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NATURAL AND MANIPULATED SOURCES OF HETEROGENEITY CONTROLLING EARLY FAUNAL DEVELOPMENT OF A SALT MARSH

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Abstract. Ecosystem recovery following wetland restoration offers exceptional opportunities to study system structure, function, and successional processes in salt marshes. This study used observations of natural variation and large-scale manipulative experiments to test the influence of vascular vegetation and soil organic matter on the rate and trajectory of macrofaunal recovery in a southern California created salt marsh, the Crown Point Mitigation Site. During the first three years following marsh establishment, macrofaunal density and species richness recovered rapidly within the *Spartina foliosa* (cordgrass) zone; densities in the created marsh were 50% of those in the natural marsh after 16 mo and 97% after 28 mo. However, the early successional assemblage had a lower proportion of tubificid and enchytraeid oligochaetes, and a higher proportion of chironomids and other insect larvae than did the mature natural marsh. Most of the colonizers arrived by rafting on sea grass and algae rather than by larval dispersal. Initial planting of *S. foliosa* had no influence on macrofaunal recovery, perhaps because of variable transplant survival. However, subsequently, both positive and negative correlations were observed between densities of some macrofaunal taxa and shoot densities of *S. foliosa* or *Salicornia* spp. (pickleweed). Salinity and measures of soil organics (belowground biomass, combustible organic matter, and chlorophyll *a*) also were correlated with macrofaunal densities and taxon richness. Of four added soil amendments (kelp, alfalfa, peat, and Milorganite), Milorganite (a sewage product) and kelp both promoted macrofaunal colonization during year 1, but effects were short lived. The most significant sources of heterogeneity in the recovering marsh were associated with site history and climate variation. Faunal recovery was most rapid in highly localized, organic-rich marsh sediments that were remnants of the historical wetland. Elevated sea level during the 1998 El Niño corresponded with similarity of macrofaunal communities in the created and natural marshes. The large spatial scale and multi-year duration of this study revealed that natural sources of spatial and temporal heterogeneity may exert stronger influence on faunal succession in California wetlands than manipulation of vegetation or soil properties.

Key words: El Niño; infauna; insect; macrobenthos; oligochaete; organic amendments; restoration; Salicornia; Spartina; *succession; tidal marsh; wetland.*

Introduction

Community structure is generally controlled by a combination of biotic and abiotic processes. However, in low-density, recruitment-limited communities, such as those that inhabit habitat fragments or that form during initial colonization of a new area, abiotic conditions may have a strong influence on community structure (e.g., Menge 2000). This may be especially relevant in intertidal, soft-bottom systems where elevation, sediment porosity, organic content, and vegetation cover interact with exposure, temperature, and light gradients to create a physiologically harsh environment (e.g., Bertness 1999). The role of physiological stress in structuring communities may be greater in warmer climates (Bertness and Leonard 1997, Bertness et al. 1999). For example, wetland systems in the Mediterranean climate of southern California frequently experience highly variable salinity and desiccation regimes (e.g., Beare and Zedler 1987, Nordby and Zedler 1991). In general, soft-bottom faunas inhabiting tidal wetlands exhibit low diversity (mainly annelids, arthropods, and molluscs), and tolerate high salinity and low-oxygen concentrations (Levin and Talley 2000). However, there is tremendous variation in faunal abundance and composition within climate regimes, within estuaries, and even within the same marsh (Levin et al. 1998, Talley and Levin 1999, Talley et al. 2000), suggesting strong local as well as regional controls on community composition.

Effective conservation and restoration efforts rely on accurate understanding of the factors that control community structure and function. Wetland systems are frequently protected, making large-scale manipulations within these systems unrealistic. Traditional research approaches have, therefore, used comparative observational methods (reviewed in Levin and Talley 2000)

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and ''natural'' experiments in which communities are studied after small-scale (e.g., Levin 1984, Smith and Brumsickle 1989, Trueblood et al. 1994) or large-scale (e.g., Sanders et al. 1980, Santos and Simon 1980) disturbances. However, mechanistic understanding and control of treatment conditions are often limited in natural experiments. Newly created (restored) ecosystems provide an unprecedented opportunity to examine the factors influencing succession on much larger (multihectare) scales than might otherwise be possible (Palmer et al. 1997, Ewel et al. 2001). This is particularly true in the coastal wetlands of California, where all wetland habitat is protected within reserves. Scale often has an important effect on colonization events (Connell and Keough 1985, Thrush and Whitlatch 2001), so extrapolation from small to large scales can be problematic (Thrush et al. 1997). In several instances, wetland scientists have incorporated relatively large-scale experiments into restoration designs to test key influences on community structure and function. Typically these experiments have tested the effects of either the presence or type of vascular plants on fauna (Levin et al. 1996) or the addition of nutrients or organic matter on vascular plant growth (Gibson et al. 1994, Broome et al. 2000).

Sediment-dwelling faunas play key roles in the ecosystem functions of wetlands; they aid decomposition and nutrient cycling and provide trophic support for higher-order consumers (Levin et al. 2001). Recovery of salt-marsh faunal communities involves time-related changes in biomass, abundance, taxonomic composition, diversity, and lifestyle. As a result, differences between created and nearby natural wetlands can persist for many years (e.g., La Salle et al. 1991, Sacco et al. 1994, Posey et al. 1997, Talley and Levin 1999). Observed faunal patterns within salt marshes are typically correlated with habitat attributes (reviewed in Levin and Talley 2000), but experiments are rarely designed to explicitly test the influence of soil, vegetation, or other properties on succession.

Here we treat restoration of a salt marsh, the Crown Point Mitigation Site (CPMS) in Mission Bay, California, USA, as a large-scale (multi-hectare) experiment to investigate controls on early succession of macrofaunal invertebrates. We evaluate (1) modes of initial recolonization, (2) soil and vegetation factors influencing faunal recruitment and succession, (3) recovery relative to an adjacent natural system, and (4) potential influence of the atypical environmental conditions associated with El Niño on recovery processes. By utilizing natural spatial heterogeneity associated with historical site conditions (mensurative approach) and manipulative experimentation (*Spartina foliosa* [cordgrass] planting and soil organic amendments), we test the null hypotheses that the rate and trajectory of faunal succession are independent of vascular plant cover, soil texture (sand content), and soil organic-matter content. The sampling period (1996–1999) included a strong El Niño year, allowing a test of the potential significance of climate variation (sea-level change) to marsh successional dynamics. In combination, the components of the study revealed that natural sources of spatial and temporal variation can overwhelm effects of soil and vegetation manipulations that are typically applied in wetland restoration efforts.

Mission Bay wetlands and experimental design

The research was conducted at the Crown Point Mitigation Site (CPMS), in the northeast corner of Mission Bay, San Diego, California, USA (32°46.8′ N, 117°14.1′ W; Fig. 1). This 2.8-ha wetland was formerly a fill site overlying an historical wetland. During the early 1990s the site was set aside as an (unsuccessful) Least Tern (*Sterna antillarum*) nesting area adjacent to a natural wetland composed of the University of California Kendall Frost Marsh Reserve (upper marsh) and the City of San Diego Northern Wildlife Preserve (NWP; lower marsh and tidal flat). The *Spartina* marsh in the NWP was used as the reference site for this study. The CPMS was excavated in fall 1995. Subtidal (from 120 cm below to 90 cm above mean lower low water) and intertidal (90–150 cm above mean lower low water) elevations were created and the site was opened to tidal flushing in December 1995. It was left unvegetated until March 1996, when a series of treatments involving *Spartina foliosa*, rototilling, and organic amendments were established. Six 25 × 12-m blocks (A, C, D, E, F, and G) were designated within the CPMS (Fig. 1), each containing eight 2 × 5-m plots with 1 × 5-m walkways between each plot. Each plot received one of eight sediment treatments, applied randomly within blocks, such that each treatment was replicated six times. Treatments were (1) unmanipulated, (2) rototilled only, (3) planted with *S. foliosa* only (referred to as planted), (4) planted and rototilled, (5) planted and rototilled with alfalfa, (6) planted and rototilled with sphagnum peat, (7) planted and rototilled with kelp (obtained from American Kelp Company, San Diego, California, USA), and (8) planted and rototilled with Milorganite (Milwaukee Metropolitan Sewerage District, Milwaukee, Wisconsin, USA), a processed sewage product. Each of the organic amendments was added in the amount of 2 kg/m^2. *Spartina foliosa* was planted at a density of 21 plants per 5 × 2-m plot. Plants were introduced as plugs obtained from three local sources (McCray 2001). Four additional 25 × 12-m blocks (H, I, J, and K) were designated within the adjacent natural marsh (Fig. 1). The experimental treatments were used to test the consequences of (a) *S. foliosa* planting, (b) organic amendments, and (c) disturbance associated with rototilling for the development of macrofaunal communities.

METHODS

Sampling took place within 1 wk, 1 mo, and 2 mo of marsh opening, and then annually from April 1996

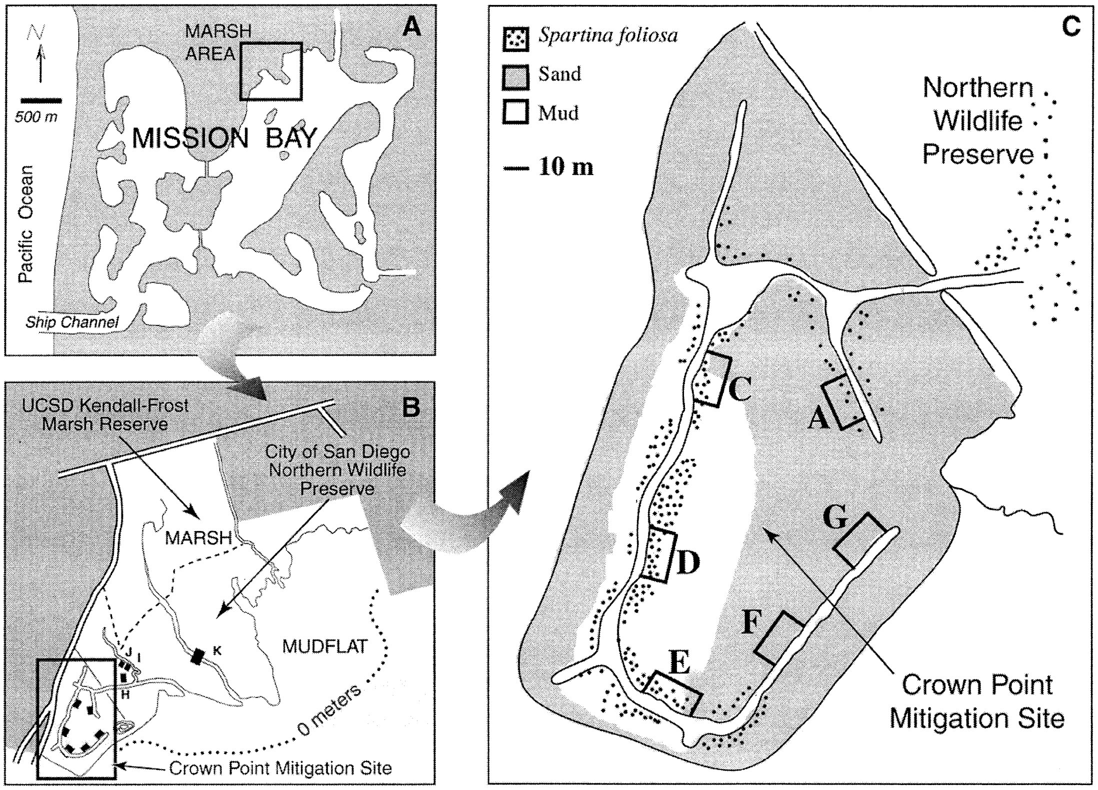

FIG. 1. Location of the Crown Point Mitigation Site (created in December 1995) and the adjacent natural marsh (City of San Diego Northern Wildlife Preserve and University of California–San Diego Kendall-Frost Marsh Reserve) in Mission Bay, California, USA. In panel C, areas without *Spartina foliosa* are vegetated by *Salicornia bigelovii*. Historic marsh sediments (mud) and remnant fill (sand) are shown. The 5 × 2-m treatment plots are located within each block (labeled black outlines) with the lower edge adjacent to the creek.

to April 1999. One 0.25-m^2 quadrat was designated randomly within each 2 × 5-m plot. Within each quadrat, measurements were made of total stem density, percentage cover, and mean stem height for each vascular plant species, and percentage cover of green algae and open space. Subsampling using smaller quadrats (0.0625 or 0.1 m^2) occurred when necessary and the data were extrapolated to 0.25 m^2. Soil salinity was measured once in each quadrat by squeezing porewater from surface sediment (0–3 cm depth) through a Whatman No. 1 qualitative grade filter (Whatman, Clifton, New Jersey, USA) with a syringe onto a hand-held salinity refractometer. Three cores were taken from each quadrat after making plant measurements, as follows. One core was taken for chlorophyll *a* (0.95 cm^2 × 2 mm depth), one for macrofauna and belowground biomass (18.02 cm^2 × 6 cm), and one for sediment grain size and organic-matter content (18.02 cm^2 × 2 cm). This yielded six macrofaunal cores per treatment (24 amended and 24 unamended) in the CPMS and four cores (natural treatment only) in the NWP on each sampling date. Macrofaunal cores were preserved (unsieved) in 8% buffered formalin with rose bengal. Sediment samples for analysis of chlorophyll *a*, grain size, and organic matter were frozen at −20°C until analysis.

Additional sampling of early invertebrate colonists took place between December 1995 and February 1996 (first two months of the study), prior to *S. foliosa* planting. Three cores were sampled from each block. Drift algae were collected by net and hand from the main channel and the mudflat surface of each block on 21 December 1995, 8 and 16 January 1996, and 6 February 1996. Algal rafts and attached fauna were preserved with 8% buffered formalin and examined to identify initial colonists.

Macrofaunal cores were washed through a 0.3-mm mesh. The animals retained were sorted from sediments using a dissecting microscope, identified to the lowest taxonomic level possible (using a compound microscope, if necessary), and stored in 70% ethanol. Live and dead belowground plant material was removed from the macrofaunal cores and dried at 65°C. Sediments for grain-size and organic-matter content analyses were homogenized and sieved though a 2-mm mesh to remove large shell and plant material. The percentage of organic matter content was determined by mass difference after combustion at 550°C for at least 10 h. The percentage of sand was determined as the dry mass of sediments retained on a 63-μm sieve (relative to total dry mass) after digestion of organics with hydrogen peroxide.

Chlorophyll *a* was extracted from the sediment cores using a solution of acetone (45%), methanol (45%), and distilled water (10%). Absorbances were measured at 665 and 750 nm wavelengths on a spectrophotometer, and measurements were converted to mg chlorophyll *a* per 10 cm^2.

Statistical analyses

Marsh (created and natural), block, and treatment (organic and vegetation) effects of macrofaunal and environmental properties were tested with analyses of variance (ANOVA) and Tukey's honestly significant difference (a posteriori) or Student's *t* tests (a priori). Differences in environmental and macrofaunal properties between each organically amended treatment and the unamended, planted, rototilled treatment (control) were determined with paired *t* tests to control for block variation. Simple regressions tested for correlations between vegetation and macrofaunal variables (e.g., percentage cover of *S. foliosa* vs. total macrofaunal density) and the linearity of relationships prior to multiple regression analysis using JMP 4 (SAS Institute, Cary, North Carolina, USA). Relationships between each macrofaunal variable and multiple environmental variables (organic matter, sand, salinity, belowground biomass, open space, and chlorophyll *a* concentrations) were explored using Statistica 4.1 (StatSoft, Tulsa, Oklahoma, USA). All numeric data were $\log_{10}(x + 1)$ transformed and proportion data were arcsine, square-root transformed prior to analyses to normalize data, homogenize variances, and emphasize multiplicative effects.

Comparisons between the created and natural marshes were made using the four unamended created-marsh treatments (treatments 1–4 above). No significant differences ($P < 0.05$) in macrofaunal or sediment properties existed among these four treatments for any sample date. Either means of these treatments were taken for each block (when marshes were compared with the six blocks as replicates) or each treatment was used separately (when blocks were compared using the four treatment plots within each block as replicates). Effects of the amended treatments (treatments 5–8 above) on macrofaunal and sediment properties were tested separately with comparisons to a single control treatment (planted, rototilled, unamended) and to the natural marsh.

We calculated the Shannon-Wiener index (H', $\log_{10}$), evenness J', and species (taxon) richness as a function of the number of individuals sampled (rarefaction) using untransformed, macrofaunal abundance data at the family level for each marsh, block, and treatment using Biodiversity Pro software (freeware).[3]

Differences in macrofaunal composition at the family level and environmental properties (organic matter, sand content, salinity, chlorophyll, belowground biomass) were tested among marshes, dates, blocks, and treatments using nonmetric multidimensional scaling (MDS) on Bray-Curtis similarity (macrofauna) and normalized Euclidean distance (environmental) indices (Primer software package, Plymouth Marine Laboratory, Plymouth, UK). Analyses were performed on double square-root transformed, unstandardized data (Clarke and Warwick 1994). Two-dimensional MDS plots are presented; a stress value is given which measures how well the two-dimensional plot represents the multidimensional distances among the data. Clarke (1993) suggests that a plot with a stress value of less than 0.2 provides a useful representation. The significance of differences between macrofaunal communities or sediment properties was calculated with Analysis of Similarity (ANOSIM). Global (whole test) sample statistics (R) and pairwise sample statistics (r) were used to determine differences between blocks or treatments (Clarke and Warwick 1994). An r value of zero signifies complete overlap of communities (replicates within groups are just as similar as among groups), while $r = 1$ signifies complete separation (replicates within groups are more similar than between groups; Clarke and Warwick 1994). The percentage of similarity between macrofaunal communities or sediment properties, as well as the taxa or sediment variables responsible for any variability, were determined with similarity percentage analysis (SIMPER, Primer-E software, Plymouth, UK).

RESULTS

Elevation and environmental properties

Elevation of sampling plots was similar in the Crown Point Mitigation Site (CPMS; mean ± 1 SE, 117 ± 2 cm) and NWP (122 ± 5 cm above MLLW; $t_{58} = 1.2$, $P = 0.24$). Interannual variation in sea level created temporal heterogeneity in inundation regime during the study. Compared to a 16-yr mean, the 1997–1998 El Niño was associated with seawater temperatures elevated by 1.1–2.6°C, a mean monthly sea-level rise of up to ~20 cm (data from University of Hawaii Sea Level Center, *available online*),[4] and 0.5–14.5 cm more precipitation in the coastal zone between November 1997 and May 1998.

Taken together, the environmental data for the CPMS differed from those in the natural marsh on all dates (ANOSIM, $P \leq 0.03$, Fig. 2A). Differences were due to lower values for organic matter, chlorophyll *a,* and belowground biomass, and higher percentages of sand and salinity in the created marsh relative to the natural marsh (SIMPER, Fig. 3A–E).

Temporal changes in the suite of environmental parameter values within the CPMS were observed between April 1996 and April 1997 (ANOSIM, $P =$

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[3] URL: ⟨http://www.sams.ac.uk/dml/projects/benthic/bdpro/⟩

[4] URL: ⟨ftp://ilikai.soest.hawaii.edu/islp/islpp.anomalies⟩

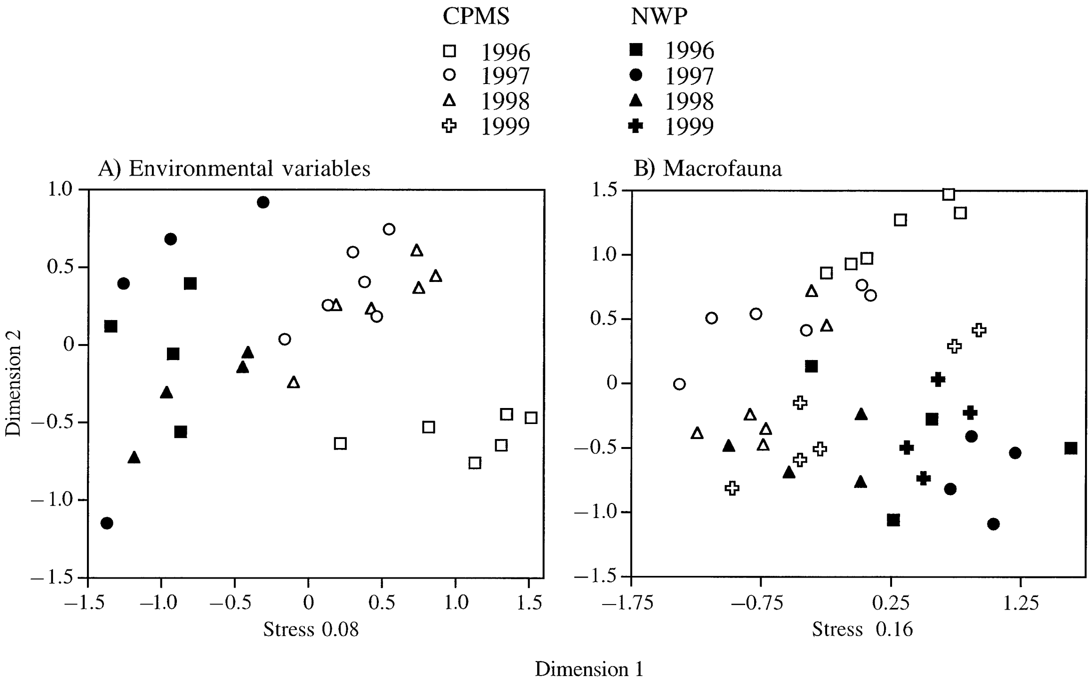

FIG. 2. Multidimensional scaling of (A) environmental variables and (B) macrofaunal communities during April of four years in the created (Crown Point Mitigation Site; CPMS) and natural (City of San Diego Northern Wildlife Preserve; NWP) marshes. Each point represents the mean of four cores (CPMS) or the value for one core (NWP). Environmental variables include percentage of organic matter content, percentage of sand content, belowground biomass, salinity, and chlorophyll *a* concentration. The stress value measures how well the two-dimensional plot represents the multidimensional distances among the data. Clarke (1993) suggests that a stress value <0.2 indicates a useful representation.

0.002) but environmental properties then remained similar from 1997 to 1998 (ANOSIM, $P = 0.576$; Fig. 2A, Table 1A). Over the two years beginning in April 1996 there were 10-fold increases in chlorophyll *a* concentration ($F_{2,69} = 129.2$, $P \leq 0.001$) and in belowground plant biomass ($F_{2,69} = 14.0$, $P \leq 0.001$). There were no significant changes in soil organic-matter content (top layer <2 mm; 3.2 ± 0.4%) or sand content (75 ± 3%) within the CPMS between 1996 and 1998.

The suite of environmental variables within the CPMS varied with the distribution of historical marsh sediments (block D, and parts of blocks C, and E) and remnant fill sediments (blocks A, F, and G, and parts of C, and E; ANOSIM, $P \leq 0.03$, Fig. 2A). Historical marsh sediments (block D) had significantly higher organic-matter content (e.g., 1996: $F_{3,31} = 40.96$, $P < 0.0001$) and lower sand content (1996: $F_{9,31} = 16.48$, $P < 0.0001$) than sediments in the other created marsh blocks during all years (Fig. 3B, C). Chlorophyll *a* concentrations were initially similar throughout the CPMS, but by 1997 and 1998, concentrations were lower in historic marsh (blocks C and D) than in remnant fill sediments ($F_{9,35} \geq 2.50$, $P \leq 0.05$; Fig. 3D). There were no consistent trends in porewater salinity across blocks, but there were three- to fivefold differences in salinity among blocks within each date (salinities ranged from 11‰ to 145‰ for all four years). Finally, belowground plant biomass did not differ within the CPMS on any date.

Vascular plant vegetation

Much of the created-marsh surface remained unvegetated and open throughout the study (Fig. 4). The percentage of unvegetated mud surface was higher in the created than natural marsh in all years ($t_8 \geq 7.53$, $P < 0.0001$). Created-marsh vascular-plant cover consisted mainly of *S. foliosa*, which grew vegetatively from plantings, and *Salicornia bigelovii* (annual pickleweed), which recruited naturally (Fig. 4). The natural-marsh plants were more diverse, with greater cover in each year of *Salicornia virginica* ($t_8 \geq 2.75$, $P \leq 0.025$), *Batis maritima* ($t_8 = 3.04$, $P = 0.016$ in 1999), and *S. foliosa* ($t_8 \geq 2.69$, $P \leq 0.027$). *Salicornia bigelovii* cover was greater in the natural than in the created marsh during 1997 ($t_8 = 4.23$, $P = 0.003$), but the pattern reversed during the 1998 El Niño ($t_8 = 3.25$, $P = 0.012$) and no differences were observed during 1999 (Fig. 4).

Invertebrate recovery

Initial colonization.—Rafted plant material, consisting largely of fragments of the sea grass *Zostera marina* and green algae, *Enteromorpha* spp. and *Ulva* spp., appeared in great abundance both on the marsh surface

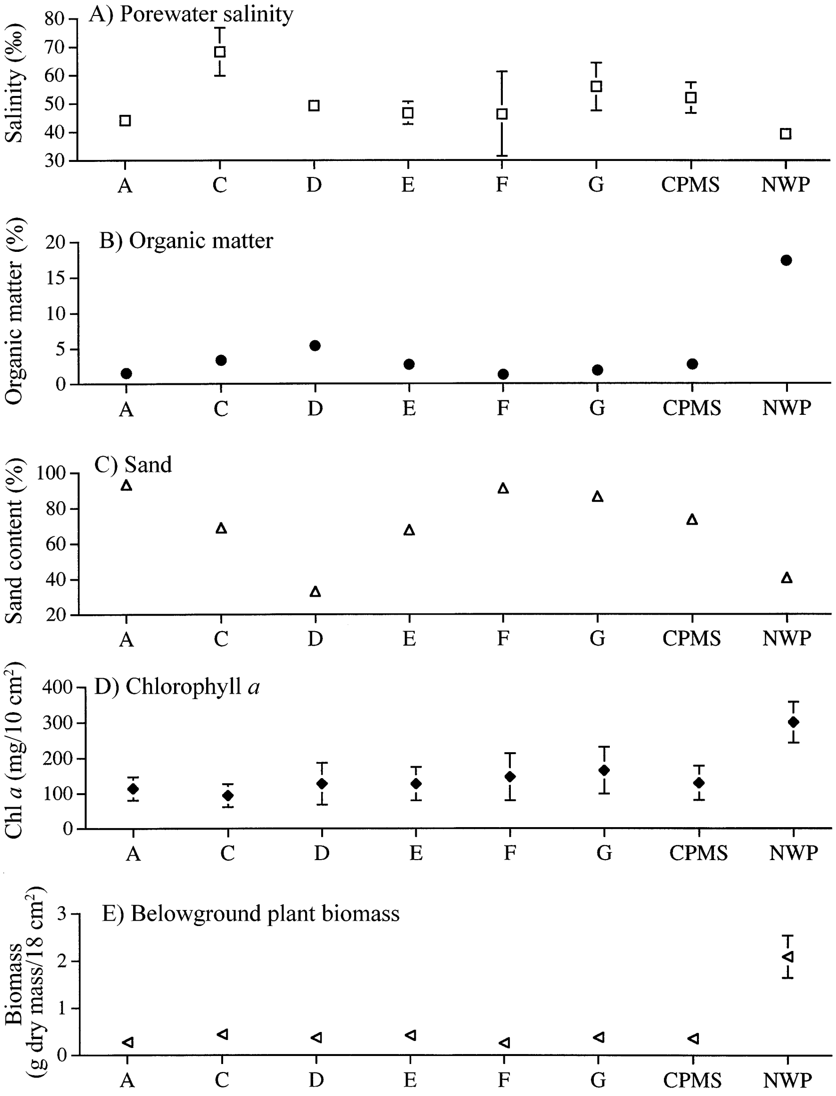

FIG. 3. Mean (±1 SE) (A) porewater salinity, (B) organic matter content, (C) sand content, (D) chlorophyll *a* concentration, and (E) belowground plant biomass in the sediments of the created (Crown Point Mitigation Site; CPMS) and natural (City of San Diego Northern Wildlife Preserve; NWP) marshes averaged over four years. Letters A, C, D, E, F, and G refer to CPMS blocks. CPMS data are for unamended treatments only. There were no organic matter, sand, or chlorophyll *a* data for 1999. Error bars are present on the organic matter, sand, and belowground biomass graphs, but are too small to see.

and in the creeks within the first week after ocean flushing was established. Also present were algae in the genera *Gracilaria*, *Ectocarpus*, *Sargassum*, *Macrocystis*, *Colpomenia*, *Gigartina*, *Porphyra*, and *Pelvetia*. During the first seven weeks after marsh opening, 160–328 macrofaunal (≥0.3 mm) individuals/g dry mass plant material were found on rafts in the created-marsh creek. The raft macrofauna was 63–83% amphipods (including *Hyale frequens*, *Pontogenia rostrata*, and *Jassa falcata*) and 4–14% tanaids (*Leptochelia dubia*), with lesser percentages (1–5%) of isopods (Cirolanidae and Anthuridea), gastropods (*Barleeia subtenuis* and *Cerithidea californica*), naidid oligochaetes (*Paranais litoralis*), polychaetes (*Eteone* sp. and *Exogone lourei*), and insects (dipteran larvae). Rafts collected from the natural marsh creek on 7 January 1996 contained a concentration of macrofauna (254 ± 93 individuals/g dry mass of plant material; mean ± 1 SE) similar to that collected in the CPMS creek (160 ± 79 individuals/g dry mass) on the same date (t_{16} = 0.45, P = 0.65), suggesting that rafting on macrofauna is also common in undisturbed settings. Proportional representation of major taxonomic groups on rafts was similar between the created and natural creeks on this date (for all t tests, $P \geq 0.27$). Rafts collected from the created marsh surface (7 January 1996) had lower concentrations (3.2 ± 0.6 individuals/g dry mass; t_{11} = 7.1, $P < 0.001$), but similar composition of macrofauna (t tests, $P \geq 0.19$) to those found in the created creeks on the same date. Notably, only gastropods (4 ± 2%

TABLE 1. Comparisons of (A) sediment and (B) macrofaunal community properties in the Crown Point Mitigation site, Mission Bay, California, USA.

A) Sediment

	Year		
Year	1996	1997	1998
1996	**93%**	0.002	0.002
1997	86%	**95%**	0.576
1998	87%	95%	**95%**

B) Macrofaunal communities

	Year			
Year	1996	1997	1998	1999
1996	**83%**	0.002	0.002	0.002
1997	64%	**73%**	0.041	0.002
1998	59%	68%	**72%**	0.106
1999	55%	63%	68%	**70%**

Notes: Data are for unamended treatments from six blocks. Bonferroni-adjusted alpha = 0.008. ANOSIM (analysis of similarity) probabilities are given above the diagonal; SIMPER within-group percentage similarities are given in bold type along the diagonal; SIMPER percentage similarities between groups are given below the diagonal.

of total raft fauna) and cnidarians (9 ± 5%) were present on algal rafts collected from the creek but not those collected from the marsh surface.

The same taxa present on algal rafts in the created marsh appeared in marsh-surface sediment cores collected during the first two months in the created marsh. These included the tanaid *Leptochelia dubia*, the oligochaete *P. litoralis*, three species of gammarid amphipods, and dipteran (chironomid and dolichopodid) larvae. All of the initial colonists were mobile taxa (amphipods, *P. litoralis*, and insects) that appeared as juveniles or adults rather than as newly settled planktonic larvae. Observations of meroplankton in pump samples taken at five locations in CPMS on 15 December 1995, 16 January 1996, and 16 March 1996 indicated that planktonic larvae of macrofaunal wetland species were rare in overlying waters (L. A. Levin and T. S. Talley, *unpublished data*). In the plankton and in larval settling tubes set out during the first six months of 1996, only spionids (*Pseudopolydora paucibranchiata* and *Polydora* spp.) and brachyuran zoea were represented (Roinestad 1999).

Community development

Density and diversity.—Macrofaunal density in the created marsh was low during April 1996 ($<12\,000$ individuals/m^2) and remained so within remnant fill sediments (blocks F and G) in 1997 (Fig. 5A). By 1997, most of the other blocks had attained densities (41 000–90 000 individuals/m^2) similar to those in the natural marsh (77 000–83 000 individuals/m^2) and did not continue to increase over time (Fig. 5A). Location (block) effects on density were evident in the created marsh in each year (ANOVA, $P \leq 0.05$; Table 2). Species richness, evaluated as the number of species per core, was lowest in 1996 (mean, 1.6 species/core), increased to 3–6 species/core in 1997, and remained relatively constant within the created marsh (Fig. 5B). Species richness per core in the created marsh was similar to that in the natural marsh (6–8 species/core) after 1996 (Fig. 5B). Similar results were observed when taxon richness was evaluated by rarefaction. Rarefaction diversity (Fig. 6) and H' within the CPMS were lower than in the NWP in 1996 ($t_4 \geq 2.7$, $P \leq 0.056$), but then became higher in 1997 ($t_8 \geq 2.34$, $P \leq 0.047$) and remained similar in 1998 and 1999. Rank-1 dominance (percentage of the most abundant species) was greater in the CPMS in 1996 ($t_8 = 2.28$, $P = 0.057$) and then similar to the NWP each year thereafter; evenness (J') never differed between the CPMS and NWP.

Composition within the Crown Point Mitigation Site (CPMS).—Macrofaunal composition varied across space and time (1996–1999; Figs. 2B and 7). Viewed as a whole, the CPMS assemblage was significantly different in 1996 than in 1997, 1998, and 1999 (Fig. 2B, Table 1B). Macrofaunal assemblages in 1997 were similar to those in 1998, and 1998 assemblages were similar to those in 1999 (Fig. 2B, Table 1B). The created-marsh macrofauna consisted largely of insects (71–72%) during 1996 and 1997 (Fig. 7, Table 3). Enchytraeid oligochaetes increased in proportion (0% in 1996 to 16% in 1999), and insects declined (72% in 1996 to 42% in 1999) over time (Fig. 7, Table 3). During 1998, increases in peracarid crustacean and polychaete representation were observed in part of the CPMS (blocks A, B, C, and D), with polychaete presence persisting into 1999 (Fig. 7). Molluscs were poorly represented in all blocks until 1999, when they occurred in abundance (21 ± 5%) in block F ($F_{5,18} = 5.03$, $P = 0.005$).

Macrofaunal assemblage structure varied with location within the CPMS (ANOSIM, global $P \leq 0.005$ for all years, Bonferroni-adjusted $\alpha = 0.013$; Fig. 2B). Faunal communities were generally similar to one another in blocks C, D, and E (ANOSIM, $r = 0.02–0.17$; 60–72% similarity), and blocks F and G (ANOSIM, $r = 0.03–0.28$; 74–76% similarity). Block A was different (ANOSIM, $r = 0.56–1.00$) from several of the other blocks on all dates (Fig. 2B). These differences were due to the patchiness of enchytraeid oligochaetes, high densities of capitellid polychaetes, naidid oligochaetes, and corophiid amphipods in block A, and higher densities of chironomid and ceratopogonid insect larvae, capitellid polychaetes, and spionid polychaetes (mostly *Polydora nuchalis*) in the historic marsh sediments (blocks C, D, and E) than in remnant fill sediments (blocks F and G; SIMPER).

Comparison with the natural marsh.—There were no differences in overall macrofaunal community structure of the natural marsh among the four years sampled (Fig. 2B, ANOSIM $P \geq 0.03$, Bonferroni adjusted $\alpha = 0.008$). The natural-marsh macrofauna was com-

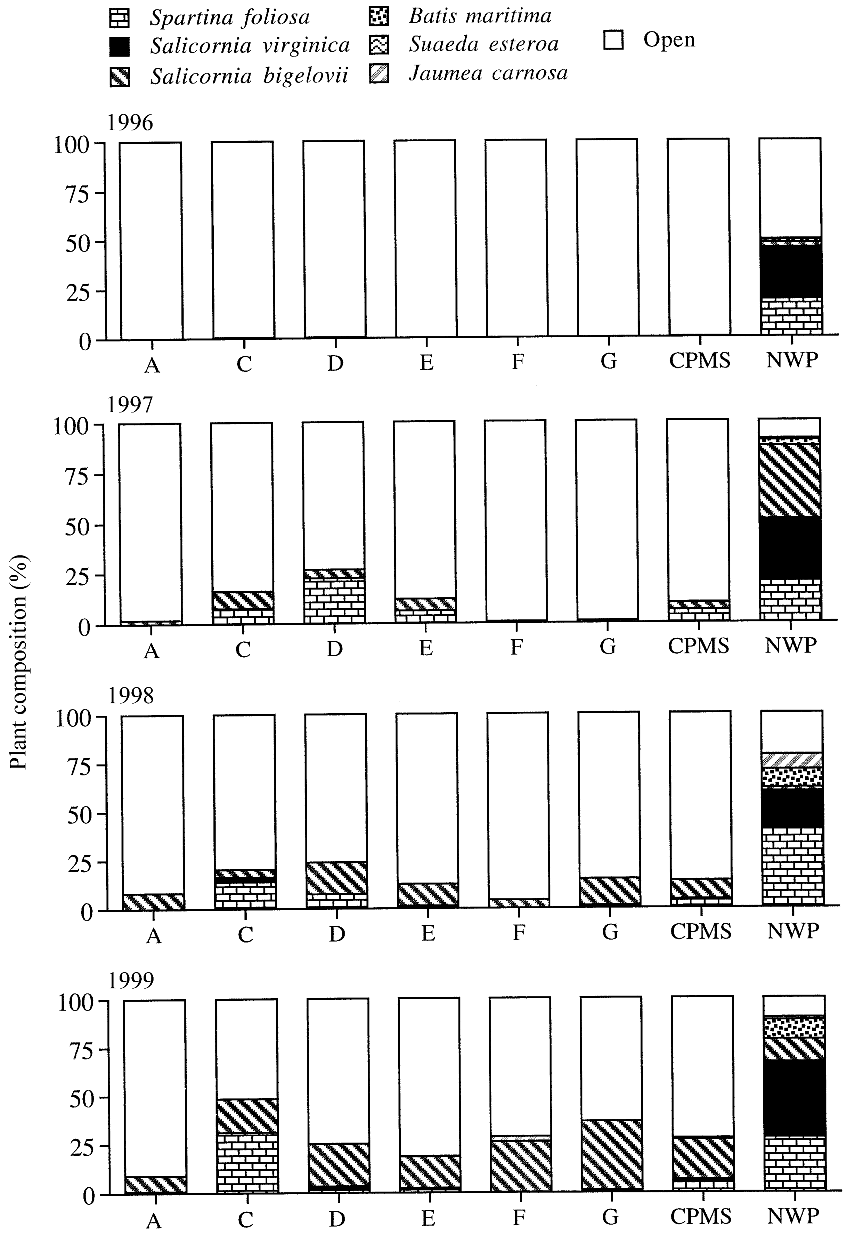

FIG. 4. Vascular plant composition during April of four years in each created marsh block (A, C–G) and pooled sample from the created (Crown Point Mitigation Site; CPMS) and natural (City of San Diego Northern Wildlife Preserve; NWP) marshes of Mission Bay. Means of three quadrats per block are plotted for April 1996, and four quadrats per block (one in each unamended treatment) are plotted for April of 1997–1999 in the created marsh. Sample size was six blocks for the CPMS and four blocks for the NWP.

prised largely of enchytraeid and tubificid oligochaetes (26–78%), as well as insects (16–32%). However, peracarid crustaceans and polychaetes were more common in 1998 (during El Niño) than in 1997 or 1999 (peracarids: 12% vs. 5–7%; polychaetes: 28% vs. 2–7%; Fig. 7). This was due largely to increased densities of the spionid polychaete *P. nuchalis* and the corophiid amphipods, *Corophium* spp. (SIMPER).

The CPMS macrofaunal assemblage did not resemble the natural-marsh assemblage, even after three years (ANOSIM, global $P < 0.0001$, $r = 0.35–0.96$; 39–44% similar in 1999; Fig. 2B, Table 3). Only during El Niño (in April 1998) did the fauna of some areas (blocks C, D, and E) in the created marsh resemble the natural-marsh fauna (Fig. 2B; ANOSIM, global $P < 0.0001$, $r = 0.10–0.33$; 54–68% similarity). Community-level differences between the created and natural marshes on all dates were due to lower densities of tubificid and enchytraeid oligochaetes and podurid insects, and higher densities of chironomid larvae and

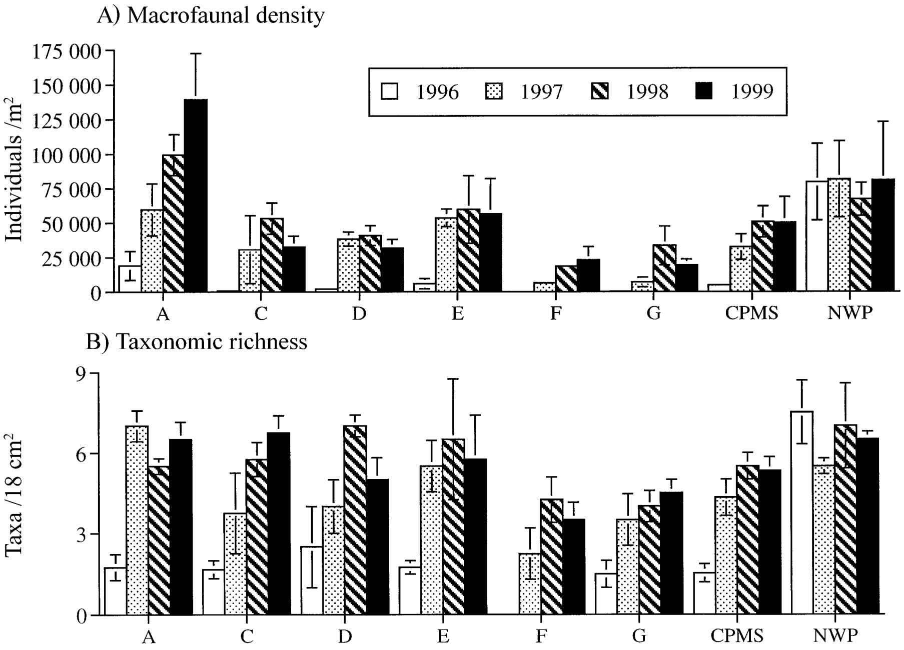

FIG. 5. Mean (±1 SE) (A) macrofaunal density and (B) number of taxa in each created marsh block (A, C–G) and for pooled samples from created (Crown Point Mitigation Site; CPMS) and natural (City of San Diego Northern Wildlife Preserve; NWP) marshes. Values for each block and for the marshes are shown. There were four (unamended) samples averaged per block (A–G) in the CPMS and one sample per block in the NWP. Sample size was six blocks for the CPMS and four blocks for the NWP.

spionid polychaetes in the created compared to the natural marsh sediments (SIMPER). Proportional representation of oligochaetes was lower ($t_8 > 2.80$, $P \leq 0.02$; Bonferroni-adjusted $\alpha = 0.02$), and representation of insects was greater ($t_8 > 2.97$, $P \leq 0.01$) in the created marsh than in the natural marsh during 1996 and 1997 (Fig. 7). No between-marsh differences in proportional composition were detected for any taxa during 1998 or 1999 (*t* tests, $P \geq 0.05$; Fig. 7).

Plant–macrofauna relationships

The potential influence of vascular plant presence on animal succession was examined by (a) comparing macrofauna in *Spartina*-planted and unplanted plots in each block, and (b) examining correlations with *S. foliosa* shoot density, *S. bigelovii* shoot density, and plant species richness. There were no differences in macrofaunal species richness, total density, or specific taxon abundances between the planted and unplanted (unamended) treatments for any of the dates tested (April 1997–April 1999; ANOVA, $P \geq 0.08$).

Relationships between shoot density and macrofaunal parameters were variable and weak, with lack of significance at the Bonferroni-adjusted alpha levels ($\alpha = 0.007$ in 1997, and $\alpha = 0.005$ in 1998 and 1999). Positive relationships were observed between insect density and plant species richness in 1997 ($r^2 = 0.31$, $P = 0.005$). There was a negative relationship between abundance of the naidid, *P. litoralis*, and density of *S. bigelovii* shoots in 1999 ($r^2 = 0.34$, $P = 0.003$). However, macrofaunal species richness was positively associated with *S. foliosa* shoot density during 1999 ($r^2 = 0.32$, $P = 0.004$) due to the appearance of capitellid and spionid (mostly *P. nuchalis*) polychaetes, *P. litoralis*, and *Corophium* spp. in the denser *S. foliosa* areas.

Benthic chlorophyll *a* concentration, a proxy for microalgal biomass, was a key environmental variable during the first spring. Macrofauna might be expected to respond to variation in microalgal concentrations as this represents an important food source for them (e.g., Page 1997). During 1996 there were positive correlations between chlorophyll *a* and total macrofaunal density ($P = 0.008$), species richness ($P = 0.048$), and densities of chironomid larvae ($P = 0.012$) but these were not significant at the Bonferroni-adjusted alpha of 0.006. The influence of microalgae on macrofaunal colonization should be explored with more intensive sampling (e.g., high replication) and experimentation.

Environmental–macrofauna relationships

The relationships between soil properties and metrics of macrofaunal community structure varied with taxon and over time. As with plant–macrofauna relationships, most correlations were not significant at the Bonferroni-adjusted alpha levels (1996, $\alpha = 0.006$; 1997, $\alpha = 0.004$; and 1998, $\alpha = 0.003$). Significant correlations included a negative correlation between salinity and naidid oligochaetes in 1996 ($r^2 = 0.35$, $P = 0.002$); a positive correlation between belowground plant biomass and density of dolichopodid larvae in 1997 ($r^2 =$

TABLE 2. Results of two-way ANOVAs testing block and treatment (organic amendment) effects on salt-marsh macrofauna of the Crown Point Mitigation Site, San Diego, California, USA.

	1996				1997			
	Block		Treatment		Block		Treatment	
Taxon	Density	Prop	Density	Prop	Density	Prop	Density	Prop
Oligochaeta					NS	**	NS	NS
Tubificidae					NS	NS	NS	NS
Naididae	*	NS	NS	NS	NS	**	NS	NS
Enchytraeidae					NS	***	NS	NS
Polychaeta					***	***	NS	NS
Polydora nuchalis					***	***	NS	NS
Streblospio benedicti					NS	NS	NS	NS
Capitellidae	NS	NS	NS	NS	***	***	NS	NS
Peracarid crustacea	NS	NS	NS	NS	NS	*	NS	NS
Insecta	*	***	NS	NS	***	**	*	NS
Chironomid larvae	*	***	NS	NS	***	**	*	NS
Ceratopogonid larvae	NS	NS	NS	NS	**	*	NS	NS
Muscidae larvae	NS	NS	NS	NS	NS	***	NS	NS
Dolichopodid larvae	*	NS	NS	NS	NS	NS	NS	NS
Total macrofauna	*		NS		***		*	

Notes: All data are for April of the given year. Macrofaunal data were examined as density (no. individuals in an 18 cm^2 × 6 cm depth core) and as proportional representation (''prop'') of the total macrofauna. $N = 8$ cores per block; $n = 6$ cores per treatment. Bonferroni-adjusted alpha = 0.001. A blank space indicates that no individuals were found.

* $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$; NS, $P > 0.05$.

0.43, $P < 0.001$); and a negative correlation of both soil organic-matter content and salinity with macrofaunal taxon richness (multiple regression, $R^2 = 0.47$, $P = 0.001$) in 1998.

Influence of organic amendments

Amendments had little persistent influence on measured sediment properties or macrofaunal community structure. In April 1996 (one month after amendments were established), organic-matter content of sediments in all four amended treatments (peat, alfalfa, kelp, and Milorganite) was significantly higher than in the unamended, planted, rototilled (control) treatment (paired t tests, $P \leq 0.010$, $t_5 \geq 2.77$; Bonferroni-adjusted $\alpha = 0.013$). However, by 1997, organic matter content of amended and unamended treatments was similar (paired t tests: $P = 0.02$, $t_5 = 3.40$ for peat; $P > 0.1$ for all other treatments). Belowground plant biomass ($\geq$0.3 mm) was higher in the alfalfa and peat amendments than in the planted and rototilled control treatment during 1996–1998 ($P \leq 0.01$, $t_5 = 3.59$, except alfalfa in 1998 when $P = 0.10$), and was higher in kelp and Milorganite treatments than in the control during 1997 ($P \leq 0.01$, $t_5 = 3.52$). The percentage of sand and chlorophyll-*a* concentration did not vary among amended and control plots, except for higher chlorophyll-*a* concentration in the Milorganite treatment during 1998 ($P = 0.002$, $t_5 = 5.95$).

Organic-matter amendments had minimal influence on the rate or trajectory of infaunal recovery in the created marsh; there were no effects in 1996. Total macrofaunal density was enhanced (paired t test, $P \leq 0.013$; Bonferroni-adjusted $\alpha = 0.013$) during 1997 in kelp- and Milorganite-amended sediments relative to the planted and rototilled control treatment, but no organic amendment effects were observed in other treatments or other years. Several taxa exhibited enhanced densities in organically amended sediments during selected years, but these were not consistent across treatments or time. Relative to the planted and rototilled control sediments, alfalfa-amended sediments had higher densities of tubificid oligochaetes in 1999 ($P = 0.018$, $t_5 = 3.49$), kelp-amended sediments had higher densities of insects in 1997 ($P = 0.001$, $t_5 = 6.89$), and peat-amended sediments had higher proportions of insects in 1999 ($P = 0.005$, $t_5 = 4.78$); (Bonferroni-adjusted $\alpha = 0.013$).

Overall, macrofaunal assemblage composition did not differ among the organically amended treatments within the CPMS on any date (ANOSIM, global $P \geq 0.59$). Amended plots differed from natural-marsh communities during 1996 and 1997 (ANOSIM, global $P \leq 0.006$; 11–27% similarity, SIMPER), but not in 1998 during El Niño conditions (ANOSIM, global $P = 0.77$; 39–52% similarity, SIMPER) or in the subsequent year (ANOSIM, global $P = 0.091$; 40–51% similarity, SIMPER).

Effects of organic additions on evenness and on taxon (family) richness (measured as number of taxa per core and via rarefaction) were examined in each year. Organic enrichment was predicted to lower diversity (Pearson and Rosenberg 1978, 1987), but there were no effects of amendments on taxon richness per core or on rank-1 dominance. During 1996, rarefaction richness tended to be higher in organically amended CPMS sediments (four species per core; all four treatments evaluated together) than in unamended sediments (two species per core; $P = 0.06$, $t_5 = 2.39$), but lower than

TABLE 2. Extended.

1998				1999			
Block		Treatment		Block		Treatment	
Density	Prop	Density	Prop	Density	Prop	Density	Prop
NS	NS	NS	NS	NS	NS	NS	*
*	***	NS	NS	NS	NS	NS	NS
***	***	NS	+	***	***	NS	NS
NS	NS	NS	NS	NS	NS	NS	*
***	***	NS	NS	***	***	NS	NS
***	***	NS	NS	NS	**	NS	NS
*	*	NS	NS	NS	NS	NS	NS
***	***	NS	NS	***	***	NS	NS
***	***	NS	NS	***	***	NS	NS
NS	*	NS	NS	NS	**	NS	*
NS	*	NS	NS	***	***	NS	**
***	***	NS	NS	NS	NS	NS	NS
NS	NS	NS	*	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS
***		NS		*		NS	

in natural-marsh sediments (six species per core; $P = 0.01$, $t_7 = 3.53$; Fig. 6). However, these differences did not persist: there were no differences in rarefaction richness between the amended and both the unamended and natural marsh during 1997–1999. Diversity (Shannon-Weiner H', $\log_{10}$) was similar in the amended and unamended plots, but lower than in the natural marsh during 1996 (Tukey's hsd, $P < 0.05$). In 1997, H' was higher in the unamended plots than in the natural marsh (Tukey's hsd, $P < 0.05$). No differences in H' were found in 1998 and 1999 among treatments, and evenness (J') did not differ among treatments at any time. These results suggest that one-time amendments may enhance macrofaunal diversity during initial colonization, but that effects are short lived.

DISCUSSION

Recolonization

In a successional context, the 2.8-ha Crown Point Mitigation Site can be viewed as a large-scale, Type II disturbance (sensu Connell and Keough 1985, Sousa

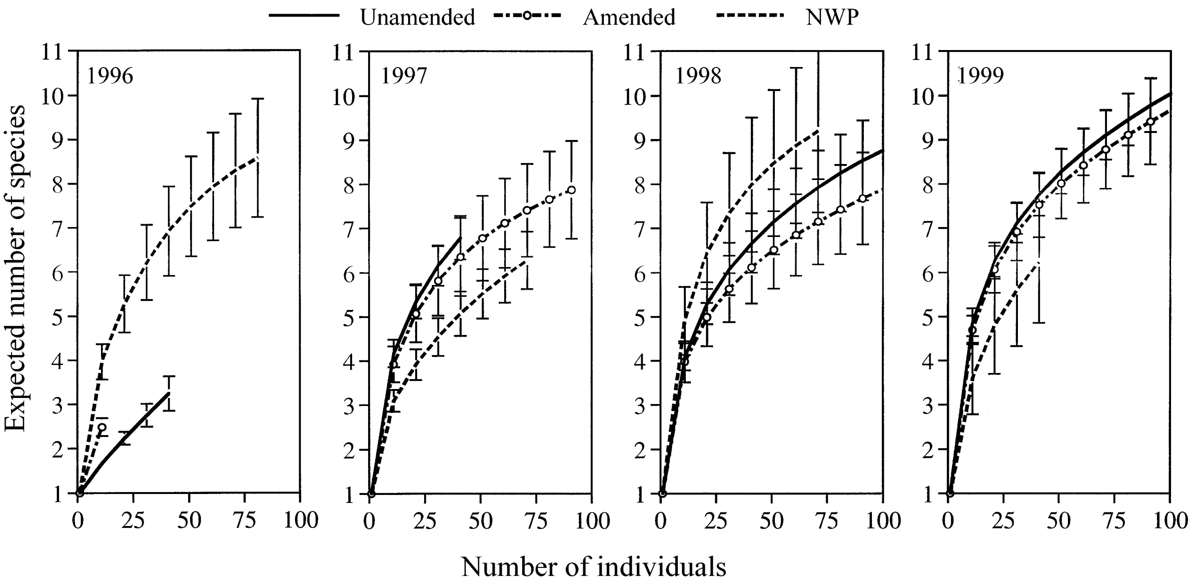

FIG. 6. Rarefaction curves showing expected number of macrofaunal species for a given sample size in the unamended and amended created (Crown Point Mitigation Site; CPMS) and natural (City of San Diego Northern Wildlife Preserve; NWP) marsh sediments during April. Curves are means (±1 SE) of six blocks in the created marsh and four blocks in the natural marsh. Only two blocks were used to calculate mean curves for the unamended curve in 1996, and three blocks for the NWP curve in 1999, due to low numbers of individuals in the other blocks.

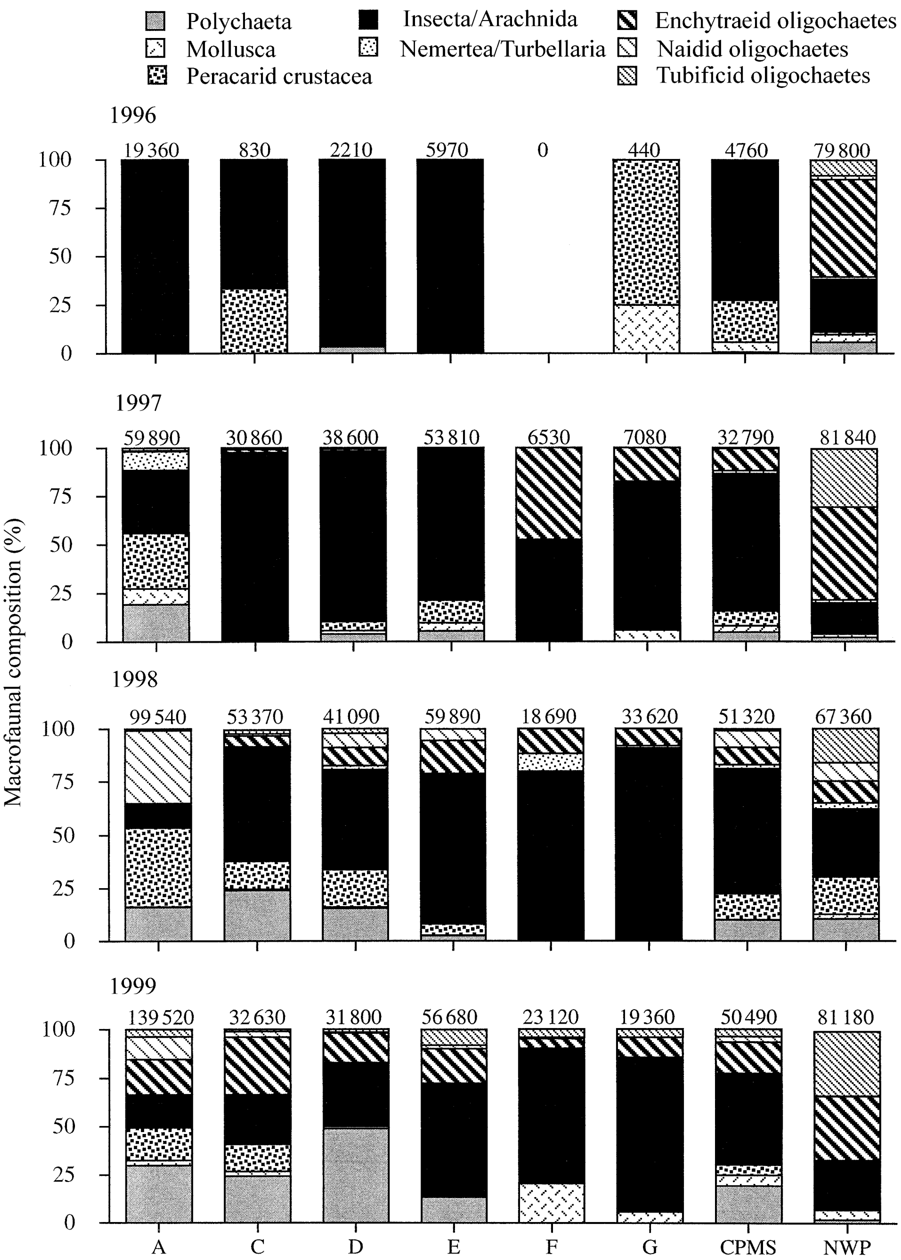

FIG. 7. Species composition of macrofaunal communities during April of four years within blocks (A, C–G) in the created (Crown Point Mitigation Site; CPMS) marsh and pooled for the created and natural (City of San Diego Northern Wildlife Preserve; NWP) marshes in Mission Bay. Data given are means of four cores per block (one from each unamended treatment) in the CPMS (Blocks A, C–G) and one core per block in the NWP. Sample size was six blocks for the CPMS and four blocks for the NWP. Mean macrofaunal density (individuals per m^2) is shown above each bar.

1985), partially because its area represents a large fraction (>20%) of the entire intertidal wetland habitat within Mission Bay, and also because it is semi-isolated from the adjacent system (Fig. 1). Colonizers of large, Type II patches are expected to immigrate through the water, largely as planktonic propagules. Migration of adults or vegetative growth is less likely when patch size is large relative to the ambit of the resident fauna (Keough 1984). However, few of the numerically dominant resident wetland species possess planktonic larval stages (Levin 1984, Talley and Levin 1999). Those that do are either more common in creeks or at lower elevations (e.g., mussels, some spionid polychaetes) or were mobile and not counted in this study (e.g., decapods). The initial salt-marsh colonizers at the Crown Point Mitigation Site (CPMS) apparently arrived as juveniles or adults via several mechanisms. Organisms rafted on drift algae or sea grass that entered from the adjacent marsh, migrated through the air as adults (insects) or migrated in the water or sediment bedload (naidid polychaetes, peracarid crustaceans). The macrofaunal species inhabiting adjacent tidal flats also exhibit limited occurrence of planktonic larval stages; many have juvenile and adult life stages adapted to colonize disturbed patches (Levin 1984, Crooks and Khim 1999).

In this study, initial colonization was by taxa present in the adjacent natural marsh rather than by exotics or opportunists not normally associated with the system (e.g., *Capitella* sp.). These results contrast with patterns of macrofaunal recovery in *Spartina alterniflora* marshes. In North Carolina and elsewhere on the Atlantic coast, early marsh colonists arrive by settlement of planktonic larvae (e.g., *Streblospio benedicti*) or are opportunists usually rare in natural sediments (e.g., *Capitella*; Sacco et al. 1994, Levin et al. 1996, Posey et al. 1997). The same is true of tidal-flat colonists (e.g., Smith and Brumsickle 1989). The diminutive size and wide separation of coastal wetlands in California appear to have selected against widespread larval dispersal capabilities of resident infauna (Levin 1984, Levin et al. 1991). The rapid colonization of the CPMS by many resident taxa stems largely from the proximity of the natural marsh and connectivity via a tidal channel (Fig. 1).

Rate and trajectory of macrofaunal recovery

The macrofauna of the CPMS exhibited rapid recovery with respect to density and species richness, the measures of community structure often used in monitoring. Within 1.5 yr, total macrofaunal density and species richness were comparable to values in the adjacent natural marsh (Fig. 5). However, diversity does not indicate functional equivalence; for example, faunal composition differed in the created and natural marshes even after 40 mo (Figs. 2B and 7). Although a broad range of taxa colonized the CPMS within a few months of establishment, insect larvae (mainly chironomids, ceratopogonids, and dolichopodids) dominated the entire marsh surface during the first few years, and through April 1999 at several locations (blocks E, F, and G; Fig. 7). Chironomid larvae were abundant in the benthic microalgal mats that developed on the sparsely vegetated, newly created marsh. Very low δ^{15}N signatures of insect larvae (L. Levin, C. Currin, T. Talley, and R. Michener, *unpublished data*) suggest they may be feeding extensively on nitrogen-fixing cyanobacteria. As vegetation cover and belowground biomass increased (Figs. 3 and 4), deposit-feeding polychaetes and enchytraeid oligochaetes replaced some of the insects (Fig. 7). This sequence was most evident in the finer grained, historic-marsh sediments (blocks C and D) and less so where sand content was higher (blocks F and G; Fig. 7).

Other restored marshes in southern California have experienced a similar faunal trajectory. A wetland established in the Tijuana Estuary in 2000 was colonized mainly by insects and *P. litoralis* during year 1 (L. Levin, S. Moseman, and C. Forder, *unpublished data*). A shift from algae-grazing insects to deposit-feeding oligochaetes was noted in a multisystem comparison of restored *Salicornia* spp. marshes by Talley and Levin (1999). In the Talley and Levin (1999) investigation, the 1- and 5-yr-old marshes were dominated by insects (the CPMS was the youngest), and the 6- and 10-yr-old marshes were dominated by naidid, enchytraeid, and tubificid oligochaetes. The 5-, 6-, and 10-yr-old *Salicornia* marshes exhibited higher macrofaunal densities than their adjacent natural counterparts, due largely to prevalence of *P. litoralis*, a naidid oligochaete (Talley and Levin 1999). Such macrofaunal density overshoots were not observed in the CPMS *S. foliosa* habitat, although the marsh was only 3.4 yr old during the final sampling (April 1999).

The dominant taxon in natural marsh sediments, Oligochaeta, was among the slowest to recover in CPMS sediments (Fig. 7). Oligochaetes lack a larval stage and produce juveniles that develop in cocoons (Giere and Pfannkuche 1982); therefore, oligochaete dispersal ability is limited. However, *P. litoralis* can reproduce asexually and may be transported in water or sediment bedload (R. Diaz, Virginia Institute of Marine Sciences, *personal communication*), or on macroalgal rafts (this study). By the final sampling date, enchytraeid oligochaetes comprised 12–32% of macrofauna throughout the CPMS, but tubificid oligochaetes were significantly underrepresented relative to the natural marsh (Fig. 7). Tubificid oligochaetes, which dominate natural *S. alterniflora* marsh sediments, were also notably slow to recolonize restored salt marshes on the Atlantic coast (La Salle et al. 1991, Levin et al. 1996).

Spatial heterogeneity: vegetation and abiotic influences on succession

Although the CPMS design included vegetation treatments that were either planted or unplanted with *S. foliosa*, and additions of four types of organic matter, most effects of these treatments were overshadowed by the spatial heterogeneity of the existing soils. Prior to 1945, the site contained salt-marsh and tidal-flat habitat (Crooks 1998). During modification of Mission Bay in 1945 to form a recreational park, bay dredge spoils were deposited on the site (Morrison 1957). Excavation during creation of the CPMS exposed a gradient in sand and organic-matter content with muddier, remnant wetland sediments exposed near blocks C, D, and parts of E. This heterogeneity appears to have driven much of the dynamics of plant (McCray 2001) and animal recovery (this study).

Studies of interactions between salt marsh plants (above- and belowground structures) and macrofauna have revealed positive, negative, or neutral associations for which a variety of mechanisms have been postulated (reviewed in Levin and Talley 2000). Planting of

TABLE 3. Densities of macrofauna from the created (Crown Point Mitigation Site, CPMS) and the natural (Northern Wildlife Preserve and Kendall Frost Marsh Reserve, NWP) marshes in Mission Bay, San Diego, California, USA.

	1996				1997			
	CPMS		NWP		CPMS		NWP	
Taxon	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Oligochaeta								
Enchytraeidae	0		43 270	18 160	900	380	30 830	4040
Naididae	60	60	970	790	390	220	0	
Tubificidae	0		4150	3290	0		34 980	25 780
Polychaeta								
Capitellidae	60	60	1800	1450	1220	970	970	350
Ctenodrilidae	0		0		0		280	280
Sabellidae	0		970	970	0		0	
Spionidae	0		0		1430	920	0	
Syllidae	0		0		0		0	
Gastropoda								
Acteocina inculta	0		0		530	260	0	
Alderia modesta	0		1110	600	0		0	
Assiminea californica	0		1520	690	50	30	830	480
Cerithidea californica	0		0		280	150	0	
Bivalvia								
Musculista senhousia	0		0		50	50	0	
Tellinidae	0		0		0		0	
Pericarid crustacea								
Corophiid	60	60	140	140	280	280	0	
Other Gammaridea	0		550	320	3730	2530	140	140
Ligiidae	0		0		0		140	140
Oniscoidea	0		0		0		0	
Tanaidae	0		0		0		0	
Insecta								
Diptera								
Chironomidae	4310	2890	4420	3700	16 640	5270	1110	1110
Cicindelidae	0		0		0		0	
Other Diptera	0		420	420	0		0	
Dolichopodidae	60	60	970	970	1110	200	0	
Ceratopogonidae	180	110	1660	810	4560	1790	140	140
Muscidae	0		550	230	600	270	140	140
Psychodidae	0		0		0		0	
Stratiomyidae	0		0		0		0	
Hemiptera	0		13 130	13 130	0		0	
Homoptera								
Coccoidea	0		0		0		0	
Hymenoptera	0		0		0		0	
Coleoptera								
Staphylinidae	0		0		230	90	0	
Collembola	0		140	140	0		10 090	9560
Arachnida								
Halacarida	0		2900	1960	0		420	420
Anemone	0		0		0		280	160
Nemertea	0		970	650	0		1240	610
Turbellaria	0		0		710	660	0	

Notes: $n = 6$ blocks in the CPMS (unamended treatments only); $n = 4$ blocks in the NWP. Values are means ± 1 SE of individuals/m^2. Where there were zero individuals/m^2, no standard error is possible, and therefore the standard error cell is left blank.

S. foliosa had no effect on macrofaunal density, richness per core, or composition relative to unplanted plots in the present study. Variable survival of the *S. foliosa* plantings may explain the lack of vegetation treatment effects on the early succession of macrofauna in the CPMS. It is notable that a four-year study of macrofaunal recovery in a *S. alterniflora* marsh also yielded similarity between *Spartina*-vegetated and unvegetated treatments (Levin et al. 1996).

However, fine-scale interactions between plants and macrofauna have been documented, largely through correlation studies. Levin and Talley (2000) reported strong positive correlations between *S. bigelovii* cover and densities of many macrofaunal taxa in three other southern California salt marshes. In the CPMS during 1999, macrofaunal taxon richness was positively associated with density of *S. foliosa*. This trend was driven by the appearance of polychaetes, *P. litoralis*, and

Table 3. Extended.

1998				1999			
CPMS		NWP		CPMS		NWP	
Mean	SE	Mean	SE	Mean	SE	Mean	SE
3000	880	6770	2610	11 890	5240	11 200	3330
7860	5910	5810	4070	2770	2100	140	140
580	240	9820	4530	1910	950	50 460	44 300
4590	2290	3870	1360	8660	4560	1380	860
0		0		0		0	
0		0		0		280	280
1520	610	2630	2450	3430	1400	0	
0		0					
50	50	0		480	430	0	
0		0		50	50	0	
0		970	790	1180	740	2490	1570
0		0		0		0	
90	70	140	140	20	20	0	
0		0		0		0	
9330	5310	9400	6920	4260	3290	280	160
0		1110	930	0		0	
0		0		0		0	
0		0		0		0	
0		0		0		0	
20 620	3910	22 120	16 430	8570	3390	2350	860
50	50	0		0		0	
0		140	140	0		0	
690	120	970	470	440	190	0	
1500	800	1240	470	230	120	830	160
0		0		140	60	0	
90	70	830	480	0		0	
0		0		0		0	
50	30	0		70	70	230	160
0		0		460	380	0	
0		0		0		0	
230	110	0		530	190	0	
0		0		0		9820	9270
250	130	0		5020	2300	1380	1020
50	30	0		0		280	280
180	100	1520	1180	50	50	0	
180	160	0		250	200	0	

corophiid amphipods (mostly surface-deposit feeders) in *S. foliosa*-vegetated areas. However, greatest *S. foliosa* survival was also associated with the finer-grained, organic remnant-marsh sediments (McCray 2001), possibly indicating a complex interaction among the plants, sediments, and macrofauna. No correlations between *S. foliosa* density and belowground habitat structure (i.e., belowground biomass) were found, but the presence of *S. foliosa* could have contributed to habitat heterogeneity on smaller (cm) scales than were measured in this study. Local habitat diversity involving even small amounts of shading, nutrient alterations, fine surface roots, and live and dead shoot material could be enough to locally enhance macrofaunal diversity.

Organic amendments had little effect on the trajectory of macrofaunal succession with the exception of two treatments. Kelp and Milorganite promoted early (16 mo) community development by enhancing macrofaunal density relative to control plots. Comparable studies of macrofaunal response to organic amendments (straw, alfalfa, and peat) were conducted in a

North Carolina *S. alterniflora* marsh (Levin et al. 1997, Broome et al. 2000, Craft 2000). Although those amendments generated low-redox conditions and inhibited macrofaunal colonization during the first few months, effects on macrofauna were minimal after six months, except in straw-amended plots (Levin et al. 1997). Eutrophication of marine sediments is expected to enhance macrofaunal densities, reduce diversity, and select for opportunistic taxa (Pearson and Rosenberg 1978, 1987). Redox was 27–77% lower in several of the organically amended CPMS treatments (Milorganite, alfalfa, kelp) than in the planted controls within six months after application (McCray 2001). However, as in North Carolina, macrofaunal responses were muted, possibly due to limited lability of the organic material or because the natural infaunal marsh assemblage is adapted to enriched conditions.

Temporal pattern

Seasonal variations in environmental conditions and propagule availability have long been recognized as key influences on intertidal succession (e.g., Ford et al. 1999), but only rarely are the consequences of higher-frequency or episodic events examined. Changes in sea level, and possibly higher temperature and increased precipitation, are likely causes for the wetter and greener appearance of the CPMS (due to growth of algae and *S. bigelovii*) in 1998 than in the previous years. During spring 1998, macrofauna in the CPMS and natural-marsh assemblages were most similar to one another with respect to composition (Fig. 2B) and species richness (Fig. 6). This was due largely to increased densities of amphipods and polychaetes (Table 3). This shift towards the natural assemblage may indicate the susceptibility of populations to change during El Niño rather than ''recovery'' because the natural assemblage simultaneously experienced change (Figs. 2B and 7). However, the compositional changes in natural-marsh macrofauna observed in 1998 did not persist. Oligochaetes regained dominance in 1999 (Fig. 7). Furthermore, the increased representation of spionid polychaetes and corophiid amphipods persisted at many locations within the CPMS through 1999 (Table 3). The reasons for the different responses of the natural and created marshes are unclear, but could involve competitive interactions among macrofauna, habitat suitability for the taxa involved, or differential predation.

One functional effect of the El Niño was to increase marsh surface access to fish and invertebrate predators on macrofauna by raising mean sea level. These predators also exhibited a composition change during the El Niño period (Talley 2000). Reduced densities of killifish (*Fundulus parvipinnis*), increased densities of mudsuckers (*Gillichthys mirabilis*), and an influx of several warmer-water species not normally present at this site (e.g., portunid crabs, mullet, and gobies; Talley 2000) may have influenced the macrofaunal composition on the marsh surface.

Wetland restoration programs are fertile ground for mensurative studies and manipulative experimentation aimed at elucidating controls on community structure and function. A particular advantage is the large area typically subject to restoration. In this study, we performed relatively large-scale manipulations (in 2 × 5 m plots), replicated in six 25 m wide blocks spread over 2.8 ha. It was the large spatial scale of the study and the multiyear study period that provided the key result—that natural spatial and temporal heterogeneity in the system are likely to exert stronger influence on early faunal succession in southern California wetlands than manipulations of vegetation or soil organic matter. Studies conducted in one area of the marsh or over a one-year period would have generated different findings. We conclude that careful characterization of site location, soil parameters and inundation regime prior to site selection, and incorporation of natural heterogeneity into wetland design, may go further in promoting rapid ecosystem recovery than expensive amendments or planting efforts.

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