, April, and August 2000 and in April and September 2001. Fifteen-meter-long transects running parallel to the main channel were placed within the *S. foliosa*-vegetated region and the adjacent unvegetated mudflat in each of the six blocks comprising the Friendship marsh and in six blocks within the natural marsh. The patchiness of *S. foliosa* in the natural marsh necessitated that blocks in that habitat be spread over about 1 km. Field measurements of *S. foliosa* density, height, and percent cover were made within 0.25-m^2 quadrats at 5-m intervals, placed randomly on either side of the transects. Salinity measurements, reported in practical salinity units, were taken within all quadrats on each transect by squeezing porewater from the upper 2 cm of sediment with a syringe and compressing it through Whatman filter paper onto a handheld refractometer. One sediment core was extracted for macrofaunal analyses per block in each marsh using a 4.8-cm diameter plastic corer (6 cm deep). The unsieved sediment core was preserved in a jar with 10% buffered formalin and contents were stained with Rose Bengal.

Preserved contents from plankton and larval collector samples were washed with distilled water through nested 63- and 300-μm mesh screens. Sediments for macrofaunal analyses were sieved on a 300-μm mesh only. Samples were sorted under a dissecting microscope at 12× magnification, counted, and identified to the lowest taxonomic level possible. Most specimens were identified to the species level except for turbellarians, nemerteans, opithobranchs, and some gastropods; these were minor members of the infaunal communities sampled.

Cores were extracted for analyses of organic matter content within each block (18.02 $cm^2 \times 2$ cm). The sediments were homogenized, sieved through a 2-mm screen, and combusted at 550 °C for at least 10 h. The percentage of organic matter was then determined by mass difference.

Below-ground detrital biomass was estimated by weighing macroscopic roots, plant detritus, and bacterial mat fragments (>300 μm) from the sediment cores.

Large pieces of material were removed by hand from sediment samples while the rest was removed via resuspension of sediment and organic particles, after sorting was completed, in a column of water. Sediment particles settled first from the water and vegetated matter was subsequently collected in a sieve to be included in the biomass sample. The material was dried in an oven at 60 °C for 24–48 h and then weighed.

2.3. Isotopic analyses

Primary producers and infaunal invertebrates were collected for stable isotopic analyses ($\delta^{13}C$ and $\delta^{15}N$) from one and sometimes two replicate plots in planted and mudflat zones in each block of the Friendship and Natural marshes during September 2000, April and September 2001, and April 2002. Macrofauna were sampled from the upper 6 cm of sediment. These were sorted live under a dissecting microscope, placed in 25-μm filtered seawater and allowed to clear their guts overnight, then washed in milli Q water and placed in preweighed silver or tin boats or combusted (500 °C for 6 h) vials, dried at 60 °C and weighed.

Primary producer isotopic signatures were obtained for suspended particulate matter collected during high tide (SPM), *S. foliosa* (living and dead), *Salicornia virginica*, and *Zostera marina* detritus, *Enteromorpha* spp., *Ulva lobosa*, and for benthic microalgae (diatoms and cyanobacteria). Plant and macroalgae samples were collected by hand, rinsed in filtered seawater in the lab to remove epiphytes, rinsed again in milli Q water, dried and powdered. Suspended particulate matter was obtained from created and natural marsh creeks by prefiltering water through a 100-μm mesh, then through ashed GFF filters. Samples were treated with 1 N HCl to remove carbonates. Benthic microalgae (BMI) were collected for isotope analysis using a variation of the density centrifugation with colloidal Si technique (de Jonge, 1979, Blanchard et al., 1988). Briefly, several grams of surficial sediment were suspended in colloidal Si (Ludox HS-40), shaken and stirred, 5 ml of distilled water were added to the top of the sediment-Ludox mixture, and the sample was centrifuged in a 50-ml centrifuge tube for 5 min at 2500 rpm. The suspended diatom and/or cyanobacterial layers were removed with a pipette and filtered through an ashed AH glass fiber filter (Whatman 934-AH). A small number of benthic microalgal samples were collected using the vertical migration techniques as described in Currin et al. (2003). All benthic microalgal samples were examined through a dissecting microscope so that detrital particles and animals could be removed. In addition, microscopic examination allowed us to qualitatively describe microalgal samples as diatom-dominated, cyanobacteria-dominated, or mixed communities composed of diatoms and cyanobacteria. Prior to combustion, all faunal samples were acidified with 10% $PtCl_2$ to remove carbonates. Macrofaunal isotope analyses were carried out on single, larger individuals or on several small individuals combined. $\delta^{13}C$ and $\delta^{15}N$ analyses were conducted using a Finnigan Conflo II continuous flow system and a Fisons NA1500 elemental analyzer.

2.4. Statistical analyses

Differences between infaunal density, diversity, or percent composition on each sampling date between treatments, and between dates were tested with *t*-tests and one-way analyses of variance using JMP 4.0. Correlations between abiotic parameters and those of the infaunal community were tested with linear regressions. Biodiversity was measured in terms of taxon richness, which closely approximated species richness. The Shannon–Weiner index and rarefaction diversity were calculated with Biodiversity Pro software (McAleece et al., 1997). For algal rafts, which varied in weight, and for larval collectors, whose lengths of deployment varied, infaunal composition was normalized via expression as percent composition. Where log arc-sin transformation of percent composition values failed to normalize data, the non-parametric Kruskal–Wallis test, approximated with the χ^2 statistic, was used.

To compare community similarity among infaunal samples, multidimensional scaling (MDS) was performed. To test for statistically significant differences in community composition between different sample types (marsh, vegetation treatment or date), an analysis of similarity (ANOSIM) was performed. Significance levels of alpha were Bonferroni-adjusted. Percent similarities and dissimilarities between groups of samples were calculated via SIMPER analyses. MDS, ANOSIM and SIMPER were calculated using PRIMER software (Clarke and Warwick, 1994).

3. Results

3.1. Abiotic factors

Porewater salinity was initially very high in the Friendship marsh (50–160 in April 2000) and was significantly higher on average than in the natural marsh (Table 2, April 2000: $t_{22} = 2.95$, $P = 0.007$). The vegetated region of the Friendship marsh displayed higher salinity than the unvegetated region (Table 2, $t_{10} = -4.78$, $P = 0.001$), probably due to higher elevation (unvegetated: <2 feet above MLLW vs. vegetated: >3 feet above MLLW). By April 2001, porewater salinity in the unvegetated region matched that in natural unvegetated areas, while salinities in the vegetated region of the Friendship marsh remained significantly greater than in the vegetated natural marsh (Table 2, April

Table 2
Average porewater salinity (with standard errors) in vegetated and unvegetated regions of the Friendship and natural marshes in April 2000 (2 months), April 2001 (14 months), and September 2001 (19 months after restoration)

	Unvegetated salinity	Vegetated salinity	Overall salinity
April 2000			
Friendship marsh	68.2 ± 2.7	97.8 ± 5.6	83.0 ± 5.4
Natural marsh	42.8 ± 1.2	44.6 ± 2.6	55.3 ± 2.3
April 2001			
Friendship marsh	53.7 ± 4.0	56.9 ± 2.4	55.3 ± 3.2
Natural marsh	48.8 ± 2.9	44.4 ± 2.4	46.6 ± 1.9
September 2001			
Friendship marsh	46.9 ± 4.2	46.4 ± 1.6	46.7 ± 2.1
Natural marsh	42.8 ± 1.9	45.1 ± 3.7	43.9 ± 2.0

2001: $F_3 = 3.39$, $P = 0.038$) until September 2001 ($t_{22} = 0.92$, $P = 0.367$). Below-ground biomass was significantly lower in the restored marsh than in the natural habitat (Wilcoxon approximation $\chi^2 = 10.15$, $P = 0.001$) until September 2001.

In its first year, the restored marsh had less organic matter in sediments (February 2000: 6.34 ± 1.05%) than the natural marsh (8.99 ± 0.69%) ($t_{22} = -2.11$, $P = 0.047$). However, by September 2001, the organic content of sediments in the restored marsh (4.68 ± 0.61%) did not differ from that of the natural marsh (3.25 ± 0.49%) ($t_{22} = 0.11$, $P = 0.107$).

There were few significant relationships between infaunal densities and abiotic parameters. An exception was a positive correlation between percent organic matter in the restored marsh and total insect densities in Spring 2001 ($r^2 = 0.59$, $P = 0.003$). No such relationship was found in Fall 2001 or in the natural marsh.

3.2. Colonization by Macrofauna

A total of 422 macrofaunal individuals were collected in 30 raft samples, 360 individuals were found in 38 larval collector samples, and only 10 individuals were detected in plankton samples during this study. However, sampling effort was lower for plankton samples than for rafts and larval collectors.

Macrofauna found on plant rafts and in larval collectors did not differ from one another in terms of family composition (ANOSIM, $P = 0.28$ in April 2000; $P = 0.55$ in August 2000). These results suggest that most taxa utilized more than one colonization mode, arriving both as hitchhikers on drifting substrate and reaching the sediment via incoming tidal waters or sediment resuspension. The naidid oligochaete, *Paranais litoralis*, the amphipod *Corophium* sp., the spionid polychaete, *Polydora* spp., and dipteran insects accounted for more than 70% of macrofauna within rafts and larval collectors (Fig. 2). The only taxon to appear in larval collectors that was not detected in rafts was the crab, *Pachygrapsus crassipes*; juveniles were found in two collectors in April 2000 and in six collectors in August 2000. These results agree with predictions that the decapod would colonize the marsh primarily through dispersal of planktonic larvae (Table 1).

Juvenile and larval *Polydora* individuals were present in plankton samples. A few *P. litoralis* individuals and turbellarians comprised the remaining meroplankters. While the *Polydora* larvae were not identified to the species level, *Polydora cornuta* is known to have planktonic larvae, while the other common spionid species in the area, *Polydora nuchalis* has direct development that occurs in adult tubes (Blake and Arnovsky, 1999). Only the former was predicted to colonize the marsh in the larval stage (Table 1; Levin et al., 1997).

3.3. Macrofaunal succession

In February 2000, when the Friendship marsh was first opened to flushing, terrestrial insects such as ants and mites occupied its sediments in low abundance. By April 2000, dipteran insect larvae dominated the Friendship marsh, constituting 73.6% of total macrofauna. In August 2000, the Friendship marsh sediment contained a moderate proportion of adult *Polydora nuchalis* (12.1%) and a very high proportion of dipteran insects (84.5% of macrofauna).

From the first to the second year in the Friendship Marsh, insects declined in relative importance while annelids increased in representation. From April 2000 to April 2001, insect percent composition significantly decreased ($\chi^2 = 14.66$, $P = 0.005$, Fig. 3). Insect densities rose from 11,111 indiv. m^{-2} in Spring 2000 (71.4% of total macrofauna) to 137 222 indiv. m^{-2} in Fall 2000 (83.2% of total macrofauna), then decreased to 39 444 indiv. m^{-2} by Spring 2001 (12.8% of total macrofauna), but rose again to 102 778 indiv. m^{-2} by Fall 2001 (30.6% of total macrofauna). Meanwhile, polychaete density consistently increased in the Friendship marsh, from 556 indiv. m^{-2} in April 2000 to 153 333 indiv. m^{-2} in September 2001 (April 2000 to April 2001: $t_{22} = -4.98$, $P < 0.001$; April 2001 to September 2001: $t_{22} = -1.79$, $P = 0.088$). Oligochaete densities increased significantly between April 2000 and April 2001 ($t_{22} = -2.10$, $P = 0.005$), driven primarily by the abundance of the naidid, *P. litoralis*. *Paranais litoralis* density fluctuated from approximately 556 indiv. m^{-2} after the first 7 months, to 137 778 indiv. m^{-2} by Spring 2001, before declining in Fall 2001 to 31 667 indiv. m^{-2}.

Total macrofaunal densities increased significantly during the first 2 years of the Friendship marsh existence (from April 2000 to April 2001, $t_{10} = -3.420$, $P < 0.0013$). Total density of macrofauna was 15 556 indiv. m^{-2}, 165 000 indiv. m^{-2}, and 307 222 indiv. m^{-2} in April 2000, August 2000, and April 2001, respectively.

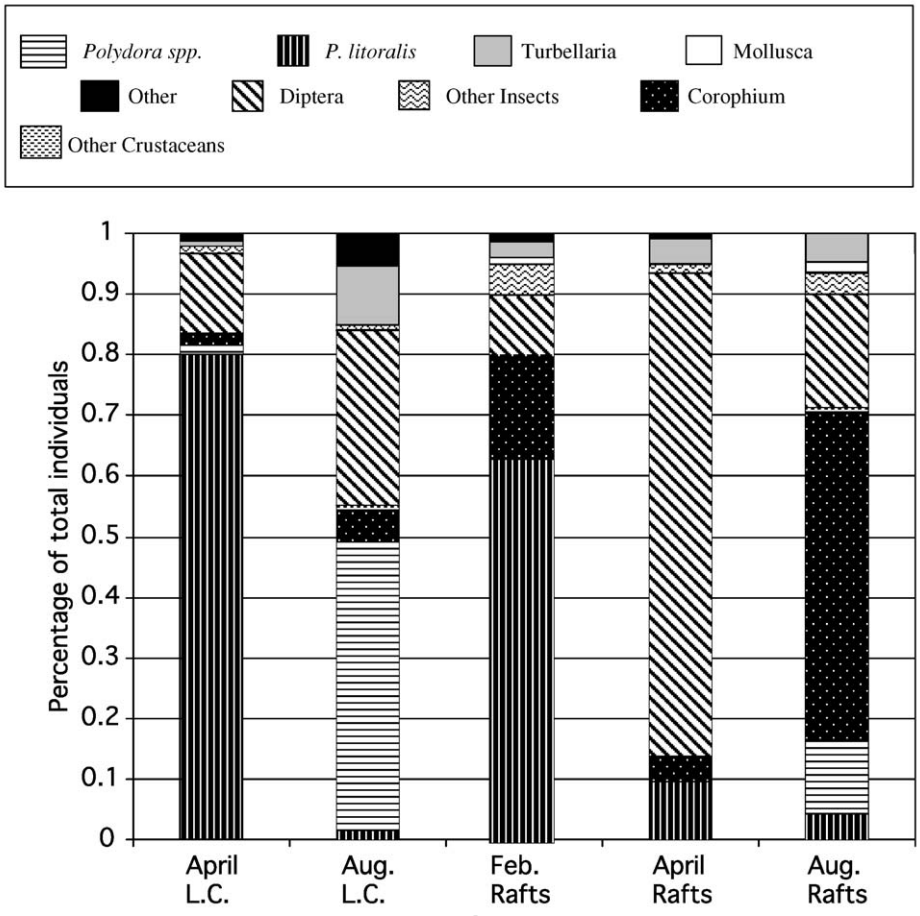

Fig. 2. Percent composition of macrofauna on plant rafts and in larval collectors (L.C.) during April and August 2000 in the Friendship Marsh (composition on rafts is also shown for February 2000).

Homogeneity of samples extracted from the restored marsh increased over time, from 20.99% at 0 months to 36.15% similarity at 19 months (SIMPER).

Seasonal variation in Friendship marsh infaunal composition was evident in its first 2 years (Fig. 3). The major taxa contributing to temporal differences between the Spring and Fall of the first year in the Friendship marsh (84.35% dissimilar) were all insects, including Ephydridae, Dolichopodidae, and Muscidae; these increased in density from Spring to Fall (Fig. 3, Table 3). Similar changes occurred from Spring to Fall of the second year (67.07% dissimilar) with most of the variation being due to dolichopodid insect larvae but also to *P. litoralis, P. nuchalis*, and *Polydora* juveniles (Fig. 3 and Table 3).

3.4. Recovery of density, composition, and diversity

Fourteen months after establishment of the Friendship marsh, in April 2001, total macrofaunal densities did not significantly differ from that of the natural marsh ($t_{22} = -0.85$, $P = 0.404$), although the Friendship marsh contained marginally lower densities by September 2001 ($t_{22} = -1.84$, $P = 0.073$).

By September 2001, compositional disparities between infaunal assemblages in the natural and Friendship marshes remained, with the Friendship marsh containing significantly higher proportions of insects (Kruskal–Wallis $\chi^2 = 5.61$, $P = 0.023$) and turbellarians ($\chi^2 = 7.14$, $P = 0.008$) but lower representation of polychaetes ($\chi^2 = 4.58$, $P = 0.032$) than the natural marsh (Fig. 3).

Species richness increased during the first 19 months of the Friendship marsh existence. After 7 months, most of the dominant species had appeared (including *P. litoralis*, several species of dipteran insects, *Corophium* sp., and *P. nuchalis*). Diversity, measured by the Shannon index (log base 10) increased slightly from $H' = 0.67$ in April 2000 to $H' = 0.75$ in April 2001. The Friendship marsh exhibited higher rarefaction diversity in Spring 2001 than in Spring 2000 (Fig. 4A) and contained species richness (per core) comparable to the natural marsh as well as a higher Shannon Index (restored: $H'_{\log 10} = 1.07$, natural: $H'_{\log 10} = 0.89$). Rarefaction diversity remained higher in the natural marsh (Fig. 4B).

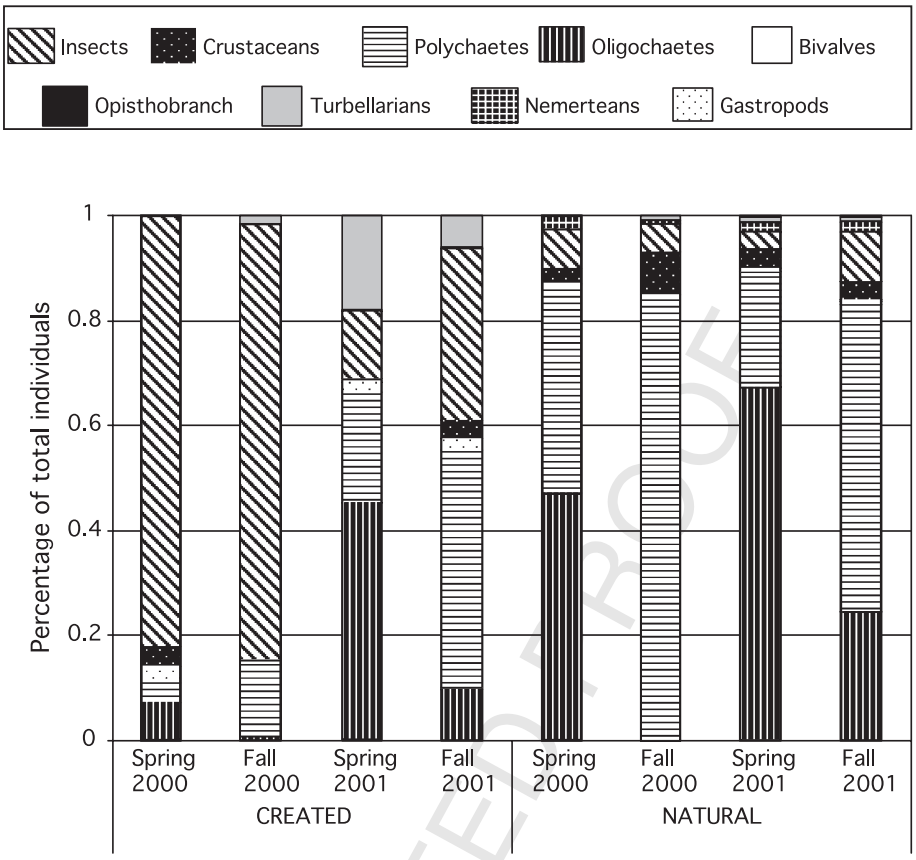

Fig. 3. Percent composition of macrofauna in both the natural and Friendship marshes over the 2-year time period of this study.

3.5. *Effect of vegetation*

After 14 months (April 2001), the average height of *S. foliosa* in the Friendship marsh was 21.21 ± 2.45 cm while that in the natural marsh was 33.46 ± 2.40 cm. The average *S. foliosa* density (indiv. 0.25 m^{-2}) in the restored and natural marshes was 4.94 ± 0.57 and 40.50 ± 11.91, respectively. Such vegetation differences remained 19 months after the marsh creation (height: $t_{10} = -2.21$, $P = 0.051$ and density: $t_{10} = -4.57$, $P = 0.001$).

Infaunal density, composition, and diversity did not significantly differ between vegetated and unvegetated regions of the Friendship marsh during its first 19 months, nor between vegetated and unvegetated regions of the natural marsh.

Macrofaunal composition appeared more similar between vegetated and unvegetated treatments than between marshes in April 2001, although none of the differences were significant (Fig. 5). September 2001 samples from the vegetated region of the restored marsh significantly differed in macrofaunal composition from those of the natural vegetated area (Table 4, ANOSIM, $P = 0.006$, $R = 0.219$).

Table 3
Percent similarities (along main diagonal) and percent dissimilarities (below diagonal) of macrofaunal communities between dates in the Friendship marsh, from February 2000 to September 2001 (Fall 2001), as determined from SIMPER

	Feb. 2000	Spring 2000	Fall 2000	Spring 2001	Fall 2001
Feb. 2000	20.99	**0.003**	**<0.001**	**<0.001**	**<0.001**
Spring 2000	97.29	23.57	**<0.001**	**<0.001**	**<0.001**
Fall 2000	97.79	84.35	34.83	**<0.001**	**<0.001**
Spring 2001	89.09	97.85	89.89	53.22	**<0.001**
Fall 2001	92.06	85.80	82.38	67.07	36.15

The significance levels of each comparison generated from ANOSIM are above the diagonal. Bold indicates significance, set at 0.005, based on the Bonferroni adjustment for number of ANOSIM tests.

3.6. *Patterns of seasonality*

In the natural marsh infaunal community, the percent composition of oligochaetes, mainly *P. litoralis*, declined (in 2000: Wilcoxon $\chi^2 = 3.56$, $P = 0.059$; in 2001: $t_{21} = 2.06$, $P = 0.052$) while the percent composition of polychaetes, mainly *Polydora* spp., increased from the Spring to the Fall seasons (in 2000: $t_{22} = -2.31$, $P = 0.031$; in 2001: $t_{21} = -2.43$, $P = 0.024$). Insect density was higher during the Fall season than in the Spring during 2001 only ($t_{22} = 2.26$, $P = 0.034$).

The Friendship marsh mirrored some of the seasonal fluctuations observed in the natural marsh. In both of its first two years, the percent representation of

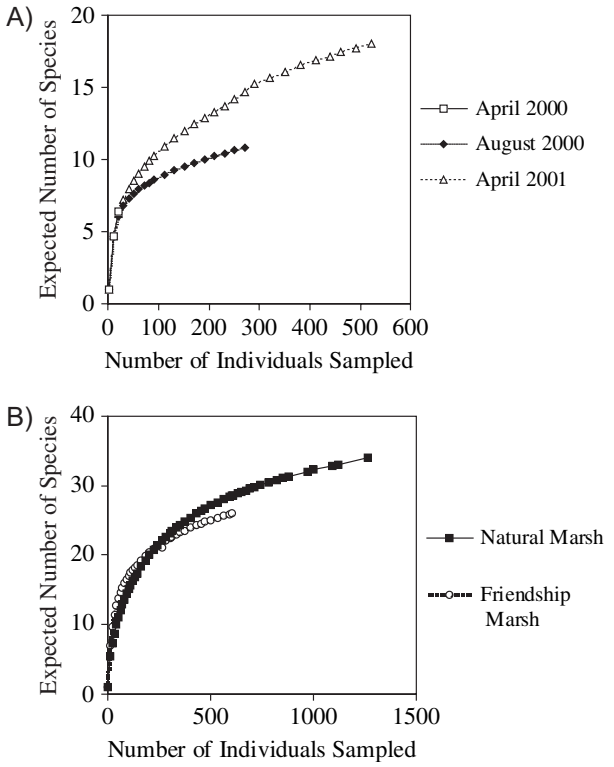

Fig. 4. Rarefaction curves for macrofauna in (a) the Friendship marsh over 3 dates from April 2000 to April 2001 and in (b) both the Friendship and natural marshes in September 2001.

oligochaetes exhibited a trend of decline from the Spring to the Fall, but this change was more notable in the second year (Fig. 6, in 2001: Wilcoxon $\chi^2 = 1.78$, $P = 0.182$). However, the significant decline in insect composition, between Fall 2000 and Spring 2001 and from Spring 2000 to Spring 2001 (Wilcoxon $\chi^2 = 14.66$, $P = 0.005$, 4 df), did not correspond with any significant seasonal change in natural insect composition and was probably more indicative of a successional transition.

3.7. Isotopic food web analyses

Primary producer $\delta^{13}C$ values ranged from −11.90 to −20.55 in September 2000 (Table 5). Most values fell within a range between −14.75 and −17.6, with the exception of (1) benthic microalgae from the Friendship marsh, which were 4.3 per mil enriched in ^{13}C relative to microalgae from the natural marsh, and (2) a single collection of suspended particulate matter (SPM) from the natural marsh (Table 5), which was depleted in ^{13}C relative to SPM collected from the Friendship marsh. Over the remainder of the study, between-marsh differences in all primary producer C isotope values were small and variable (Table 5), with little separation between taxonomic groups.

In contrast, $\delta^{15}N$ values allowed better separation of primary producer groups, and also exhibited greater marsh effects (Table 5). Benthic microalgae from the Friendship marsh exhibited the most depleted $\delta^{15}N$ values, between 1.8 and 5.1 per mil. In September 2000, 7 months after marsh establishment, $\delta^{15}N$ values of benthic and planktonic microalgae were readily distinguishable from macroalgae (*Enteromorpha*) and *Spartina*, which exhibited relatively enriched $\delta^{15}N$ values of over 7.9 per mil (Table 5). Over the remainder of the study period, most primary producers collected from the natural marsh exhibited a consistent enrichment of 1−3 per mil in their $\delta^{15}N$ values relative to those of the Friendship marsh, and benthic microalgae remained relatively depleted in ^{15}N compared to *Spartina* and *Enteromorpha* (Table 5).

In September 2000, infaunal macrobenthos from the Friendship marsh exhibited $\delta^{13}C$ values that were on average 4.5 per mil heavier (mean = −9.8) and $\delta^{15}N$ values 5.1 per mil lighter (mean = 4.92) than those in the natural marsh (mean $\delta^{13}C = -15.65$, mean $\delta^{15}N = 11.14$). Comparable between-marsh differences were observed among the gastropod *Cerithidea californica*, chironomid and dolichopodid insect larvae, the amphipod *Corophium* sp. and other gammarid species, the spionid polychaetes *P. cornuta, P. nuchalis, and Streblospio benedicti* (Fig. 6). Only ephydrid insect larvae had identical signatures in the two marshes. Because microalgae were the only primary producers to exhibit a similarly large, between-marsh isotopic difference, and benthic microalgal isotope values were closest to those of infauna collected in September 2000 (Fig. 7), these data suggest that microalgae were the primary food source for the small, short-lived macrobenthos in the Friendship marsh. However, between-marsh $\delta^{15}N$ differences were less for microalgae (all taxa grouped) than those observed for the infauna. Macrofaunal signatures may reflect selective consumption of cyanobacteria in the restored marsh. Cyanobacteria have relatively depleted $\delta^{15}N$ signatures (Currin et al. submitted) as a result of their N_2-fixing activity.

Over 18 months, $\delta^{15}N$ remained more enriched in the natural than restored marsh for a number of invertebrate taxa (dolichopodid insects, *Polydora* spp. and *Paranais litoralis* (Fig. 6). However, during this same period the $\delta^{13}C$ values converged, with seasonal $\delta^{13}C$ averages of −14.2 to −14.9 in the Friendship marsh and −15.0 to −15.9 in the restored marsh. Isotopic signatures suggest that the trophic structure of the Friendship marsh at the lowest levels very rapidly came to resemble that of the natural system.

Another feature of the natural marsh is the apparent seasonality of isotopic signatures in some taxa. In general microalgae and invertebrates exhibited lighter $\delta^{15}N$ signatures in Fall (September) than in Spring (April) (Fig. 6). Causes might include greater abundance and consumption of nitrogen-fixing cyanobacteria, or less input from anthropogenic sources (sewage,

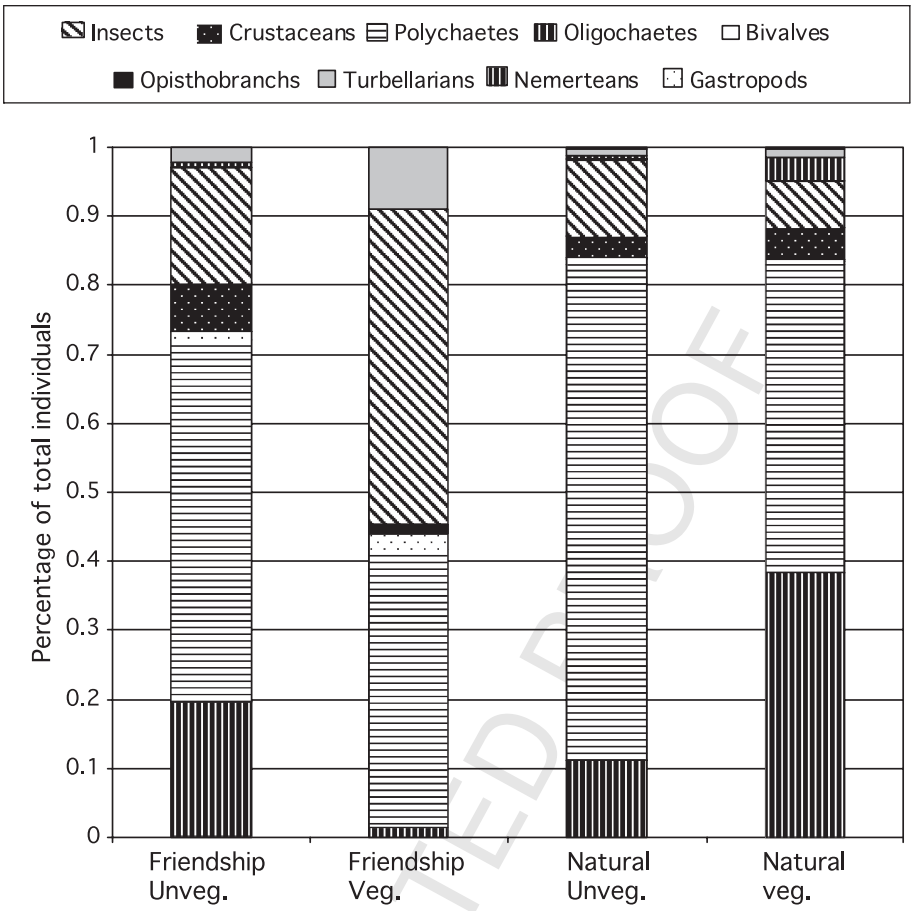

Fig. 5. Percent composition of macrofauna in vegetated and unvegetated regions of the Friendship and natural marshes in April 2001.

groundwater, agricultural runoff) enriched in ^{15}N, during Fall than Spring.

4. Discussion

4.1. Mechanism of colonization

Based on the presence of most taxa in both larval collectors and on rafts, and the lack of long-lived planktonic larvae in most species (Table 1), we infer that most colonists arrived passively as post-larval stages by a combination of bedload transport, water column or water-surface transport, and rafting. The presence of active adult dispersers, such as *P. litoralis* and *Corophium* sp., on algal rafts suggests that the distances those individuals are able to disperse may be enhanced by passive rafting, or that the individuals secondarily occupied the rafts after arriving in the Friendship marsh. Since the naidid oligochaete swims as an adult and reproduces asexually (Levinton et al., 1995), its high dispersal potential and development mode contribute to rapid colonization in southern California marshes (Talley and Levin, 1999; this study).

The scarcity of organisms in plankton samples was characteristic of the infaunal community in Tijuana Estuary; resident species largely lack planktonic dispersal stages. Nonetheless, the presence of a few *Polydora* sp. larvae in the water column in the spring plankton sample was consistent with peaks of larval abundance for *P. cornuta* observed during the spring in a Mission Bay mudflat (Levin, 1984). Another taxon with planktonic larvae was the lined-shore crab *Pachygrapsus crassipes*. Although its larvae were found in

Table 4
Percent similarities of macrofauna within vegetation treatments of the natural and Friendship marshes (along main diagonal) and percent dissimilarities between vegetation treatments of the habitats in September 2001 along with their significance levels (on opposite sides of the diagonal) from SIMPER and ANOSIM

	Nat. veg.	Nat. unveg.	Created veg.	Created unveg.
Nat. veg.	33.91	$P = 0.848$	***P = 0.006****	$P = 0.516$
Nat. unveg	61.78	35.22	$P = 0.383$	$P = 0.346$
Created veg.	75.01	69.54	30.90	$P = 0.565$
Created unveg.	66.73	64.55	67.23	33.93

Bold indicates significance, set at $\alpha = 0.008$, based on the Bonferroni adjustment for number of ANOSIM tests).

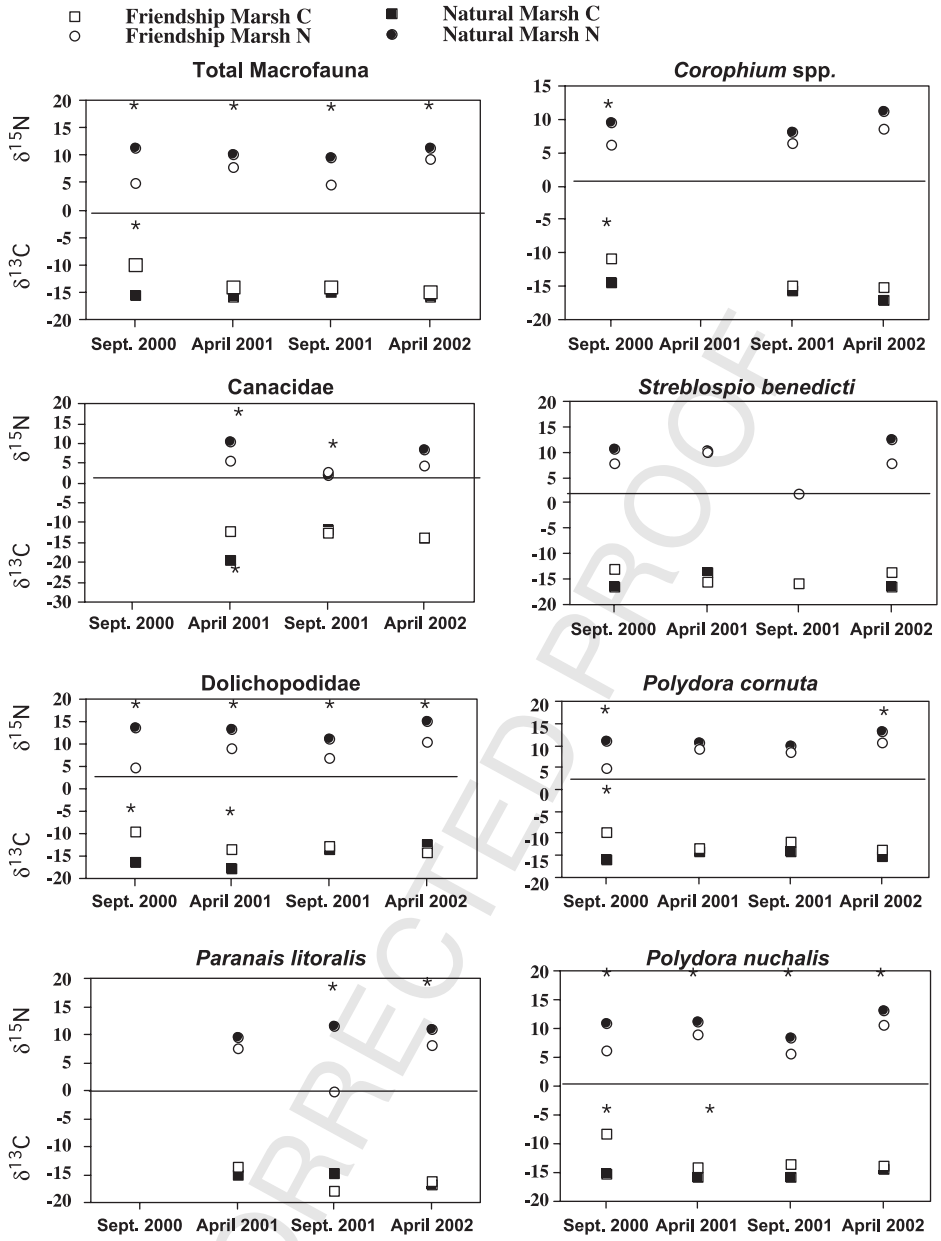

Fig. 6. Average isotopic signatures ($\delta^{15}N$, $\delta^{13}C$) of total macrofauna and the most abundant macrofaunal taxa in the Friendship and adjacent natural marsh habitats as a function of time. The Friendship marsh was opened to flushing in February 2000. Sample data from *Spartina*-vegetated and unvegetated sediments have been pooled. Asterisks indicate significant differences between the Friendship and natural marshes.

larval collectors but not in plankton samples, only one sampling period was conducted for plankton in this study. Further, the absence of *P. crassipes* on rafts supports the predictions that it would colonize mainly via planktonic larvae (Table 1; Levin et al., 1997). In contrast to Tijuana Estuary, dominance by infauna with planktotrophic modes of development over other forms was shown for an early successional marsh in North Carolina (Levin et al., 1996; Craft and Sacco, 2003).

Adult individuals of *P. nuchalis*, a species with direct development, reached the marsh by August in the first year but were not found on rafts nor in larval collectors, so this species' colonization mechanism remains undetermined. The created marsh consistently contained a greater proportion of the planktotrophic *P. cornuta* among total *Polydora* adults in its second year than the natural marsh (25.3 vs. 18.1% in April 2001 and 21.7 vs. 12.4% in September 2001, respectively). The greater success of *P. cornuta* than *P. nuchalis* at colonizing the Friendship marsh in its first 2 years is consistent with its known opportunistic behavior and planktonic dispersal ability (Zajac, 1991).

The only taxa found arriving exclusively on rafts were the oligochaete, *Tubificoides fraseri*, and the gastropod,

Table 5
Average $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures (± 1 standard error) of primary producers in the Friendship marsh and nearby natural marsh habitats of the Tijuana Estuary

	$\delta^{13}C$				$\delta^{15}N$			
	Sept. 2000	April 2001	Sept. 2001	April 2002	Sept. 2000	April 2001	Sept. 2001	April 2002
Suspended particulate organic matter								
Friendship	−17.62 (1)	−14.92 ± 1.31 (2)	–	–	2.46 (1)	7.72 ± 0.44 (2)	–	–
Natural	−20.55 ± 0.79 (2)	–	–	–	3.34 ± 0.7 (2)	–	–	–
Spartina foliosa (live)								
Friendship	−14.75 ± 0.52 (3)	−14.25 ± 0.41 (2)	−13.10 (1)	–	11.04 ± 0.57 (3)	8.65 ± 0.19 (2)	5.76 (1)	–
Natural	−14.84 ± 0.25 (5)	−14.38 ± 1.04 (2)	−13.34 (1)	–	9.39 ± 0.44 (5)	8.03 ± 2.55 (2)	9.15 (1)	–
Benthic microalgae								
Friendship	−11.90 ± 0.63 (14)	−15.50 ± 0.46 (16)	−15.76 ± 0.42 (29)	−17.29 ± 0.48 (15)	1.76 ± 0.33 (14)	5.09 ± 0.42 (16)	4.01 ± 0.36 (29)	4.09 ± 0.52 (15)
Natural	−16.16 ± 1.27 (9)	−14.85 ± 0.40 (11)	−16.29 ± 0.54 (14)	−17.55 ± 0.55 (6)	3.59 ± 0.63 (9)	7.77 ± 0.37 (11)	5.51 ± 0.79 (14)	7.31 ± 0.52 (6)
Enteromorpha sp.								
Friendship	−15.18 ± 0.38 (5)	−16.81 ± 0.43 (3)	−16.74 ± 0.29 (2)	–	7.93 ± 0.63	10.70 ± 0.11 (3)	6.72 ± 1.28 (2)	–
Natural	−16.54 (1)	−14.46 (1)	−15.87 ± 1.01 (2)	−16.20 ± 1.03 (8)	8.63 (1)	11.30 (1)	8.49 ± 1.18 (2)	11.47 ± 0.38 (8)

Numbers of observations are given in parentheses.

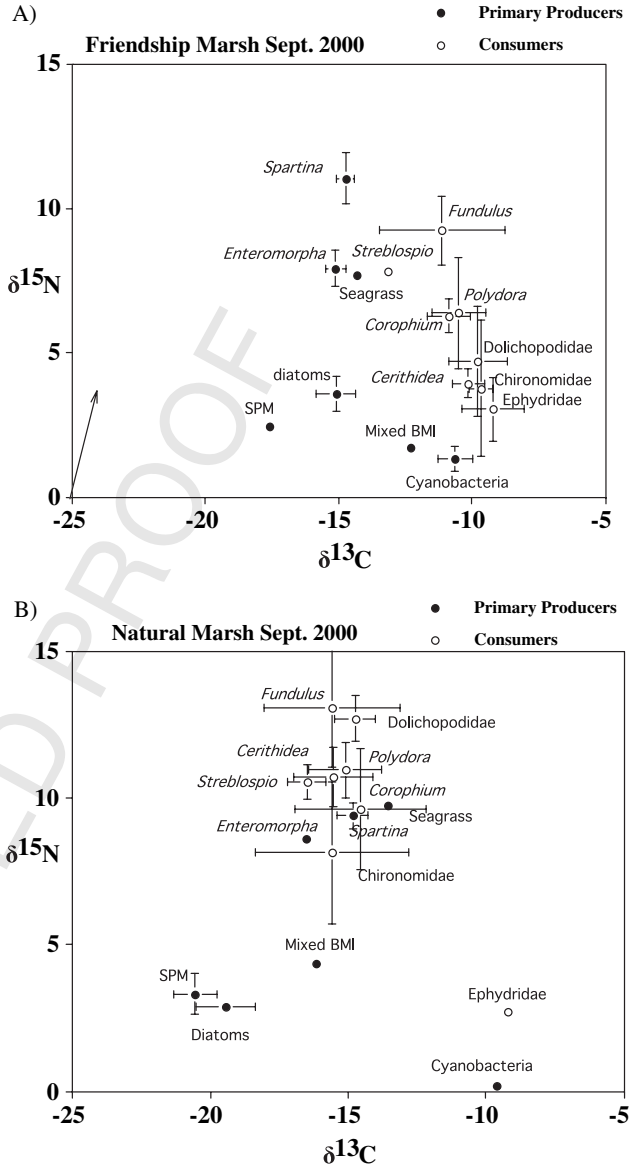

Fig. 7. Dual plot of $\delta^{13}C$ versus $\delta^{15}N$ for average macrofauna (open) and primary producer signatures (filled) with standard error in the (a) Friendship and (b) natural marsh of Tijuana Estuary in September 2000.

Cerethidia californica. *Tubificoides fraseri* was correctly predicted to have poor colonization potential (Table 1), as only one individual was found within the sediments of the Friendship marsh during its first 2 years, and its identification on algal rafts is consistent with its lack of planktonic larvae and active dispersal. In contrast, *C. californica* was unlikely to have been restricted to colonizing by rafts since this direct developer was ubiquitous throughout the natural and created marshes; it probably colonized the Friendship marsh by a variety of mechanisms (rafting, transplant in *Spartina* culms, etc.).

The dipteran insect larvae that dominated the infauna during the first year of the Friendship marsh, including

Dolichopodidae, Muscidae, Ephydridae, and Chironomidae, were unique compared to other colonists in their ability to arrive via adult flight. Adult insects were not readily sampled by the techniques employed in this study, but dispersal by flight is the most likely means by which the dipteran insects initially arrived at the marsh and deposited larvae.

4.2. Order of succession

The successional trajectory observed in the Friendship marsh consisted of early dominance by insects and the naidid oligochaete, *P. litoralis*, followed by an increase in polychaete abundance and the appearance of tubificid and enchytraeid oligochaetes. The pattern generally agreed with that documented in created *Salicornia* marshes (Talley and Levin, 1999) and a *Spartina foliosa* marsh in nearby Mission Bay, California (Levin and Talley, 2002). The appearance of spionid polychaetes after insects in the Friendship marsh may represent an intermediate successional stage that had not been documented in *Salicornia* marshes (Talley and Levin, 1999), but was seen in a created *S. foliosa* marsh in Mission Bay (Levin and Talley, 2002). This stage was probably due to the preference of polychaetes for the lower elevations and wetter conditions of *S. foliosa* zones. Rapid recovery of surface-deposit feeders, particularly polychaetes, has also been found in *S. alterniflora* marshes (Craft and Sacco, 2003).

4.3. Abiotic and biotic influences on succession

Porewater salinity levels in the created marsh were initially high enough (up to 165 in April 2000) that they likely restricted the types and numbers of taxa that could colonize the habitat. A study in Mission Bay, California found a positive correlation between salinity and insect density in *S. foliosa* habitat and a negative correlation between salinity and densities of polychaetes and peracarid crustaceans (Levin and Talley, 2000). This is consistent with our observation that the highly saline, early successional sediments of the Friendship marsh were dominated by insects while polychaetes characterized a more advanced successional stage that was obtained after salinity levels declined in the second year.

Numerous other studies have attributed structural differences in infaunal communities between artificial and natural habitats to distinctions in sediment organic content (Moy and Levin, 1991; Sacco et al., 1994; Levin et al., 1996; Levin and Talley, 2000). The positive relationship found in our study between percent organic matter of sediment and total insect densities in the created marsh supports the positive correlations between macrofaunal abundance and organic content that have been documented in Brazilian salt marshes (da Cunha Lana and Guiss, 1991) and *Salicornia* habitats (Talley and Levin, 1999), and between total insect densities and percent organic content in created and natural *Spartina* marshes (Talley and Levin, 1999).

In spite of the plethora of studies that have revealed the influence of vascular vegetation on infaunal communities in intertidal salt marsh habitats (reviewed in Levin and Talley, 2000), the infaunal community of both the created and natural *S. foliosa* habitats did not differ between vegetated and unvegetated areas (Fig. 5). The similarity of infauna from different vegetation treatments of each marsh is consistent with the absence of vegetation effects in created *S. alterniflora* and *S. foliosa* marshes (Levin et al., 1996 and Levin and Talley, 2002, respectively). Lack of direct sampling of the *Spartina* culms, cited as one possible reason for failure to detect effects (Levin et al., 1996), may apply in this study as well. Alternatively, vegetation density may have been too low in both the created and natural *S. foliosa* habitats to influence infaunal communities.

Given the limited influence of abiotic and biotic factors on the communities, modes of colonization by infauna and their order of arrival may have been a key determinant of successional trajectories.

4.4. Rate of recovery

The recovery of infauna in the Friendship marsh, assessed in terms of density, composition, and diversity, was relatively rapid considering the large size of the restored marsh (20 acres). Total macrofaunal densities and species richness were similar between the Friendship and natural marshes by the time the restored marsh was 19 months of age. Created salt marshes in North Carolina, for instance, have maintained significantly lower macrofaunal densities for as long as 25 years (Craft and Sacco, 2003). One created *S. alterniflora* marsh was found to achieve similar densities and species richness after only 6 months, while compositional differences with a natural marsh remained after 4 years, but this marsh only occupied 2.2 acres (Levin et al., 1996).

Recovery of the Friendship marsh may appear more rapid than if a continuous cordgrass marsh had been the natural reference site. The natural *S. foliosa* patches studied in Tijuana Estuary had lower organic matter content (average ranged from $3.25 \pm 0.14\%$ in September 2001 to $14.26 \pm 1.44\%$ in April 2000) and higher salinity (average ranged from 43 ± 0.39 in April 2000 to 46 ± 0.55 in April 2001) than more continuous *S. foliosa* marshes sampled nearby in San Diego Bay, California (% organic matter $= 13.3 \pm 0.7$, salinity $= 30.8 \pm 0.4$) and Mission Bay, California (% organic matter $= 18.0 \pm 1.3$, salinity $= 24.7 \pm 1.4$) (Levin and Talley, 2000). However, the patchy natural reference sites were selected because they constituted the natural *Spartina* and adjacent mudflat habitats in Tijuana Estuary that most closely shared the tidal flushing, exposure,

sedimentation, and disturbance regimes of the Friendship marsh (L. Levin, personal observation).

The complete recovery of infaunal composition, particularly representation of subsurface-deposit feeders, was not achieved by 19 months in the Friendship marsh. Compositional disparities were documented in a created *S. alterniflora* marsh in North Carolina at the age of 3 years; there was greater representation of surface deposit-feeders, evident in the diet of higher consumers, than in a natural reference (Moy and Levin, 1991). Compositional differences between created and natural *Salicornia* marshes, with higher insect proportions in the artificial habitats, persisted in 5- and 6-year-old systems (Talley and Levin, 1999) and only converged after 10 years, suggesting that the created habitats require a longer period for recovery of infaunal composition than infaunal density and diversity (Levin and Talley, 2002). However, compared to other *S. foliosa* salt marshes that have been studied, which contain as much 37–85% oligochaetes (Levin et al., 1998; Levin and Talley, 2002), tubificid and enchytraeid oligochaetes did not represent a significant proportion of the natural *S. foliosa* infauna in the Tijuana Estuary (consistently less than 10% of total macrofauna), highlighting the lack of a significant functional role, sub-surface deposit feeding, in that habitat.

4.5. Stable isotopic studies of trophic structure

The isotopic signatures of macrofauna in the Friendship marsh highlight benthic microalgae, and cyanobacteria in particular, as the dominant food source of macrofauna in the early successional marsh (Fig. 7). The enriched $\delta^{13}C$ values obtained for macrofauna in September 2000 suggest that benthic microalgae were the most important source of nutrition for macrofauna during the early stages of marsh succession. Previous work by Kwak and Zedler (1997) identified macroalgae and microalgae as a major organic matter source for invertebrates in the natural marsh of Tijuana estuary. Page (1997) also reported microalgae to play a key nutritional role for invertebrates in another southern California marsh. With the exception of samples obtained in September 2000 from the Friendship marsh, macrofaunal $\delta^{13}C$ signatures overlap with those of a variety of primary producers (benthic microalgae, SPM, macroalgae, seagrass, and *Spartina*). Quantitative estimates, via mixing models, are not provided for this system, as the number of potential primary producers contributing to the food web is greater than the number of sources that can be modeled with two isotopes, and the variance about the mean value for fauna is sometimes greater than the difference between end-member values (Table 5). However, by grouping macroalgal and *Spartina* into a single category of 'marsh macrophytes', a number of three-source mixing models were generated, including one whose apices represented values describing 100% assimilation of either benthic microalgae, suspended particulate matter, or marsh macrophytes (Phillips and Koch, 2002). In September 2000, only one macrofaunal taxon (*Streblospio*) and only two taxa (*Cerethidea* and chironomids) out of eight fell within this mixing triangle for the Friendship and Natural marsh, respectively. Other three-source mixing models constructed from different endmembers generated similar results. The number of macrofauna values which fall outside the mixing triangle demonstrates the inability of a three-source mixing model to adequately describe the complex marsh food web (Phillips and Kock, 2002) and suggests a significant dietary role for cyanobacteria (with lighter C and heavier N than the other food sources). However, qualitatively, the faunal values in the natural marsh fall closest to the 'marsh macrophytes' endmember, while macrofaunal values in the Friendship marsh fall closest to the BMI endmember.

The $\delta^{15}N$ values of macrofauna from both marshes throughout the study were generally 10 per mil or less (Figs. 6 and 7) and thus suggest utilization of a food resource with a $\delta^{15}N$ value of 8 per mil or less, given a 2–3 per mil trophic enrichment (DeNiro and Epstein, 1981; Hart and Lovvorn, 2002; McCutchan et al., 2003). Microalgae and SPM had $\delta^{15}N$ values that ranged between 1.8 and 7.8 per mil, while $\delta^{15}N$ values of *Spartina* and *Enteromorpha* frequently exceeded 7 per mil (Table 5), further supporting a conclusion that benthic microalgae were an important part of the food web supporting macrofauna throughout the study in both marshes. Both primary producers and macrofauna from the natural marsh were enriched in ^{15}N relative to samples from the Friendship marsh throughout the study, most likely as a result of differential input of anthropogenically-derived nitrogen (McClelland et al., 1997), but also possibly due to less nitrogen fixation by cyanobacteria. The critical importance of algae in southern California marsh trophic webs is consistent with the high ratio of algal to vascular plant production in Pacific marshes (reviewed by Sullivan and Currin, 2000).

The strong initial enrichment of microalgal $\delta^{13}C$ signatures and initial depletion of invertebrate $\delta^{15}N$ signatures in the Friendship marsh relative to the Tijuana Estuary natural marsh may be a characteristic feature of created marshes in southern California. Similar studies in a 7-acre created *Spartina* marsh in Mission Bay, California, revealed similarly heavy $\delta^{13}C$ and light $\delta^{15}N$ of microalgae, macroalgae, suspended particulate organic matter and invertebrate consumers (relative to an adjacent natural system) during the first few years after establishment (Currin et al., submitted). Between-marsh isotopic differences persisted in Mission Bay for about 6 years, unlike the Tijuana system, where created and natural marsh trophic structures apparently have converged within the first year. Seasonality of macrofaunal isotopic signatures, with lighter $\delta^{13}C$ and $\delta^{15}N$ in

Fall, was also evident in Mission Bay. The temporal shifts that occur in macrofaunal signatures may possibly be attributed to decreasing importance of cyanobacteria over time (Currin et al., submitted).

5. Conclusion

To establish mechanistic understanding of the influence of abiotic and biotic environmental parameters on infaunal communities in wetlands, future studies must continue to adopt manipulative approaches. This study employed marsh restoration as a large-scale manipulation and found that salinity and organic matter set constraints for the general succession of infauna in the Friendship marsh, but that the biotic influence of vegetation was not significant at the scale and stage observed. Instead, the successional sequence documented, of opportunistic insects and naidid oligochaetes followed by surface-deposit feeding spionid polychaetes, may have been more strongly governed by dispersal potential and seasonal availability of colonists than by abiotic and biotic factors.

While recovery of the Friendship marsh was rapid with respect to density and diversity, polychaetes remained underrepresented in terms of percent composition, and microalgae, particularly cyanobacteria, constituted a larger portion of infaunal diets than in the natural marsh after 18 months. The rapid recovery rate of structural equivalency in the Friendship marsh, and any restored wetland, must not mask functional disparities, which may be best ascertained by a combination of approaches such as the use of stable isotopes for evaluating trophic recovery, manipulation of environmental factors on a variety of spatial scales, and careful consideration of temporal variability.

6. Uncited references

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