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Publication Date

2005-01-12



SeaGrant Final Report

Recovery of Trophic Function in Restored Pacific Wetlands R/CZ 173

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INTRODUCTION

Given the increasingly widespread wetland restoration activities in California (Zedler 1996), it is imperative that reasonable measures of success be adopted. In the past, monitoring of restored wetlands has focused on superficial indicators of structure, such as density or species number. Functional measurements have been more elusive (Zedler 2000). In this study we compared the trophic structure and function of a 6-7 year old created salt marsh and adjacent natural marsh in Mission Bay, San Diego, California in an effort to develop means to assess recovery of trophic function. The major objectives of the study were to (1) evaluate of benthic community structure (density, composition and diversity), (2) track seasonal and interannual changes in trophic structure based on natural abundance stable isotopic analyses, (3) conduct isotopic enrichment experiments to identify consumers of specific food sources (microalgae, cyanobacteria, *Spartina* and other bacteria), (4) perform of plant cover manipulations to evaluate the mechanisms by which *Spartina* influences benthic processes, and (5) improve conceptual understanding of trophic successional processes associated with restoration. In combination these research results allow us to assess the extent to which the Crown Point Mitigation Site (CPMS) in Mission Bay California has come to resemble the natural wetland (Northern Wildlife Preserve [NWP] and Kendall Frost Marsh) and the mechanisms underlying this recovery.

METHODS

Biannual sampling was conducted in spring (April) and fall (September) between April 2001 and April 2003. Four transects (5 quadrats per transect) were established in the restored and natural marsh at lower marsh elevations (*Spartina* habitat) and at upper marsh elevations (*Salicornia*, *Batis*, *Jaumea* habitat). During this period we documented plant cover, soil properties (grain size and organic matter) and benthic invertebrate community structure. Methods for benthic sampling and soil and invertebrate sample processing are described in Levin and Talley (2002). Samples were collected for analysis of stable isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of dominant plants, fish, snails and infauna to assess recovery of food web structure. Methods for isotope collections and analyses are given in Levin and Michener (2002) and Currin et al. (submitted).

Stable isotope enrichment experiments were conducted in situ in the CPMS and NWP during November 2001 and May 2002 to identify major consumers of different wetland primary producers. On the first date we labeled benthic microalgae by spraying

^{13}C bicarbonate (Middelburg et al. 2000) and tracked consumption of ^{13}C -labeled algae by infaunal consumers over time (1, 3, 6 and 57 da). On the second date we labeled cyanobacteria in enclosed cores with $^{15}\text{N}_2$ gas, microalgae with ^{13}C bicarbonate, *Spartina* with $^{15}\text{NH}_4$ (injected 6 wk prior to harvest), and bacteria with ^{13}C acetate (2 cm below the sediment surface). Experiments were conducted with paired labels (microalgae + cyanobacteria, *Spartina* + bacteria) and infauna were sampled and analyzed for evidence of consumption of different food source over a time series (0, 3, 6, 11 and 72 da).

Spartina foliosa and *Salicornia virginica* are frequent restoration targets, in part because they provide habitat required by the endangered clapper rail or Belding's Savannah sparrow for nesting. Measurements of plant cover, stem density, light reduction, salinity, temperature and chlorophyll a were made in 10 quadrats each of *Spartina*, *Salicornia* and unvegetated habitat in the Kendall Frost reserve in Dec. 2003. A plant cover and light manipulation experiments was conducted in 2002 to examine the influence of *Spartina* cover on sediment properties and infaunal communities. Three treatments were replicated in 8 blocks in *Spartina* stands of the Kendall Frost Marsh (natural habitat): (a) clipped, unshaded plots; (b) clipped plots with shade cloth designed to mimic *Spartina* shading effects and (c) unclipped control plots. Chicken wire supports, required to hold shade cloth in treatment (b), were mounted in all 3 treatments to control for experimental artifacts. Treatments were maintained by weekly clipping for a 4-month period and plant cover, soil temperature, salinity, redox, water content and pigment concentrations and macrofaunal community structure were examined between May and November 2002.

RESULTS

Plants and Soil

Spartina foliosa and *Salicornia virginica* plant cover did not differ between restored and natural marshes, however, *Salicornia bigelovii* cover was higher in the CPMS than in the NWP at upper elevations in April 2002 and in *Spartina* transects in Sept. 2002 ($P < 0.05$). Also, the incidence of open (unvegetated) space was higher at upper elevations in the CPMS than NWP in April 2001 and Sept. 2002. Vascular plant species richness was comparable in the CPMS and NWP at all elevations and years except in the high marsh during Sept. 2002, where it was lower in the CPMS (2.50 spp. per 0.25 m² quadrat) than in the NWP (4.85 spp. per quadrat). Porewater salinity was typically higher in the CPMS than NWP; this was significant in *Spartina* transects in Sept. 2001, in upper-marsh transects in Sept. 2002, and in both transects in April 2003. Chlorophyll a concentrations did not differ between marshes or elevations.

The organic matter (<2mm) and percent sand content ($\geq 63\mu\text{m}$) were analyzed for April 2001. The natural had a greater % organic matter content than the created marsh (8.94 vs 3.63, $P = 0.0342$) but there was no statistical difference for percent sand content (52.00 vs 61.91, $P = 0.5029$). When comparing the same parameters by vegetations zones between the two marshes, the natural-created marsh differences in organic matter content were found only in the upper mixed vegetation zone (NWP (6.25%) > CPMS (2.73%), $P = 0.0545$).

Benthic Invertebrate Communities

California horn snail (*Cerithidea californica*) densities were equivalent in the restored and natural marshes in all years except 2003, when upper marsh densities in the CPMS exceeded those in the NWP. During 2001 and 2002, average macro-infaunal densities (animals > 0.3 mm) were lower in the restored marsh at *Spartina* elevations ($27,445 \pm 13,886$ ind. m⁻² in 2001 and $24,055 \pm 3,672$ in 2002) than in the upper marsh ($51,504 \pm 16,348$ in 2001 and $104,445 \pm 39,805$ in 2002). These densities were also lower than those in the natural *Spartina* marsh ($128,481 \pm 31,825$ in 2001 and $133,667 \pm 13,981$ in 2002) or the natural upper marsh ($92,875 \pm 11,450$ in 2001 and $83,241 \pm 26,686$ in 2002) ($P < 0.0001$).

Macrofaunal diversity was slightly lower in the restored than natural marsh in both years, but not significantly so (2001 H' natural [log base 10] = 0.88, 2001 H' restored = 0.67; 2002 H' natural = 0.78, 2002 H' restored = 0.64). The same was true for community evenness (2001 J' natural = 0.69, 2001 J' restored = 0.70; 2002 J' natural = 0.64, 2002 J' restored = 0.64). Rarefaction curves reflect significant interannual variability in patterns of diversity (Fig. 1).

Benthic communities were compared across elevation zones (*Spartina* vs Upper marsh), marsh types (natural vs restored) and years (99 [previous study], 2001 and 2002) using multivariate statistical approaches. At upper marsh elevations there were restored vs natural marsh differences in invertebrate composition during April 2001 (ANOSIM, $P = 0.001$) (Fig. 2a) but not in 2002 ($P = 0.093$) (Fig. 2b). Differences in invertebrate composition were observed between natural and restored *Spartina* marshes in both 2001 and 2002 (both $P = 0.001$) (Fig. 2), driven largely by higher abundances of amphipods, polychaetes, oligochaetes and insect larvae in the natural marsh. Within a marsh type, there were no between-year differences in a comparison of 2001 and 2002, as well as with data collected previously from 1999 ($P > 0.20$). However, given that the restored and natural marsh infaunal communities were not different in 1999 ($P = 0.13$; Levin and Talley 2002), the 2001 and 2002 results reflect possible degradation of conditions in the restored marsh.

Trophic recovery: natural abundance stable isotope analyses

Isotopic analyses carried out in 1996-98 (1-2 years after marsh establishment) revealed major differences in $\delta^{13}\text{C}$ and to a lesser extent, $\delta^{15}\text{N}$ signatures of producers and consumers between the restored and natural marsh (Fig. 3; Currin et al. submitted). Although some of these differences persisted through the start of this study in April 2001, most of them had disappeared by Sept. 2002 and April 2003 (Fig. 3a, b, c), providing a semblance of trophic recovery. By the final year only Enchytraeidae (oligochaetes) and *Cincindela* (insect) continued to exhibit lighter $\delta^{13}\text{C}$ in the created than natural marsh, and this was significant only during Sept. Only *Cincindela* exhibited heavier $\delta^{15}\text{N}$ in the created than natural marsh, and again only in Sept.

Trophic complexity (diversity and redundancy) among the infaunal assemblages of the NWP and CPMS can be compared via dual natural abundance isotope plots. We plotted 2001-2003 average isotope signatures for each macrofaunal species inhabiting the

Spartina zone and defined 10 trophic guilds representing distinct food sources (Fig. 4). We observed that trophic diversity (calculated as H' using the number of species in each guild) was greatest in the 7-yr old created marsh, least in the newly created marsh (2y) and intermediate in the natural marsh. The 7y-old created marsh supported a similar number of guilds (10) as in the natural marsh (8), but functional redundancy was less – i.e. there were fewer taxa in each guild (Fig. 4). Functional redundancy (dominance) was greatest in the natural marsh, where half of all species fell into a single consumer guild.

Diet Preferences: Isotope Enrichment Experiments

Initial isotope enrichment experiments (Nov. 2002) labeled microalgae with ^{13}C to identify microalgal consumers. A time series of infaunal $\delta^{13}\text{C}$ signatures from labeled plots revealed insect larvae (chironomids and ceratopogonids) to be the most voracious microalgal consumers. Spionid polychaetes and amphipods were moderate consumers of labeled algae, and oligochaetes largely avoided microalgal consumption (Fig. 5).

In a second isotope enrichment experiment we successfully labeled 4 primary producer sources in 2 dual labeling studies: microalgae [^{13}C] + cyanobacteria [^{15}N] and subsurface sediment bacteria [^{13}C] + *Spartina* detritus [^{15}N] (Table 1). Among the common taxa in the system, only the insect larvae consumed large amounts of ^{15}N -labeled cyanobacteria. Initial *Spartina* detritus consumers included *Collembola* (springtails), the amphipod *Orchestia*, and enchytraeid oligochaetes. Consumers of bacteria and *Spartina* label included enchytraeid oligochaetes, capitellid polychaetes, and *Polydora* sp. (Table 1). We also learned that N leached from detritus is rapidly consumed by algal epiphytes on the detritus, and that microalgae can consume ^{13}C glucose heterotrophically (results courtesy of lipid analysis by Kevin Carman, LSU).

Vascular plant influence on benthos

Mensurative sampling in the natural marsh revealed that *Salicornia*- and *Spartina*-vegetated sediments experience much greater light reduction than unvegetated sediments ($P < 0.0001$), and this corresponds to lower soil temperature ($P < 0.0001$) and salinities ($P < 0.0003$). A negative relationship between plant cover and soil temperature was observed ($r^2 = 0.85$, $P \leq 0.0001$). Plant cover had no significant effect on microalgal biomass, measured as chlorophyll a, although highest concentrations were observed in plant-shaded sediments.

Experimental removal of the *Spartina* canopy without subsequent shading led to significant elevation of soil temperature (Fig. 6a) and salinity (Fig. 6b), reduced water content (Fig. 6c) and mortality of algal mats. The benthic community lost annelid and crustacean components but insect larvae increased in relative importance (Fig. 7). In treatments lacking *Spartina* plants but provided shade, most of the abiotic effects were ameliorated, and soil properties and macrofaunal assemblages resembled those of control plots, where *Spartina* remained intact (Figs. 6, 7).

DISCUSSION

Assessing Functional Recovery of Restored Wetlands

After 7 years of development, several structural measures reflect similarity of the Crown Point Mitigation Site and the adjacent natural Northern Wildlife Preserve. Vascular plant cover, plant species richness and snail densities are among these. For some taxa, such as *Salicornia bigelovii*, and *Cerithidea californica*, densities in the restored marsh exceeded those in the natural marsh. However, total macrofaunal densities were lower and composition differed when cross-marsh comparisons were made within elevation zones. It appears that higher elevations recovered more rapidly than low elevations in this system (Fig. 2).

Since its inception, the Crown Point Mitigation site has experienced macrofaunal succession, from an initially insect-dominated assemblage to one characterized by more annelids, particularly oligochaetes. In some instances mites have also become more prevalent. This change corresponds to a loss of open space, increasing vascular plant cover, and a buildup of belowground plant detrital biomass, as well as increasing microalgal biomass. The combination of natural abundance and isotopic enrichment studies allows us to identify the feeding preferences of invertebrate fauna characteristic of different successional stages. The early dominance by ceratopoginid and chironomid insect larvae represents an initial colonizing stage dependent on microalgal mats, and cyanobacteria in particular. This is reflected in exceptionally heavy $\delta^{13}\text{C}$ and light $\delta^{15}\text{N}$ signatures in animal tissues during the first few years of CPMS existence (Figs. 3, 4). Similar dependence on cyanobacteria (with heavy carbon isotope signatures) was observed for infauna colonizing the Friendship Marsh in Tijuana R. Estuary during the first year of flushing (Moseman et al. in press).

Oligochaetes (mainly Enchytraeidae and Tubificidae) and mites, which became abundant in the restored marsh after 5-7 years, appear associated with plant detritus based on visual observations during sorting. Both natural abundance and enrichment experiments indicate oligochaete reliance on non-algal food sources, including *Spartina* detritus and bacteria (Fig. 5, Table 1). Taxa such as the spionid *Polydora nuchalis*, *Capitella* sp. and the amphipod *Corophium* spp. have mixed food sources in Mission Bay, that may include some benthic microalgae, macroalgae, bacteria and suspended POM (Currin et al. submitted). These taxa were uncommon or rare in the restored marsh during April 2001 and 2002, but were important mid-stage colonists in the Tijuana Friendship Marsh (Moseman et al. in press).

In Mission Bay, it took 5-7 years for isotopic signatures and food web structure of the restored and natural marshes to become similar (Figs. 3, 4). In the nearby Tijuana Friendship marsh, similarity of isotopic signatures was achieved in just 2 years (Moseman et al. in press). Reasons for this difference may be related to the high exposure to flood-related disturbance of both the restored and natural habitats sampled in the Tijuana Estuary, stronger interconnectivity of natural and restored marshes in Tijuana River Estuary relative to Mission Bay, or possibly to the lower elevations studied in the Tijuana R. Estuary.



Vascular Plant Cover

The importance of plant cover to soil conditions and the infaunal assemblage is evident from (a) mensurative measurements made under different plant cover conditions (Levin and Talley 2000, this study), (b) successional patterns observed as the restored marsh develops, and (c) manipulative experiments that modify plant cover. Results of canopy removal experiments suggest that *Spartina* effects on benthos are largely light-mediated, but interactions may be direct (through change in abiotic conditions) or indirect, via altered supply of microalgae or other food sources. Our observation that *Salicornia* and *Spartina* have somewhat similar effects on soil salinity and temperature if elevation is held constant may not extend to other aspects of the benthos. Future studies are needed to distinguish effects of different types of plant cover (e.g., *Salicornia* vs *Spartina*). Cover manipulation experiments involving both species are underway to examine these issues.

Project findings suggest that development of plant cover is key to the creation of fully functional salt marsh ecosystems in southern California. While some plant species, such as *S. bigelovii* are rapid, effective colonizers, other such as *Spartina* will need active planting efforts to take and spread. Salt marsh plants are known to ameliorate harsh environmental conditions in arid wetlands (Bertness and Callaway 1994), but have not previously been shown through manipulations to influence benthic infaunal composition.

Plant cover appears to control development of the food web in salt marshes. In restored wetlands, initial open stages with little plant canopy support mainly cyanobacterial consumers. Subsequent development of plant cover promotes succession by annelids and other detritivores. Thus bottom-up processes exert significant influence on recovery of restored marsh communities.

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Table 1. Average isotopic signatures of major consumer taxa exposed to isotopically enriched food sources. Isotopic signatures of enriched food sources were: *Spartina* +345 to +860, microalgae +26 to +101, cyanobacteria +71 to +576. Bacteria signatures are not available. Time 0 data reflect background isotope levels of consumers. Bold indicates high uptake of labeled food sources. CPMS = Created Marsh, NWP = Natural Marsh

TAXON	TIME SINCE START	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Treatment A: ^{13}C Acetate (bacteria) + ^{15}N <i>Spartina</i>			
CPMS			
<i>Capitella</i> spp.	0	-13.62	7.70
	3 DAY	-7.33	20.67
	6 DAY	5.06	50.26
	72 DAY	-9.09	34.01
Ceratopogonidae larvae	0	-13.95	6.08
	3 DAY	-3.32	29.34
	6 DAY	0.49	35.00
<i>Corophium</i> spp.	0	-7.63	9.13
	72 DAY	-12.82	12.52
Dolichopodidae larvae	0	-15.20	6.41
	3 DAY	-7.30	15.85
	6 DAY	-13.92	10.20
	72 DAY	-15.00	8.43
<i>P. nuchalis</i>	0	-12.41	11.67
	3 DAY	35.45	39.71
	6 DAY	-7.59	18.23
	72 DAY	-12.06	18.34
NWP			
Enchytraeidae	0	-22.31	8.25
	3 DAY	-7.12	13.27
	6 DAY	-18.37	34.01
	72 DAY	-21.78	23.30
Halacaroida	0	-19.29	10.39
	3 DAY	-19.09	15.52
	72 DAY	-29.48	4.43
<i>O. traskiana</i>	3 DAY	-23.70	156.45
Podurids	3 DAY	-20.27	128.26
	6 DAY	-19.74	7.34

Table 1. Continued

TAXON	TIME SINCE START	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Treatment B: ^{13}C Microalgae and ^{15}N Cyanobacteria (labeled 3da later)			
CPMS			
Dolichopodidae larvae	11/8 DAY	46.49	82.59
Ceratopogonidae larvae	0	-13.21	4.21
	3 DAY	62.67	4.22
	11/8 DAY	80.70	128.28
	72/69 DAY	-10.18	4.99
Ceratopogonidae pupae	0	-14.06	4.01
	11/8 DAY	36.32	108.85
<i>M. rubroniveus</i>	0	-11.40	5.82
	3 DAY	-14.75	5.99
<i>P. nuchalis</i>	3 DAY	1.24	8.21
Nemertean	0	-7.18	10.02
	11/8 DAY	-14.68	10.94
NWP			
Enchytraeidae	3 DAY	-19.54	6.18
	72/69 DAY	-20.09	6.95

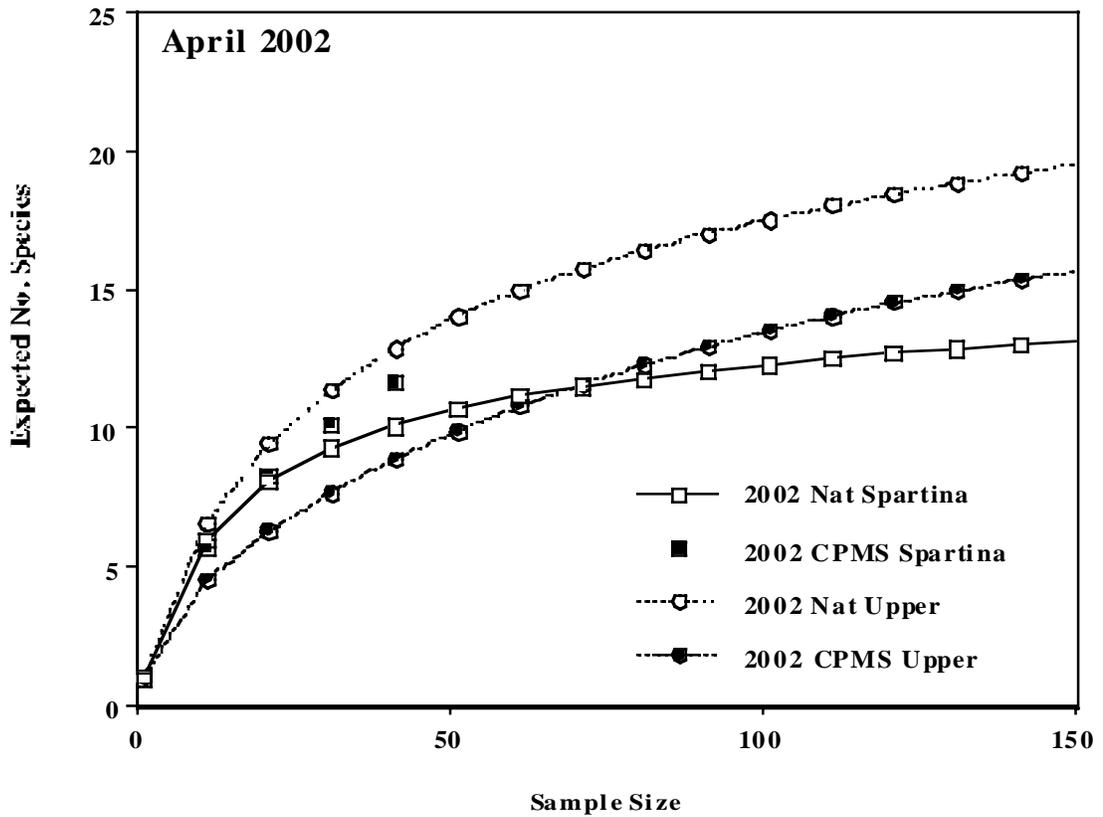
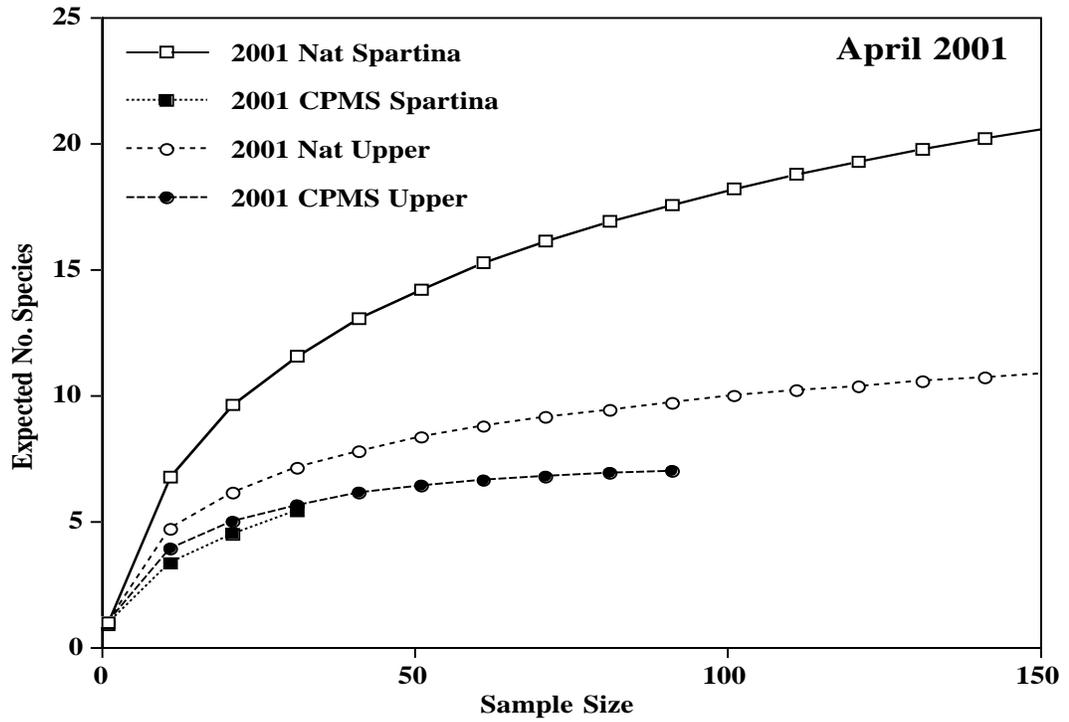


Figure 1. Rarefaction curves for macrobenthos from natural and created marsh sediments at lower (*Spartina*) and upper elevations.

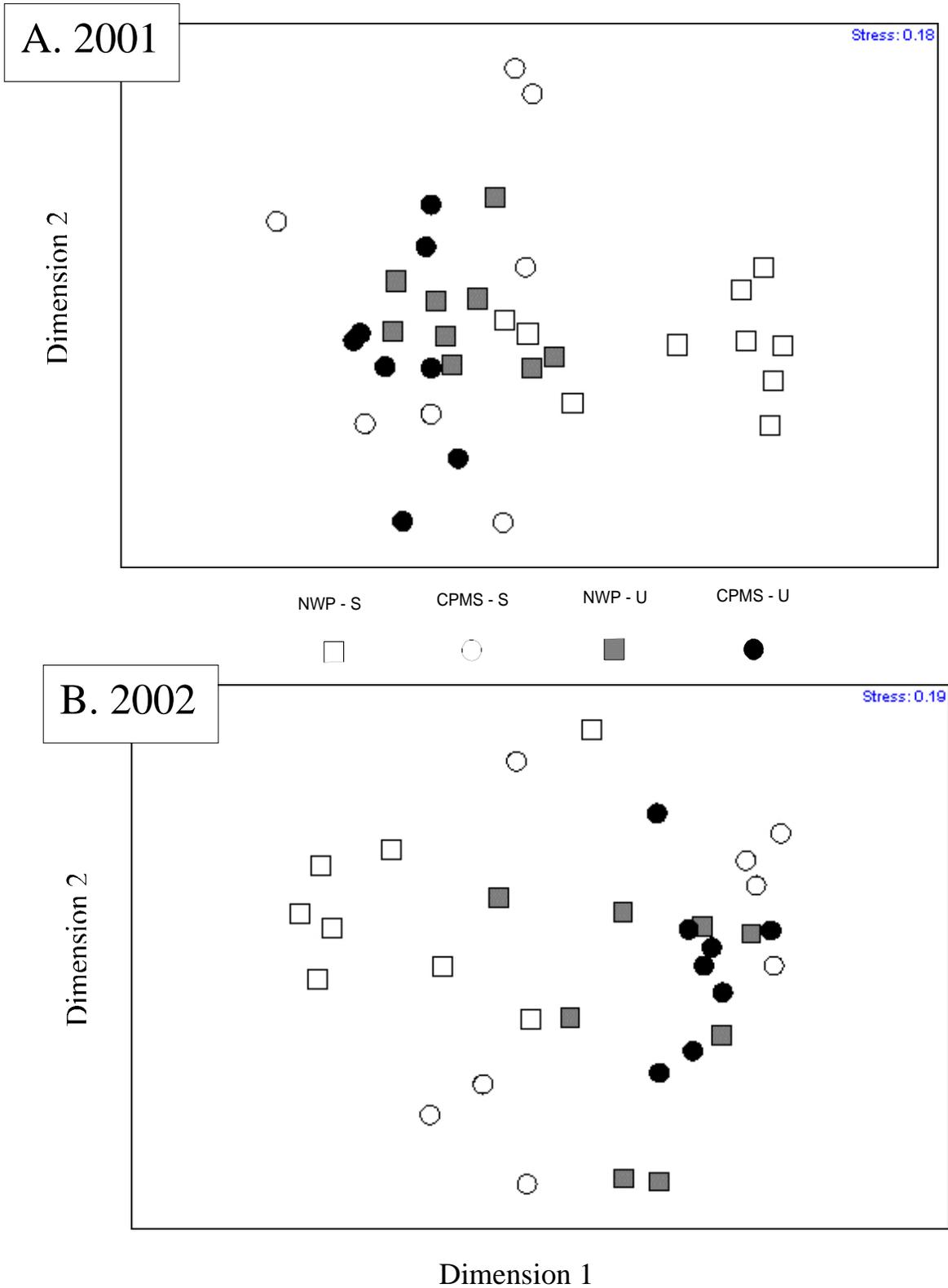


Figure 2. Multidimensional scaling plot of macrobenthos (> 300 microns) from lower (*Spartina* - S) and upper (mixed vegetation - U) elevations in the created (CPMS) and natural (NWP) salt marshes of Mission Bay, California.

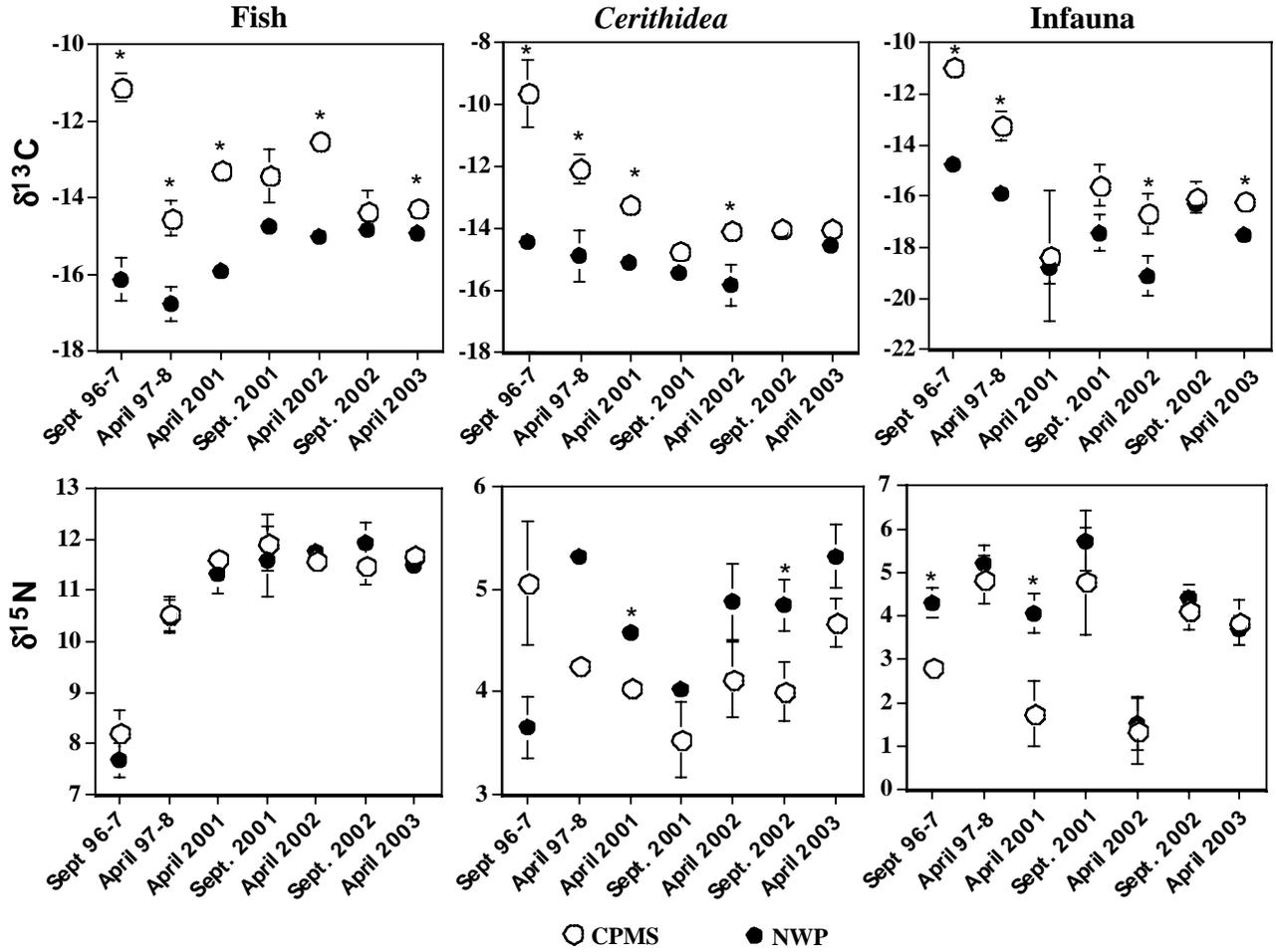


Figure 3. Temporal sequence of average C and N isotopic signatures for snails (*Cerithidea*), macrobenthos (>0.3 mm), and fish (*Fundulus*) in the created and natural marsh in Mission Bay: Sept. 96 through April 2003. Created marsh establishment was in Dec. 1995. Asterisks indicate significant created vs natural marsh differences.

Species Average Isotope Signatures

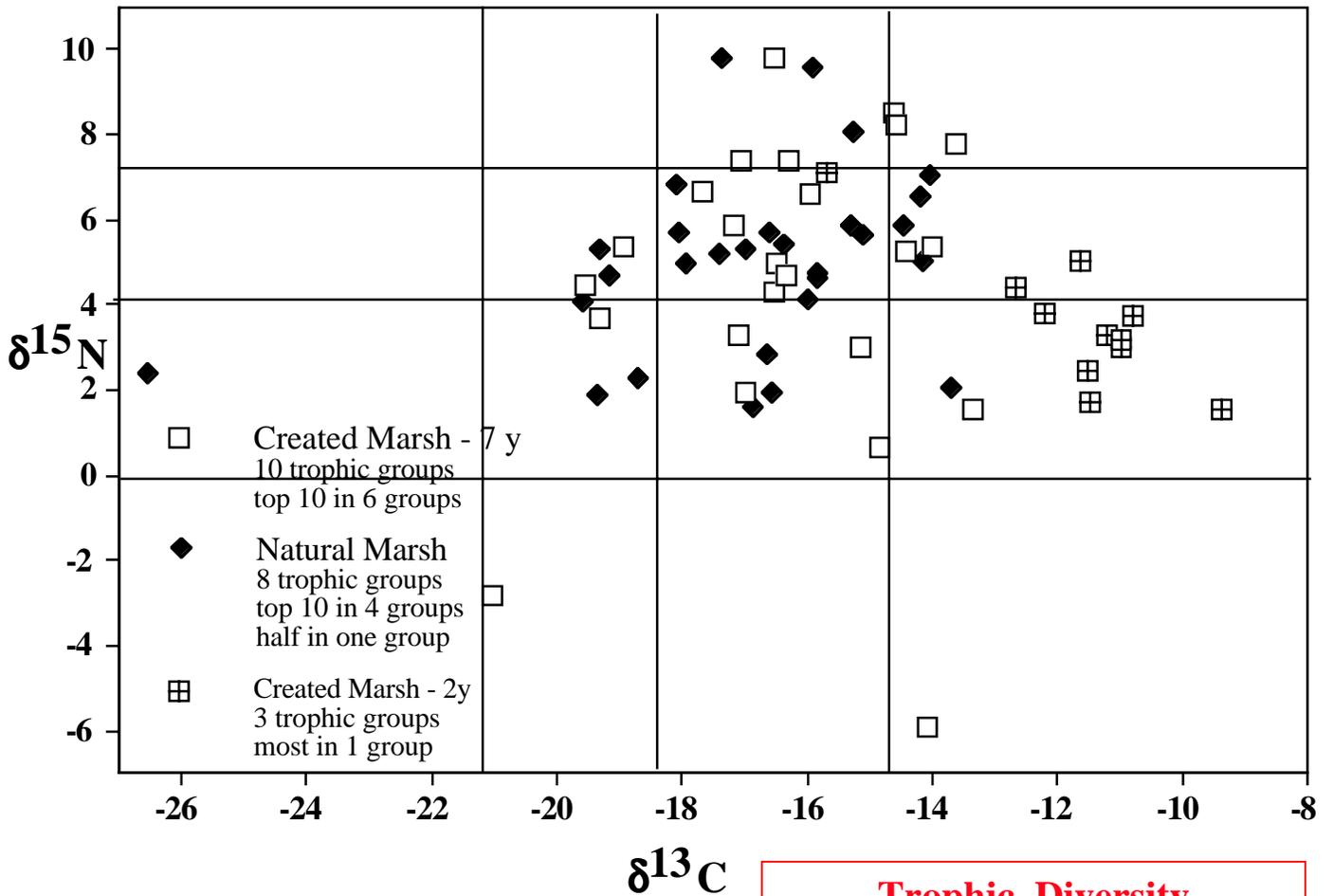


Figure 4. Changes in created marsh trophic diversity over time and in relation to the natural marsh. Each point reflects the average isotope signature for a single species. Note reduced trophic diversity in the restored marsh at 2 years and maximal diversity at 7 years, relative to the natural marsh. The greatest functional redundancy occurs within the natural marsh. Trophic diversity (H' log 10), evenness (J') and number of functional groups (F) are calculated using the number of species in each trophic category, defined by the boxes on the grid.

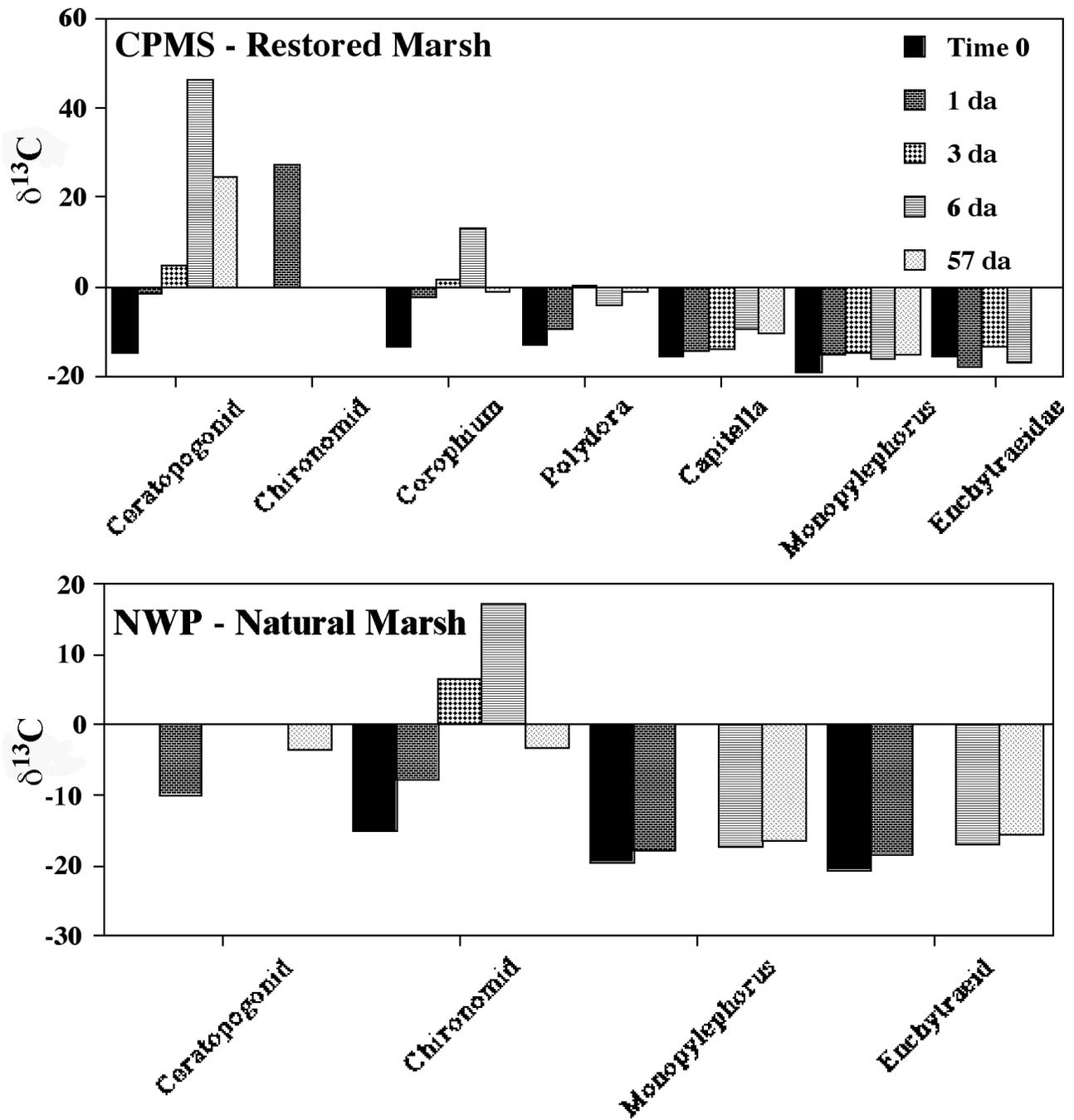


Figure 5. Time series of average $\delta^{13}\text{C}$ signatures of dominant macrofauna in the restored and natural marsh following labeling of microalgae with ^{13}C bicarbonate. Time 0 values reflect background signatures. Data are given for insect larvae (Ceratopogonidae, Chironomidae), amphipod (*Corophium* spp.), polychaetes (*Polydora nuchalis*, *Capitella* sp.) and oligochaetes (*Monopylephorus*, Enchytraeidae).

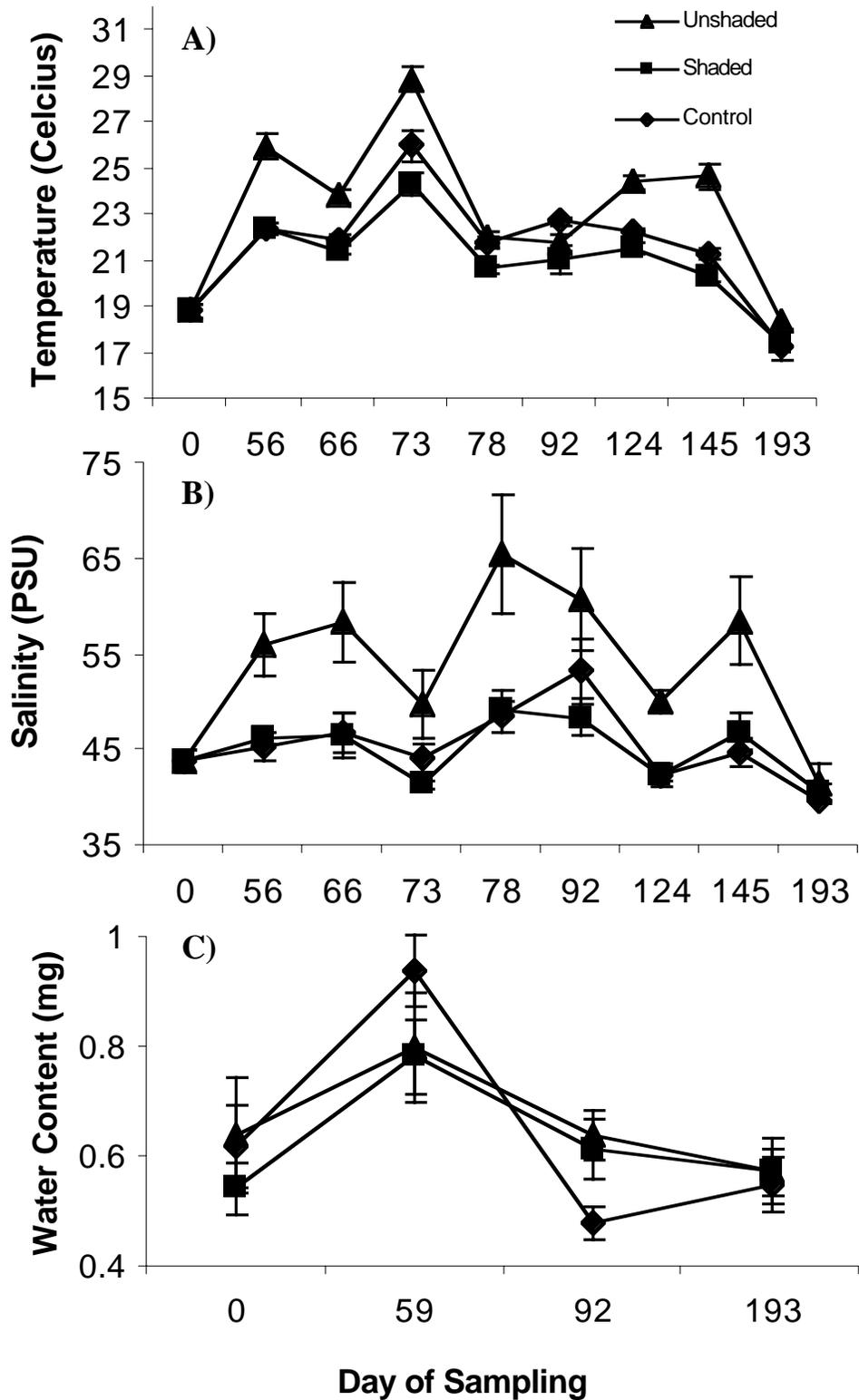


Figure 6. Temperature (A), salinity (B), water content (C) of soils subjected to *Spartina* manipulations initiated in May 2002, Kendall Frost Marsh, Mission Bay, CA. Unshaded=clipped *Spartina*, Shaded=clipped *Spartina* + shade cloth, Control=unclipped *Spartina*

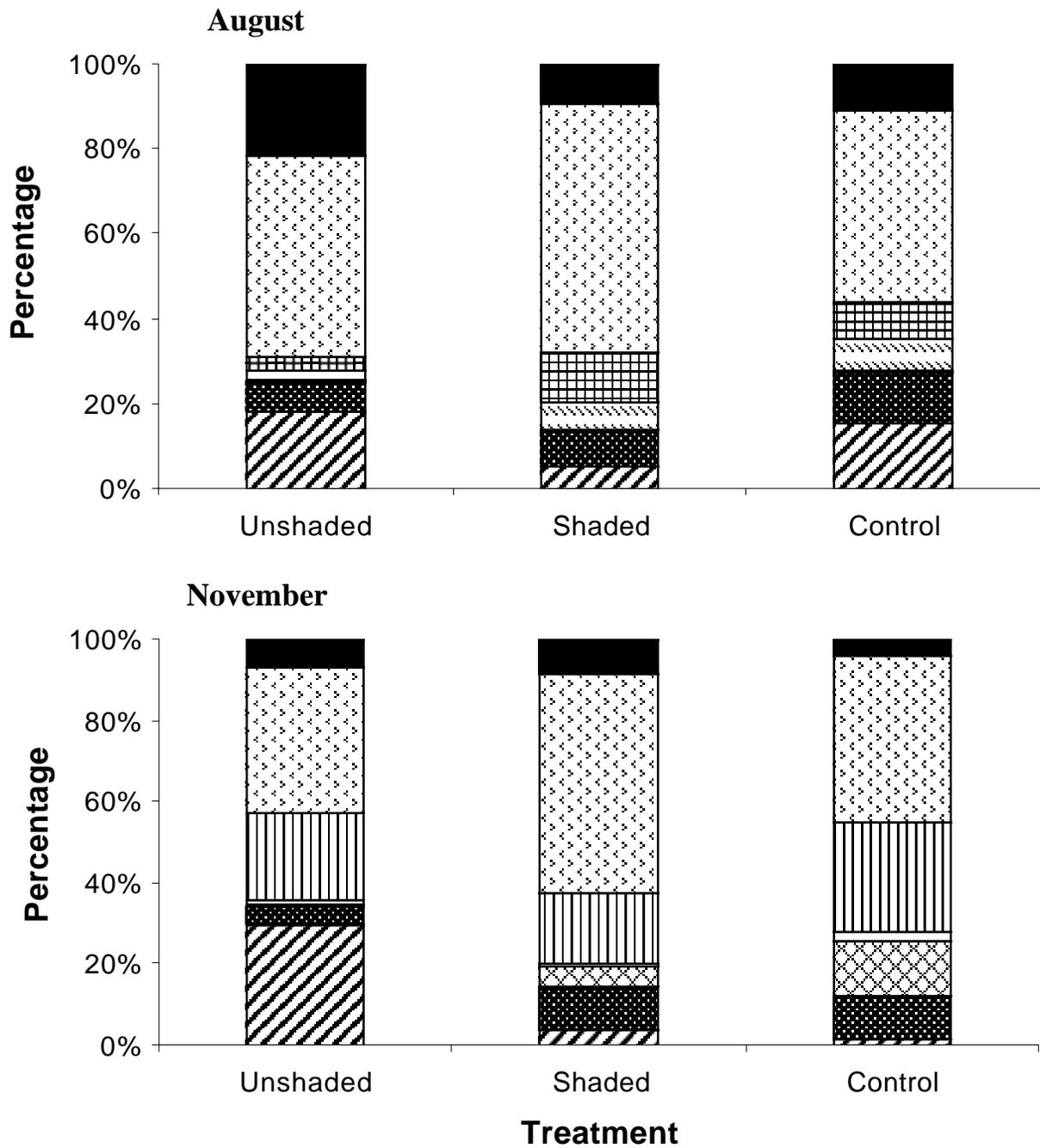


Figure 7. Percent macrofaunal composition in sediments underlying experimental treatments in the *Spartina* zone of the natural Kendall Frost Marsh, Mission Bay, CA. Unshaded=clipped *Spartina*, Shaded=clipped *Spartina* + shade cloth, Control=unclipped *Spartina*