Ecology, 88(4), 2007, pp. 904–917

REGULATION OF BENTHIC ALGAL AND ANIMAL COMMUNITIES BY SALT MARSH PLANTS: IMPACT OF SHADING

Christine R. Whitcraft[1] and Lisa A. Levin

Integrative Oceanography Division, Scripps Institution of Oceanography, La Jolla, California 92093-0218 USA

Abstract. Plant cover is a fundamental feature of many coastal marine and terrestrial systems and controls the structure of associated animal communities. Both natural and human-mediated changes in plant cover influence abiotic sediment properties and thus have cascading impacts on the biotic community. Using clipping (structural) and light (shading) manipulations in two salt marsh vegetation zones (one dominated by *Spartina foliosa* and one by *Salicornia virginica*), we tested whether these plant species exert influence on abiotic environmental factors and examined the mechanisms by which these changes regulate the biotic community. In an unshaded (plant and shade removal) treatment, marsh soils exhibited harsher physical properties, a microalgal community composition shift toward increased diatom dominance, and altered macrofaunal community composition with lower species richness, a larger proportion of insect larvae, and a smaller proportion of annelids, crustaceans, and oligochaetes compared to shaded (plant removal, shade mimic) and control treatment plots. Overall, the shaded treatment plots were similar to the controls. Plant cover removal also resulted in parallel shifts in microalgal and macrofaunal isotopic signatures of the most dynamic species. This suggests that animal responses are seen mainly among microalgae grazers and may be mediated by plant modification of microalgae. Results of these experiments demonstrate how light reduction by the vascular plant canopy can control salt marsh sediment communities in an arid climate. This research facilitates understanding of sequential consequences of changing salt marsh plant cover associated with climate or sea level change, habitat degradation, marsh restoration, or plant invasion.

Key words: abiotic properties; biodiversity; cordgrass; light; macrobenthos; microalgae; pickleweed; plant cover; Salicornia virginica; Spartina foliosa; *stable isotope*.

Introduction

Vascular plants have major structuring roles in both marine and terrestrial ecosystems (Clements 1991, Bruno and Bertness 2001). On land, the role of plants in altering the physical environment is well-understood, and ecologists are working toward a detailed understanding of how plants affect the complete sediment system (e.g., Swift and Anderson 1993, Hooper et al. 2000). Although vascular plants are recognized as a structuring force in coastal benthic communities (Bertness 1991*a*, *b*, 1992, Smith et al. 2000, Snelgrove et al. 2000, Bortolus et al. 2002), a detailed mechanistic understanding of plant–animal relationships has not been developed, especially for salt marshes. For coastal wetlands, it is known that the presence of plants affects ecosystem-level processes such as hydrology, sedimentation rate, and nutrient cycling (Bertness 1988, Leonard and Luther 1995, Levin and Talley 2000). Plant shoots and detrital material partially fuel the salt marsh food web (Peterson et al. 1985, Levin and Talley 2000, Levin et al. 2006). In addition, vascular marsh plants modify the amount and quality of light reaching the sediment, thus affecting temperature (Gallagher 1971, Bertness and Hacker 1994) and algal growth (Lüning 1980, Seliskar et al. 2002). On a larger scale, critical salt marsh functions, such as nursery habitat provision, coastal stabilization, runoff filtration, and trophic support, are directly and indirectly tied to the presence of vascular plants (Gleason et al. 1979, Warren and Neiring 1993).

Experimental work has shown that plant community disturbance affects abiotic sediment properties and positive interactions between different plant species (Bertness 1988, 1991*a*, *b*, 1992, Bertness and Callaway 1994). However, few studies have experimentally studied the responses of benthic algae and belowground invertebrates to plant disturbance (Pagliosa and Lana 2005). Comparing a restored and an adjacent natural wetland system in southern California, Levin and Talley (2002) inferred the influence of vascular salt marsh vegetation on the rate and trajectory of macrofaunal recovery. They observed that during early succession when the marsh had little plant cover, the macrofaunal assemblage had a lower proportion of oligochaetes and a higher proportion of insect larvae as compared to the assemblage in the neighboring mature marsh. As the vegetation expanded and the created marsh matured, the percentage of insect larvae decreased, and the percentage

Manuscript received 31 December 2005; revised 6 September 2006; accepted 7 September 2006. Corresponding Editor: C. R. Hupp.

[1] E-mail: cwhitcra@ucsd.edu

of polychaetes and amphipods increased. Similar trajectories have been observed in other southern California systems (Talley and Levin 1999, Moseman et al. 2004). Our study was designed to experimentally identify the mechanisms behind the observed macrofaunal community changes and to test whether this trajectory occurs under small-scale disturbance scenarios.

We designed field manipulations of light levels and structure to explore the role of aboveground vegetation in determining environmental conditions and algal and macrofaunal diversity. These manipulative experiments tested the hypotheses that (1) modification of plant cover would alter environmental conditions and microalgal assemblages, (2) these environmental and algal modifications would lead to changes in the abundance and composition of the macrofaunal community, (3) structure and light removal would have differing effects, and (4) plant effects on algal and macrofaunal communities would be equivalent for the dominant grass (*Spartina foliosa*) and succulent (*Salicornia virginica*, also known as *Sarcoconia pacifica* in California) species in southern California. We predicted that plant influence on benthos should be especially strong in the arid mediterranean climate regime characteristic of southern California relative to wetter Atlantic systems, where much related research has been conducted (i.e., New England and the Southeast, USA). Describing the functional role of plants in salt marsh ecosystems is crucial to ecological understanding and highly relevant to conservation issues associated with restoration, invasions, marine reserves, and biodiversity maintenance.

Methods

The mediterranean climate of southern California, USA, with mild, wet winters and warm, dry summers, supports two dominant vascular plant species within the salt marsh environment: pickleweed (*Salicornia virginica*) and Pacific cordgrass (*Spartina foliosa*). *Salicornia virginica* dominates in mid-marsh habitat and under conditions of episodic inlet closure, while *Spartina foliosa* occupies the low marsh zone and requires regular flushing; it disappears in the absence of ocean water influx (Zedler et al. 1992). The research was conducted in the 6.5-ha Kendall Frost Mission Bay Marsh Reserve, an intertidal salt marsh in the northeast corner of Mission Bay, San Diego, California (32°47′35″ N, 117°13′00″ W), where both plant species co-occur.

Experimental design

To determine mechanisms by which plants influence sediments, algae, and macrofauna, we conducted parallel experiments in adjacent *Spartina foliosa*- and *Salicornia virginica*-dominated habitats. Within the marsh, eight experimental blocks were established in patches of *Spartina foliosa* (at least 90% cover) growing with other mixed vegetation (*Salicornia* spp., *Batis maritima*), and eight blocks were established in existing patches of *Salicornia virginica* (again at least 90% cover). Three different 1-m^2 treatments were created within each vegetation type: (1) absence of plant cover and structure (clipped, unshaded), (2) absence of plant structure (clipped, shaded), and (3) control (unclipped, no shade manipulation). Hereafter, these will be referred to as unshaded, shaded, and control treatment plots, respectively. In the unshaded and shaded treatment plots, all species present in the plot (*Spartina foliosa*, *Salicornia virginica*, etc.) were clipped at the soil surface, leaving belowground biomass intact. These two treatments were maintained by weekly clipping for the duration of the study (six months). The clipped plant roots continued to resprout and require clipping, indicating that the plants remained alive belowground and suggesting limited decay of underground plant matter.

Spartina foliosa plant removal treatments were maintained from May 2002 until May 2003; *Salicornia virginica* treatments were maintained from May 2004 until May 2005. Weekly maintenance included removal of detrital material trapped on shade cloth and/or chicken wire over treatments. Sampling took place three months and six months after establishment of the treatment plots. Plant habitat elevations, measured for each plot using an automatic level (SAL series, CST/Berger, Watseka, Illinois, USA), were on average 0.3 m lower in the *Spartina foliosa* plots (2.00 ± 0.03 m below mean low water) than in the *Salicornia virginica* plots (2.27 ± 0.15 m below mean low water).

Light measurements, made immediately prior to clipping in May, revealed that natural plant cover reduced incident light by ~94% in *Spartina foliosa* patches (94.1% ± 2.1%) and 85% in *Salicornia virginica* patches (85.7% ± 5.0%) (*Spartina foliosa* > *Salicornia virginica*; $\chi^2 = 17.396$, $P < 0.0001$). Shaded treatments, designed to mimic light reduction, had a set of four poles suspending a chicken wire frame and a 90% reduction shade cover (two layers of 70% reduction shade cloth) over the plot. To equalize experimental artifacts, unshaded and control treatment plots also had a set of four poles suspending only chicken wire, allowing light to penetrate to the ground. Light measurements were made on a cloudless day using a Quantum Scalar Laboratory 100 Irradiance Meter (4 pi steradians sensor; Biospherical Instruments, San Diego, California, USA) in each replicate. Ambient light readings were taken immediately preceding light measurements under the canopy, and all light readings were an average of three measurements.

Measurement of abiotic and sediment properties

Within each treatment plot, soil salinity of the top 0.5 cm (±1 practical salinity units [psu]) was measured weekly by squeezing porewater from the sediment surface through a Whatman number 1 qualitative grade filter onto a hand-held salinity refractometer. Temperature (±0.1°C) at 2 cm depth was measured weekly using

a portable digital thermometer (Ingold Mettler-Toledo, Bedford, Massachusetts, USA). Water content of the top 0.5 cm was determined at three months and six months by mass loss after drying a known volume of sediment (Buchanan 1984). Redox potential was measured at three months and six months at 1-cm depth with a portable Mettler Toledo millivolt meter. These millivolt readings were corrected to the standard hydrogen electrode value by adding 207 mV (Giere et al. 1988). Redox potential has been used to indicate the degree of oxygenation in wetland soils (Gambrell and Patrick 1978) and is known to be influenced by wetland plant rhizomes (Lovell 2002). One sediment core (4.8 cm diameter × 6 cm) was collected within each treatment plot at three months and six months for analysis of particle size and organic-matter content using methods of Neira et al. (2005). Belowground plant detrital biomass (dry mass) was calculated by removing all plant detritus (>300 μm) from macrofaunal cores (4.8 cm diameter × 6 cm), drying the material at 60°C, and weighing it on an analytical balance.

Algae collection and analysis

In each treatment plot at three months and six months, separate cores (0.95 cm^2 × 5 mm and 0.56 cm^2 × 5 mm, respectively) were taken for chlorophyll *a* (a proxy for microalgal biomass) and for analysis of algal pigments by high-performance liquid chromatography (HPLC) to indicate microalgal functional group composition and diversity (Cariou-LeGall and Blanchard 1995). Once back in the laboratory, chlorophyll *a* was extracted with 90% acetone and the concentration was determined spectrophotometrically (Plante-Cuny 1973). Pigment separation was conducted according to Janousek (2005). For HPLC data presented, detector outputs (in millivolts) were converted to mass (in nanograms or micrograms) of pigment using pigment-specific calibrations generated independently with purified pigment material (Janousek 2005).

Macrofauna sampling

At three months (August) and six months (November), macrofaunal cores were taken in each treatment plot using a cylindrical push core (4.8 cm diameter, 18.1 cm^2) inserted to a depth of 2 cm. We selected a 4.8 cm diameter core to target macrofauna typically in the 1–2 mm size range, recognizing that this is likely to exclude megafauna, such as large clams or crabs. This core size is consistent with published literature on macrobenthos from this and nearby marshes (Levin et al. 1998, Talley and Levin 1999, Levin and Talley 2002, Levin and Currin 2005). Most (78–89%) of the macrofauna in southern California *Spartina foliosa* marshes is found in the top 2 cm of sediment (Levin et al. 1998). Cores were preserved (unsieved) in 8% buffered formalin with Rose Bengal. For macrofaunal quantification, the core sediments were washed through a 0.3-mm mesh. The animals retained were sorted under a dissecting microscope at 12× magnification, identified to the lowest taxonomic level possible, counted, and stored in 70% ethanol. Most insects collected were larvae; identifications of these were at the family level only. For other organisms, identifications were to species level, although putative names were used in some cases. The biomass of each species was measured on an analytical balance as wet mass (nearest 0.01 mg) after rehydrating the organisms in water and then blotting on a cotton wipe for ~30 s. Wet mass was assessed to avoid variability associated with previous ethanol storage. The error incurred for repeated measurements of wet mass, assessed for representatives of four phyla, was less than ±4% (C. R. Whitcraft, *unpublished data*). Storage in ethanol for 1–2 years will have reduced actual biomass, but differences among treatments are considered valid.

Stable isotope analysis

Stable isotopic analyses were used to assess (a) whether signatures of the primary producers change with plant cover, (b) which consumer species rely on microalgae as a food source (i.e., species whose signatures track changes in microalgae caused by treatments), and (c) whether microalgae grazers are influenced by changing plant cover more than other feeding groups (detritivores, predators, or plant grazers). Samples of sediment organic matter, microalgae, macroalgae, and macrofauna were collected in March 2005 in the *Salicornia virginica* habitat within each treatment using collection methods described below and were analyzed for $\delta^{13}C$ and $\delta^{15}N$ signatures. The $\delta^{15}N$ signatures were analyzed statistically for differences among treatments (as discussed below) but revealed no significant patterns, so results are not included in this paper.

Microalgae were collected using density centrifugation with ludox (colloidal silica) (Currin et al. 1995), providing a pure algal sample (devoid of sediment). Macrofaunal invertebrates were sieved on a 0.3 mm mesh, sorted live, and identified to species. All animals were kept alive in seawater and allowed to evacuate guts for up to 24 h. Animal material was washed in Milli-Q water (Millipore, Billerica, Massachusetts, USA) and frozen in combusted vials (500°C for 4 h) or tin boats until analysis. Larger organisms were removed from the shell or carapace, dried at 65°C, and then ground with a mortar and pestle. All samples were treated with Pt Cl_2 to eliminate inorganic C. Isotopic composition of animal and algal samples was analyzed using a PDZ Europa 20-20 mass spectrometer connected to an elemental analyzer (PDZ Europa ANCA-GS, Northwich, UK). Stable isotope abundance is expressed in parts per thousand in a ratio of heavy to light isotope content (^{15}N:^{14}N or ^{13}C:^{12}C). Working standards, sucrose and ammonium sulfate, were $\delta^{13}C = -23.83‰$ vs. Vienna Pee Dee Belemnite Standard or $\delta\ ^{15}N = +1.33‰$ vs. air N_2. Typical sample precision is better than 0.1‰.

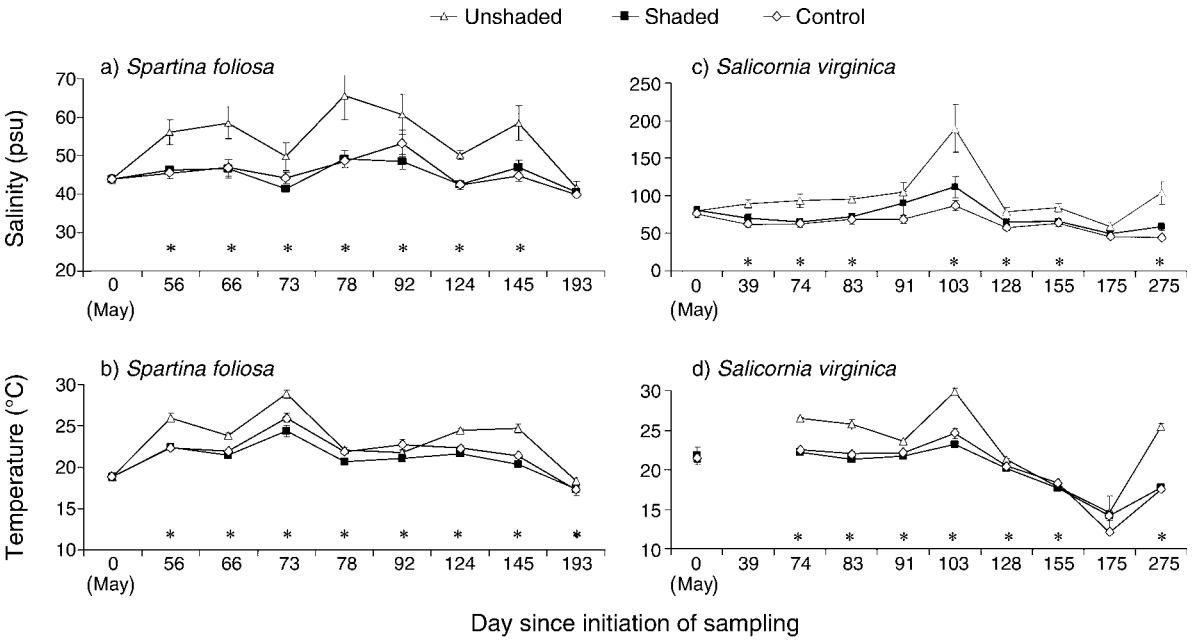

FIG. 1. Porewater salinity (practical salinity units, psu) and temperature (mean ± SE) of upper 2 cm of sediment in three treatments in *Spartina foliosa* and *Salicornia virginica* treatment plots. Values designated with asterisks indicate that unshaded treatment values are significantly different from shaded and control treatment values (Wilcoxon rank sum, $P < 0.05$). The research was conducted in the 6.5-ha Kendall Frost Mission Bay Marsh Reserve, an intertidal salt marsh in the northeast corner of Mission Bay, San Diego, California, USA. Temperature data were not collected on day 39 in *S. virginica* habitat due to equipment malfunction.

Statistical analysis

All univariate tests were conducted with JMP 5.1 statistical software (SAS Institute, Cary, North Carolina, USA). Data were tested for normality, and square-root or $\log_{10}$-transformed as needed prior to analysis. If no transformation yielded normal data, nonparametric Wilcoxon tests were utilized. Comparisons of abiotic, sediment, and algal properties, macrofauna percent composition, and macrofauna species-level density and biomass data among treatments were conducted with one-way ANOVAs or nonparametric Wilcoxon tests followed by a posteriori Student's *t* tests. Whole-core measurements of species richness and diversity (Simpson's D [$D = 1/\sum P_i^2$]) were calculated from count data, and comparisons among treatments were conducted using one-way ANOVAs or nonparametric Wilcoxon tests, again followed by a posteriori Student's *t* tests. Relationships among abiotic and biotic factors were analyzed for significance using Spearman's rho. Species were used as replicates for analyses of treatment effects on stable isotope ($\delta^{13}C$) signatures in one-way ANOVAs and Wilcoxon nonparametric tests with a posteriori Student's *t* tests. We present as significant the increase in microalgae $\delta^{13}C$ signatures in plant removal treatments ($P = 0.082$) because power analysis shows that with four additional samples, P would have been 0.05. One standard error about the mean is presented for all data unless otherwise noted.

Multivariate analyses were conducted on macrofaunal count and biomass data (both fourth-root transformed) using Primer 5 (Clarke 1993, Clarke and Warwick 1994). Analyses are based on Bray-Curtis similarity indices (Clarke 1993). Pairwise comparisons of overall community similarity were made using analysis of similarity, ANOSIM.

RESULTS

Abiotic sediment properties

Light reduction was significantly greater in the shaded and control treatments relative to the unshaded treatments (*Spartina foliosa*, unshaded 36.8% ± 8.0%, shaded 82.9% ± 3.0%, control 94.1% ± 2.1%, $\chi^2 = 12.12$, $P = 0.002$; *Salicornia virginica*, unshaded 14.7% ± 4.5%, shaded 85.0% ± 3.9%, control 85.7% ± 5.0%, $\chi^2 = 13.12$, $P = 0.014$). Prior to experimentation, no differences existed among *Spartina foliosa* treatments with respect to salinity (ANOVA, $F_{2,21} = 0.21$, $P = 0.811$), temperature (Wilcoxon, $\chi^2 = 2.61$, $P = 0.272$), or among *Salicornia virginica* treatments with respect to salinity (ANOVA, $F_{2,21} = 0.38$, $P = 0.687$), temperature (ANOVA, $F_{2,28} = 0.03$, $P = 0.968$), or redox potential (Wilcoxon, $\chi^2 = 1.36$, $P = 0.508$). Redox potential in *Spartina foliosa* plots was not measured before establishment of the experiment. Following removal of plants, the unshaded treatment plots in *Spartina foliosa* and *Salicornia virginica* habitats demonstrated consistently higher temperatures and porewater salinities

TABLE 1. Comparison of responses (mean with SE in parentheses) to unshaded, shaded, and control treatments by sediment properties, abiotic physical parameters, and the algal community after three months (August) and six months (November) in (a) *Spartina foliosa* and (b) *Salicornia virginica* habitat.

Property	Three months				
	Unshaded	Shaded	Control	χ^2_2 or $F_{2,21}$	P
a) *Spartina foliosa*					
Grain size (% mud)	93.6 (3.3)	97.0 (1.2)	96.6 (0.9)	$\chi^2 = 1.19$	0.553
Organic matter (%)	30.2 (5.7)	31.4 (4.3)	32.6 (4.8)	$\chi^2 = 0.47$	0.793
Salinity	50.1 (1.2)[a]	42.5 (0.8)[b]	42.4 (1.2)[b]	$F = 13.06$	0.002
Temperature (°C)	24.4 (0.3)[a]	21.6 (0.1)[b]	22.3 (0.2)[b]	$F = 17.75$	0.0001
Water content (g/core)	0.64 (0.03)[a]	0.62 (0.05)[a]	0.48 (0.04)[b]	$F = 3.86$	0.038
Redox (Eh)	19 (63.08)	−25.63 (65.81)	−27.63 (82.95)	$\chi^2 = 0.38$	0.829
Chl *a* (μg/g sediment)	305.6 (92.6)	346.6 (107.8)	214.4 (53.2)	$\chi^2 = 1.1$	0.560
Fucoxanthin (μg/cm^2)	4.32 (0.64)	5.26 (1.53)	4.74 (0.59)	$\chi^2 = 0.42$	0.811
Density (no./18.1 cm^2)	35.3 (21.2)[a]	120.3 (23.5)[b]	64.9 (17.5)[b]	$\chi^2 = 0.39$	0.0006
Species richness (no. spp./18.1 cm^2)	5.50 (0.57)[a]	8.88 (0.58)[b]	8.50 (0.89)[b]	$\chi^2 = 10.1$	0.0006
Biomass (mg/18.1 cm^2)	7.57 (3.50)[a]	21.42 (5.76)[b]	22.13 (7.75)[b]	$\chi^2 = 5.96$	0.050
Diversity (Simpson's *D*)	0.58 (0.09)	0.62 (0.06)	0.69 (0.07)	$\chi^2 = 1.23$	0.539
b) *Salicornia virginica*					
Grain size (% mud)	92.1 (4.9)	93.0 (4.0)	92.7 (3.6)	$\chi^2 = 1.65$	0.513
Organic matter (%)	29.8 (2.4)	28.5 (2.8)	30.4 (3.1)	$\chi^2 = 2.19$	0.293
Salinity	79.4 (5.1)[a]	65.0 (3.7)[b]	57.0 (2.8)[b]	$F = 8.2$	0.002
Temperature (°C)	21.3 (0.1)[a]	20.2 (0.3)[b]	20.5 (0.2)[b]	$F = 8.73$	0.002
Water content (g/core)	0.49 (0.07)	0.43 (0.06)	0.50 (0.06)	$F = 0.43$	0.659
Redox (Eh)	−7.5 (55.36)	−34.43 (43.18)	−40.50 (57.21)	$F = 0.11$†	0.895
Chl *a* (μg/g sediment)	27.1 (6.9)	37.3 (7.0)	31.8 (9.2)	$F = 0.43$	0.654
Fucoxanthin (μg/cm^2)	0.67 (0.21)[a]	1.5 (0.60)[b]	1.26 (0.29)[b]	$\chi^2 = 2.62$	0.0009
Density (no./18.1 cm^2)	21.4 (8.2)[a]	75.9 (19.3)[b]	55.3 (16.1)[ab]	$\chi^2 = 5.93$	0.050
Species richness (no. spp./18.1 cm^2)	3.63 (0.75)	1.63 (1.05)	4.00 (0.89)	$F = 0.31$	0.736
Biomass (mg/18.1 cm^2)	4.08 (1.44)	137.80 (124.67)	7.76 (2.38)	$\chi^2 = 2.59$	0.274
Diversity (Simpson's *D*)	0.42 (0.11)	0.29 (0.11)	0.28 (0.10)	$\chi^2 = 0.87$	0.648

Notes: Superscripted letters indicate a posteriori differences among treatments ($P < 0.05$). The research was conducted in the 6.5-ha Kendall Frost Mission Bay Marsh Reserve, an intertidal salt marsh in the northeast corner of Mission Bay, San Diego, California, USA.

† Degrees of freedom for this F test were 2, 16.

compared to the shaded or control treatment plots over the duration of the experiment (Fig. 1). The unshaded treatment plots had lower water content relative to the shaded and control treatment plots in both *Spartina foliosa* and *Salicornia virginica* habitats (three months, *Spartina foliosa*, $F_{2,21} = 3.86$, $P = 0.038$; six months, *Salicornia virginica*, $\chi^2 = 9.78$, $P = 0.008$).

Prior to treatment establishment, the standing stock of belowground plant detritus did not differ between *Spartina foliosa* (13 800 ± 1400 g/m^2) and *Salicornia virginica* (11 015 ± 3000 g/m^2) habitats (Wilcoxon, $\chi^2 = 0.89$, $P = 0.345$). Neither the removal of shade nor the removal of aboveground plant structure was associated with any soil organic matter or particle size changes during the experiment (Table 1). Redox potential measurements were extremely variable among *Salicornia virginica* blocks and treatments and did not demonstrate treatment effects. The redox data (unshaded, mean = −7.5, range = −165 to 116; shaded, mean = −34.4, range = −222 to 111; control, mean = −40.5, range = −262 to 126) indicate that the soils in unshaded and shaded treatments did not become more reduced than control sediments.

Algal community

Prior to treatment establishment, there were no treatment differences in sediment chl *a* concentrations (all values in micrograms per gram sediment) for both *Spartina foliosa* (unshaded, 167.0 ± 35.5 μg/g; shaded, 272.4 ± 50.2 μg/g; control, 266.6 ± 91.7 μg/g) and *Salicornia virginica* habitats (unshaded, 53.0 ± 11.6 μg/g; shaded, 54.3 ± 12.5 μg/g; control, 53.72 ± 12.5 μg/g) (Wilcoxon, *Spartina foliosa*, $\chi^2 = 1.40$, $P = 0.498$; *Salicornia virginica*, $\chi^2 = 0.05$, $P = 0.978$). After three and six months, the *Spartina foliosa* treatment plots had greater chlorophyll *a* concentrations than *Salicornia virginica* plots (ANOVA, three months, $F_{1,46} = 79.57$, $P < 0.0001$; ANOVA, six months, $F_{1,45} = 32.93$, $P < 0.0001$). The removal of plant cover did not alter chlorophyll *a* concentrations in any habitat or season (Table 1). All pigments that are indicative of a single functional group were tested for significant difference among treatments, but only significant pigment data are presented. The HPLC pigment data at three and six months suggest a shift from a cyanobacteria-dominated to a more diatom-dominated community in the unshaded treatments. Microalgal communities in the unshaded treatment plots exhibited increased fucoxanthin pigment concentrations at three months in the *Spartina foliosa* habitat and decreased zeaxanthin pigment concentrations at three months in the *Salicornia virginica* habitat (Fig. 2), indicating diatom and euglenoid abundance

TABLE 1. Extended.

Six months				
Unshaded	Shaded	Control	χ^2_2 or $F_{2,21}$	P
94.5 (2.8)	96.2 (3.7)	98.1 (1.1)	$\chi^2 = 0.79$	0.659
29.2 (4.7)	30.6 (6.1)	31.4 (2.3)	$\chi^2 = 2.45$	0.334
41.6 (1.8)	40.5 (1.1)	39.9 (0.5)	$F = 0.25$	0.882
18.4 (0.3)[a]	17.3 (0.3)[b]	16.8 (0.6)[b]	$F = 7.16$	0.028
0.58 (0.06)	0.57 (0.04)	0.55 (0.05)	$F = 0.08$	0.927
−84.50 (46.82)	−162.63 (39.22)	−151.04 (49.33)	$F = 0.87$	0.435
334.2 (91.5)	283.7 (95.3)	185.2 (33.8)	$\chi^2 = 1.58$	0.454
10.90 (2.11)[a]	7.53 (1.91)[ab]	4.55 (1.24)[b]	$\chi^2 = 2.08$	0.021
123.1 (17.5)	133.8 (23.5)	174.6 (21.2)	$\chi^2 = 2.95$	0.229
7.75 (0.53)	7.50 (0.7)	8.75 (0.80)	$\chi^2 = 1.06$	0.587
1139.61 (640.15)	11.31 (2.73)	26.75 (5.59)	$\chi^2 = 4.34$	0.114
0.58 (0.04)	0.53 (0.08)	0.48 (0.06)	$\chi^2 = 1.46$	0.482
		(no data)		
		(no data)		
59.1 (5.9)	49.3 (2.9)	44.8 (1.9)	$F = 5.24$	0.070
14.6 (2.1)	14.2 (0.7)	12.1 (0.3)	$F = 3.87$	0.144
0.52 (0.04)[a]	0.70 (0.02)[b]	0.69 (0.05)[b]	$\chi^2 = 9.78$	0.008
−14.2 (29.4)	−29.38 (35.86)	−22.06 (43.81)	$F = 0.13$	0.723
81.3 (19.3)	63.4 (16.4)	26.5 (11.3)	$F = 3.05$	0.069
4.56 (1.31)	5.39 (0.82)	5.24 (1.28)	$\chi^2 = 0.86$	0.651
46.3 (15.7)	65.4 (9.3)	77.9 (22.5)	$F = 0.91$	0.420
5.00 (1.15)	6.63 (0.68)	6.50 (0.82)	$F = 0.99$	0.386
7.10 (2.39)	16.92 (4.08)	279.25 (262.88)	$\chi^2 = 4.63$	0.099
0.64 (0.10)	0.66 (0.09)	0.46 (0.10)	$\chi^2 = 1.83$	0.400

increases and cyanobacteria abundance decreases relative to shaded and control treatment plots.

Macrofaunal community response

Macrofauna in the upper 0–2 cm exhibited similar responses across habitats and seasons so all results are summarized together below with details of season and habitat type given in Tables 1 and 2 and the Appendix. Relative to the shaded and control treatment plots, unshaded treatment plots exhibited a reduction in species richness (Wilcoxon, *Spartina foliosa*, unshaded $<$ shaded and control, $P = 0.0006$ after three months), decreased density of organisms (Wilcoxon, unshaded $<$ shaded and control, $P < 0.05$ at three months, both habitats), reduced biomass (Wilcoxon, *Spartina foliosa*, unshaded $<$ shaded and control, $P = 0.05$ after three months), and altered macrofaunal community composition based on count and biomass data (ANOSIM, unshaded $\neq$ shaded and control, $P < 0.05$ in all seasons and vegetation zones except *Salicornia virginica* after six months). Density, biomass, and richness changes in unshaded treatment plots involved a significant loss of amphipods (*Corophium* spp., species of Gammaridae), loss of tubificid oligochaetes, and an increase in insect larvae (Fig. 3, Table 2, Appendix).

We observed relationships between temperature, salinity, water content, and macrofaunal density and diversity when seasonal data were pooled within vegetation zone. Increases in temperature and salinity

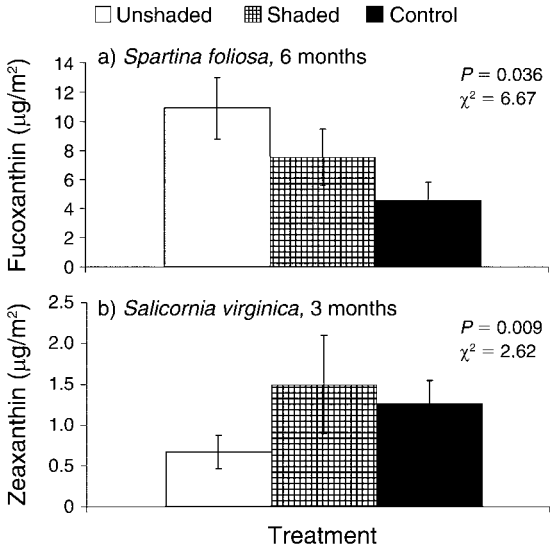

FIG. 2. Pigment abundance (mean ± SE) of (a) fucoxanthin in *Spartina foliosa* at six months and (b) zeaxanthin in *Salicornia virginica* at three months as determined through high-performance pigment chromatography: only significant ($P < 0.05$) results are shown. Letters indicate a posteriori differences among treatments ($P < 0.05$) in pigment abundance values. Graphs indicate increased importance of diatoms in unshaded treatment plots relative to control and shaded treatment plots.

TABLE 2. Comparison of responses (mean with SE in parentheses) to unshaded, shaded, and control treatments by the macrofaunal community (density, composition, and biomass) after three months (August) and six months (November) in (a) *Spartina foliosa* and (b) *Salicornia virginica* habitats.

Parameter	Three months				
	Unshaded	Shaded	Control	χ^2_2	*P*
a) *Spartina foliosa*					
Crustacea					
Density	0.8 (0.6)[a]	7.4 (3.5)[b]	4.8 (2.4)[b]	5.75	0.023
Biomass	3.00 (2.96)	5.53 (1.70)	10.92 (5.78)	4.59	0.101
Total density (%)	2.2 (1.7)	7.6 (3.3)	8.0 (4.2)	4.08	0.130
Gastropoda					
Density	0.1 (0.1)	0.5 (0.3)	0.5 (0.3)	1.31	0.519
Biomass	0.01 (0.01)	0.03 (0.02)	0.16 (0.10)	1.06	0.590
Total density (%)	0.7 (0.7)	0.6 (0.3)	0.5 (0.4)	0.78	0.677
Insecta					
Density	6.4 (1.8)	6.5 (1.5)	10.0 (4.3)	0.12	0.944
Biomass	3.25(0.04)	11.61 (0.03)	4.05 (0.02)	2.70	0.259
Total density (%)	22.8 (6.0)	6.2 (1.1)	17.7 (6.3)	3.55	0.170
Oligochaeta					
Density	17.9 (9.8)[a]	84.9 (30.3)[b]	35.0 (11.3)[b]	10.27	0.006
Biomass	0.34 (0.20)	1.64 (0.52)	1.10 (0.60)	5.59	0.061
Total density (%)	42.5 (12.2)	63.3 (7.2)	50.1 (8.4)	1.22	0.317
Polychaeta					
Density	2.6 (1.5)[a]	10.1 (2.6)[b]	7.5 (2.6)[b]	6.01	0.050
Biomass	1.50 (0.82)	3.12 (1.16)	5.86 (3.69)	2.43	0.297
Total density (%)	10.9 (5.6)	13.7 (4.8)	10.4 (2.1)	1.51	0.470
Other					
Density	7.5 (4.2)	10.9 (2.8)	9.0 (3.3)	1.59	0.452
Biomass	0.08 (0.0001)	0.01 (0.03)	0.07 (0.03)	1.64	0.440
Total density (%)	20.9 (10.4)	8.7 (2.1)	13.2 (4.8)	0.15	0.928
b) *Salicornia virginica*					
Crustacea					
Density	0.0 (−)[a]	1.9 (1.2)[b]	1.5 (0.6)[b]	5.75	0.023
Biomass	0.0 (−)[a]	4.92 (3.63)[b]	3.23 (2.09)[b]	7.48	0.024
Total density (%)	0.0 (−)[a]	3.2 (1.5)[b]	18.3 (12.1)[b]	4.08	0.020
Gastropoda					
Density	1.3 (0.9)	4.6 (3.3)	0.3 (0.2)	1.31	0.610
Biomass	0.13 (0.08)	2.50 (1.73)	0.021 (0.01)	1.18	0.553
Total density (%)	5.8 (3.6)	9.0 (5.2)	0.4 (0.3)	0.78	0.589
Insecta					
Density	4.8 (2.3)	2.6 (1.2)	3.9 (3.2)	0.12	0.331
Biomass	3.30 (1.15)	1.40 (0.89)	1.53 (0.94)	3.14	0.209
Total density (%)	30.2 (11.7)	4.2 (2.3)	5.8 (3.7)	3.55	0.044
Oligochaeta					
Density	14.9 (6.3)	61.6 (19.3)	46.6 (14.5)	10.27	0.101
Biomass	0.45 (0.53)	1.84 (1.65)	1.40 (1.23)	4.01	0.135
Total density (%)	40.8 (12.1)[a]	77.7 (10.5)[b]	69.6 (12.5)[b]	1.22	0.041
Polychaeta					
Density	0.4 (0.3)	1.0 (0.6)	0.8 (0.8)	6.01	0.380
Biomass	0.58 (0.56)	2.03 (2.00)	1.10 (1.10)	1.92	0.383
Total density (%)	0.7 (0.5)	1.3 (0.7)	0.6 (0.6)	1.51	0.367
Other					
Density	3.9 (3.6)	1.5 (0.8)	1.4 (0.7)	1.56	0.867
Biomass	0.04 (0.04)	0.09 (0.08)	0.01 (0.005)	1.54	0.462
Total density (%)	10.0 (7.0)	1.8 (0.7)	5.1 (4.1)	0.15	0.940

Notes: Density and biomass per core (18.1 cm^2) are reported. Superscripted letters indicate a posteriori differences among treatments ($P < 0.05$).

TABLE 2. Extended.

Six months				
Unshaded	Shaded	Control	χ^2_2	P
0.6 (0.3)[a]	7.3 (4.3)[ab]	24.5 (12.6)[b]	7.45	0.024
0.11 (0.09)[a]	0.11 (0.09)[ab]	2.16 (0.77)[b]	7.04	0.030
0.5 (0.2)[a]	5.1 (2.0)[ab]	13.7 (7.1)[b]	6.67	0.036
0.0	0.0	0.0	n/a	n/a
0.0	0.0	0.0	n/a	n/a
0.0	0.0	0.0	n/a	n/a
22.8 (8.1)[a]	3.6 (1.3)[b]	3.3 (1.0)[b]	8.65	0.013
132.80 (125.27)	3.43 (1.66)	5.79 (4.09)	2.43	0.296
29.5 (9.6)[a]	4.0 (1.2)[b]	1.9 (0.6)[b]	8.80	0.012
82.3 (20.8)	101.4 (22.2)	122.4 (24.7)	0.95	0.623
3.33 (1.3)	2.30 (0.48)	3.31 (0.92)	0.67	0.717
58.7 (9.3)	71.7 (7.4)	70.1 (10.6)	1.50	0.472
6.6 (3.4)	14.8 (7.2)	17.9 (5.0)	3.54	0.171
1003.01 (654)	3.36 (1.29)	9.36 (4.81)	3.26	0.196
4.7 (2.2)	10.7 (5.2)	10.3 (2.8)	3.26	0.196
6.1 (2.9)	5.6 (2.3)	5.8 (2.0)	0.14	0.931
0.06 (0.03)	0.06 (0.02)	0.05 (0.02)	0.34	0.846
6.0 (3.0)	8.4 (5.2)	3.3 (1.1)	0.02	0.992
1.3 (1.0)	1.3 (0.6)	1.8 (0.5)	3.13	0.209
1.40 (0.94)	2.07 (1.20)	5.52 (2.28)	5.29	0.071
3.7 (2.8)	2.4 (1.0)	4.3 (2.4)	2.13	0.345
3.3 (1.8)	3.3 (2.0)	2.6 (0.9)	0.74	0.691
1.86 (1.01)	0.61 (0.32)	1.97 (0.98)	1.63	0.443
7.8 (4.7)	6.8 (3.9)	5.8 (2.5)	0.43	0.807
15.4 (7.5)	22.4 (5.4)	4.8 (0.9)	4.40	0.111
2.19 (1.44)	7.12 (2.55)	16.29 (14.13)	3.44	0.179
27.8 (8.0)	35.1 (6.3)	10.9 (4.1)	3.98	0.137
24.5 (9.0)	30.9 (7.6)	59.4 (23.0)	1.46	0.482
0.89 (0.28)	0.89 (0.19)	1.66 (0.72)	0.14	0.934
44.1 (9.5)	43.7 (9.2)	64.5 (9.9)	1.68	0.432
0.5 (0.5)	3.4 (1.6)	2.4 (1.5)	2.74	0.254
0.72 (0.72)	6.21 (3.57)	253.71 (249.49)	2.29	0.318
0.4 (0.4)	5.6 (2.4)	5.0 (4.3)	3.07	0.216
0.3 (0.2)	1.0 (0.5)	7.0 (6.4)	1.91	0.385
0.003 (0.003)	0.01 (0.005)	0.07 (0.06)	1.75	0.416
0.9 (0.6)	1.7 (1.1)	9.4 (7.2)	1.70	0.427

for both vegetation zones and decreases in water content for *Salicornia virginica* were correlated with decreased macrofaunal density (Fig. 4a–d, f). Although these are significant regressions, the r^2 values for several of the relationships are very low with slopes close to zero (Fig. 4b, f, h, i). Increased temperature in *Salicornia virginica* habitat and increased salinity for both vegetation zones were correlated with decreased macrofauna species richness (Fig. 4g–i, j). A positive correlation was found between chl *a* and macrofauna density in the *Salicornia virginica* habitat after three months ($r^2 = 0.167$, $P = 0.047$).

Stable isotope analysis

Among the three primary, nonvascular plant food sources available to macrofauna (sediment organic matter [SOM], benthic microalgae, and the macroalgae, *Ulva* spp.), only benthic microalgae demonstrated significant change in $\delta^{13}C$ with experimental treatment (Table 3). There was a 2–3‰ increase in $\delta^{13}C$ of microalgae in the unshaded and shaded treatment plots after 11 months ($F_{2,21} = 2.83$, $P = 0.082$; Fig. 5a). Averaged signatures of all macrofauna within shaded and unshaded treatment plots mimicked the shift in microalgae signatures, with significantly enriched $\delta^{13}C$ values compared to the control treatment plot ($F_{2,84} = 7.79$, $P = 0.0008$; Fig. 5b). Among invertebrate groups, $\delta^{13}C$ signatures of oligochaetes and insects in the shaded and unshaded treatment plots also mimicked this $\delta^{13}C$ enrichment (oligochaetes, $F_{2,11} = 4.02$, $P = 0.049$; insects, $\chi^2 = 7.79$, $P = 0.012$), indicating a probable reliance on microalgae as a primary food source. Crustaceans and polychaetes exhibited no shift in $\delta^{13}C$ signatures among treatments (crustaceans, $F_{2,3} = 0.15$, $P = 0.869$; polychaetes, $F_{2,2} = 1.48$, $P = 0.403$; Fig. 5c). Most invertebrate species exhibiting shifts in $\delta^{13}C$ signatures were those with significant changes in overall density and biomass in the unshaded treatment plots, suggesting that microalgae influenced abundance responses. In the unshaded treatment plots, organisms that increased in abundance (insects) were more enriched in $\delta^{13}C$ (resembling the microalgal signatures) compared to organisms that decreased in abundance (crustaceans) or showed no shift (polychaetes, molluscs; Fig. 5d). Oligochaetes were the exception with declines in density but clear $\delta^{13}C$ enrichment. Finally, comparison of the taxa by feeding group revealed differentiation of $\delta^{13}C$ signatures in the unshaded treatment plots; microalgal grazers had more enriched signatures relative to the detritus and plant grazers ($F_{3,8} = 8.24$, $P = 0.008$; Fig. 5e).

DISCUSSION

Our manipulative experiments provide direct evidence that plant–animal interactions mediated by soil and algal properties are important structuring forces in southern California salt marshes. We show that plant cover influences the microhabitat of the sediment by controlling the amount of light reaching the sediment surface and that these changes in key abiotic environmental factors appear to induce changes in the sediment biotic community. Such changes can occur as quickly as three months after plant cover loss.

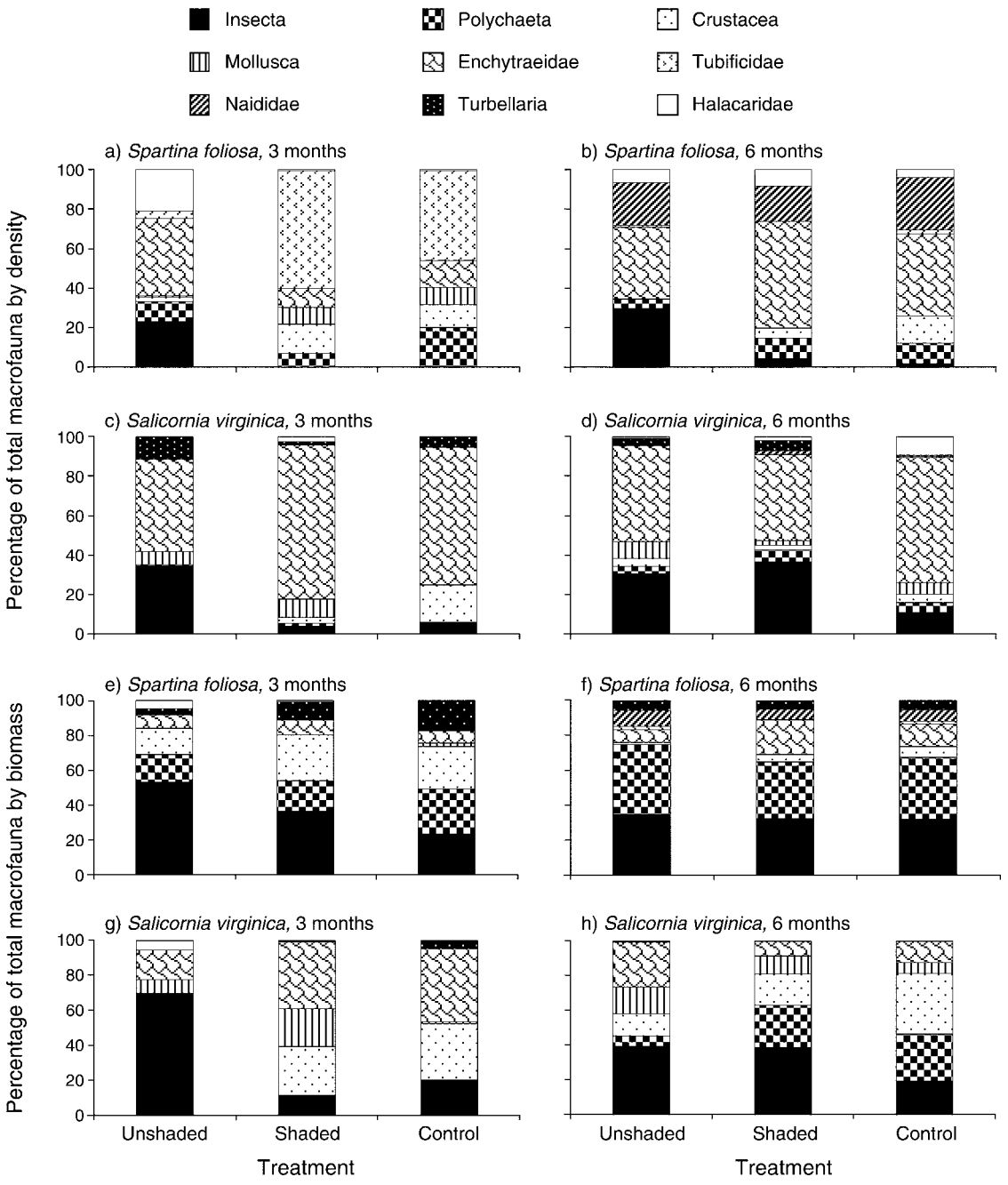

FIG. 3. Macrofaunal community composition (a–d) based on counts or (e–h) based on biomass in three treatments three and six months after experiment initiation: unshaded (absence of plant cover and structure), shaded (absence of plant structure), and control (plants intact) in *Spartina foliosa* and *Salicornia virginica* treatment plots.

Note: Enchytraeidae, Tubificidae, and Naididae are Oligochaeta.

In the absence of shading, removal of plant cover induced higher soil temperature, increased porewater salinities, and lower water content, most likely due to the increased sun exposure and subsequent evaporation. These changes are analogous to conditions seen in unvegetated patches or plant removal experiments in New England salt marshes (Bertness 1991*b*) and to naturally occurring conditions observed in bare patches in Mission Bay (Janousek 2005). However, none of the studies mentioned above considered the effect of these alterations on the associated macrofaunal communities. In this study, these significant physical alterations were correlated with changes in macrofaunal density, biomass, and species richness.

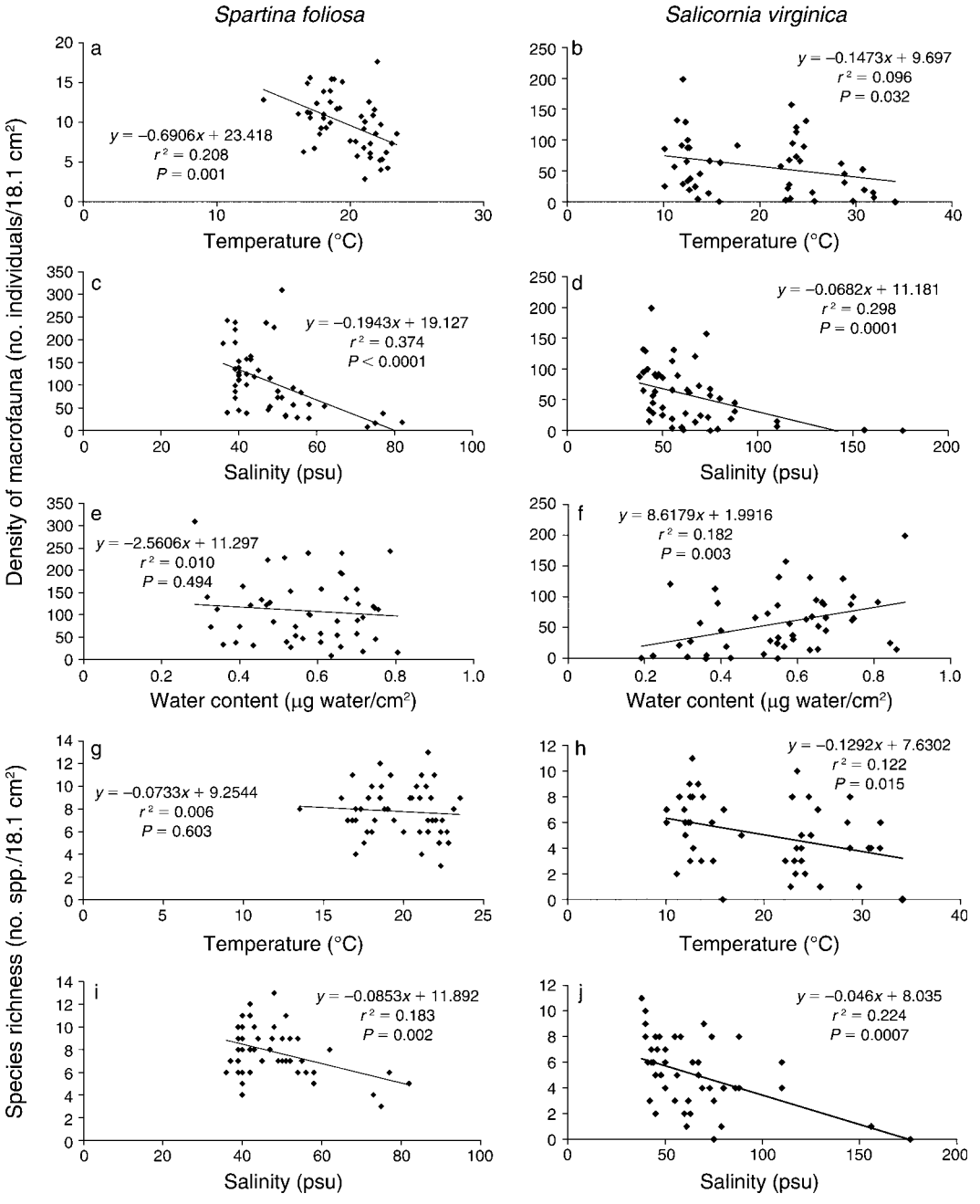

FIG. 4. Regressions showing relationships between macrofauna density and (a, b) temperature, (c, d) salinity, and (e, f) water content; and between macrofaunal species richness and (g, h) temperature and (i, j) salinity. Data were pooled across treatments and seasons.

Algal mats beneath the marsh plants experienced community composition shifts (increased diatom abundance or decreased cyanobacteria abundance) in the absence of shade. While these changes are complex, other experiments in riverine and forested areas have demonstrated similar shifts away from diatom-dominated communities under low light intensity, with green algal communities dominating under higher light intensities (Lamberti et al. 1989, Franken et al. 2005). In addition to the dramatic shifts in the physical environment, the changes in the microalgae, which are a crucial food source for marsh consumers (Kwak and Zedler 1997, Moseman et al. 2004), represent a second important potential mechanism by which plant cover affects macrofaunal community dynamics.

The plant-induced changes in environmental conditions and in microalgal communities were correlated with changes in the macrofauna community composi-

TABLE 3. The $\delta^{13}C$ signatures of macrofauna (mean with SE in parentheses) with abundance changes indicated for unshaded treatment plots relative to control plots after three and six months in *Salicornia virginica* habitat.

Species (class or order)	Unshaded $\delta^{13}C$	Shaded $\delta^{13}C$	Control $\delta^{13}C$	Feeding group	Abundance changes†
Enchytraeidae (Oligochaeta)	−19.53	−22.71 (0.045)	−23.38 (0.33)	detritivore[1]	decrease
Tubificoides browniae (Oligochaeta)	−21.89 (1.77)	−21.49 (0.34)	−23.75 (0.54)	detritivore[2]	decrease
Polydora nuchalis (Polychaeta)	−19.7	−20.23	−22.78	detritivore[3]	no change
Traskorchestia traskiana (Amphipoda)	−24.75	−21.39 (0.35)	−22.05 (0.15)	plant feeder[3]	decrease
Dolichopodidae larvae (Insecta)	−18.57 (0.29)	−21.66 (1.74)	−20.38 (0.81)	predatory[4]	increase
Staphylinidae adult (Insecta)	−21.73 (0.25)	n/a	−22.89 (0.74)	predatory[5]	no change
Ceratapogonidae larvae (Insecta)	−18.98 (0.73)	−20.25 (0.65)	−23.72 (0.85)	microalgal feeder[6]	increase
Muscidae larvae (Insecta)	−17.22	−19.77 (0.86)	−20.03 (3.35)	microalgal feeder[6]	increase
Cincindelidae adult (Insecta)	−18.04	−18.45 (0.62)	n/a	microalgal feeder[6]	no change
Staphylinidae larvae (Insecta)	−16.83 (0.22)	−21.10 (1.67)	−21.43 (1.25)	microalgal feeder[6]	no change
Stratiomyidae larvae (Insecta)	n/a	−25.45	−20.22 (0.94)	microalgal feeder[6]	no change
Ephydridae larvae (Insecta)	−18.95 (1.04)	−19.21 (0.82)	−18.40 (1.76)	microalgal feeder[6]	no change
Assiminea californica (Gastropoda)	−19.09 (1.66)	n/a	−19.73 (0.11)	microalgal feeder[6]	no change

Notes: When no SE is reported, $n = 1$. Superscript numbers indicate references: 1, Dash and Cragg (1972); 2, Wavre and Brinkhurst (1971); 3, Levin and Currin (2005); 4, Bickel and Dyte (1989); 5, D. Holway (*personal communication*); 6, Moseman et al. (2004). The abbreviation "n/a" indicates "not available."

† For a table of macrofaunal densities in treatment and control plots, see the Appendix.

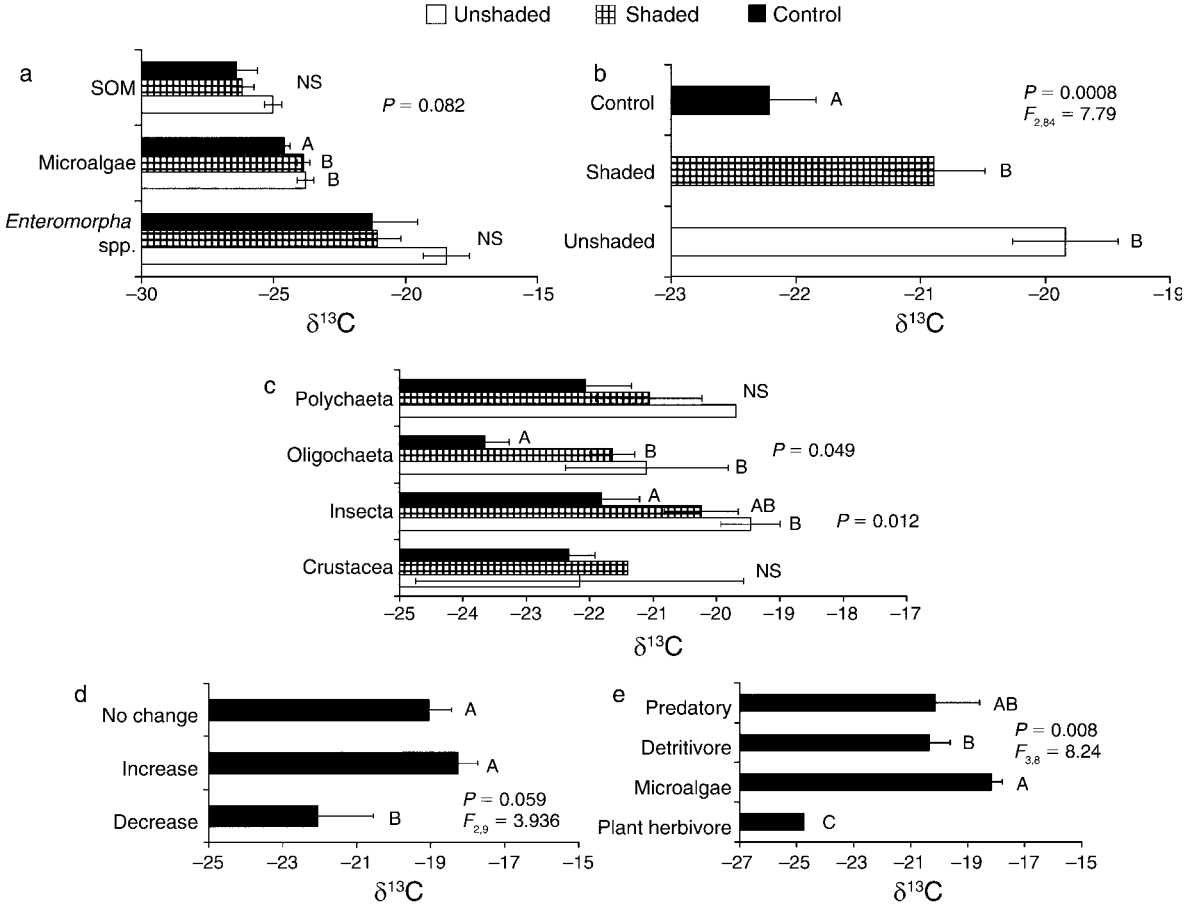

FIG. 5. Stable isotope signatures ($\delta^{13}C$; mean ± SE) of sediment, microalgae, macroalgae, and selected macrofauna in *Salicornia virginica* habitat 11 months after treatment initiation. Natural abundance $\delta^{13}C$ values are given for (a) macrofaunal food sources (SOM, sediment organic matter), (b) total combined macrofauna, (c) major macrofaunal taxa, (d) macrofauna grouped by response to unshaded treatment, and (e) macrofauna grouped by feeding mode. Uppercase letters to the right of error bars indicate significant ($P < 0.05$) a posteriori differences in $\delta^{13}C$ values among treatments.

tion, richness, and diversity (Fig. 4). In both seasons, the macrofauna in unshaded treatments resembled communities seen in newly restored *Salicornia virginica* (de Szalay et al. 1996) and *Spartina foliosa* (Levin and Talley 2002) salt marshes in southern California; as plant cover increases, oligochaetes, crustaceans, and polychaetes increase, and insects decrease in representation (Talley and Levin 1999, Levin and Talley 2002, Moseman et al. 2004). Similar compositional shifts in the macrofaunal community were observed in our experiments conducted in both grass- and succulent-dominated marsh habitats, reinforcing the generic role of plant cover in ameliorating harsh physical conditions in a manner essential to the development and maintenance of a natural sediment ecosystem (Bertness and Hacker 1994).

In our experiment, redox, belowground plant structure, and detrital biomass did not differ among treatments. The fact that redox values did not become more reduced in the plant removal treatments indicated little degradation of remaining belowground plant material during the experiment. However, higher photosynthetic oxygen inputs in the unshaded treatments may have masked some degradation. In restored, invaded, or degraded systems in which plant community shifts involve a dramatic canopy loss or conversion to vegetated area, belowground root biomass and detritus will also change. Such alterations have the potential to drive large trophic shifts through alterations to the detritivore food supply (Levin et al. 2006) and space limitation (Brusati and Grozholz 2006).

Our results provide a mechanistic understanding of the plant-induced shifts in abiotic and biotic factors and also inform us about controlling factors in this particular marsh environment. Changes in physical properties due to changing light regimes appear to mediate changes in the sediment biotic community. Several other plant effects that may be important in structuring the benthic ecosystem were not studied, such as the effects of plants on detrital food supply, on predators, or on flow regime (Leonard and Luther 1995, Nomann and Pennings 1998, Neira et al. 2006). However, the Mission Bay marsh system has low hydrodynamic energy, potentially reducing the importance of plant structure effects on flow and elevating the importance of light and evaporation as structuring agents.

Stable isotopic techniques have recently been used to assess trophic succession in created and invaded salt marshes (Currin et al. 2003, Moseman et al. 2004, Levin et al. 2006). The enriched $\delta^{13}C$ isotope values seen in the unshaded and shaded treatment plots relative to the control plots have several possible explanations. Typically, heavier $\delta^{13}C$ values in microalgae are indicative of faster photosynthetic rates (increased light) accompanied by carbon limitation, increased cyanobacterial content, less utilization of remineralized plant matter, higher salinity, or less nitrogen fixation (Beardall et al. 1998, Raven et al. 2002). In this experiment, unshaded treatment plots had increased salinity and algal community shifts. However, because the $\delta^{13}C$ enrichment was observed in the shaded and unshaded treatment plots (Fig. 5), it is more likely that the enrichment is due to the influence of aboveground plant structure rather than light.

The isotope data provide two potential explanations for plant-induced shifts in macrofaunal abundances. In the absence of aboveground plant structure and shade (unshaded treatments), algal mat samples shifted to more diatom-dominated communities and fresh detrital food sources were reduced by removal of aboveground biomass. Detrital grazers such as amphipods and oligochaetes decreased overall. Insect larvae, typically microalgal grazers, increased in abundance and exhibited an isotopic shift similar to that of the microalgae (Fig. 5). These results support a major role for microalgae in structuring animal response to changing plant cover. These plant canopy-induced changes in microalgae and macrofauna can have effects that extend to higher trophic levels. For example, structural differences in macrofaunal communities between natural and created systems have been shown to translate to higher trophic levels by altering foraging patterns of fish (Moy and Levin 1991).

Much research has been focused on the role of interspecific interactions, facilitation, and subsequent zonation among vascular plant species within the salt marsh environment (Bertness 1991*a*, *b*, 1992, Pennings et al. 2005). Equally important to consider is plant facilitation and zonation of the sediment system for sessile or limited-mobility invertebrates. Many of the early studies mentioned above that revealed plant effects on edaphic factors such as substrate redox potential and salinity were conducted within New England salt marshes. Studies in Brazilian marshes have identified changes in macrobenthos associated with plant biomass, detrital input, grain size, predation pressure, sediment organic matter, and freshwater input (Lana and Guiss 1992, Pagliosa and Lana 2005). In southern California where there are significantly higher salinities and less predictable redox than in these other systems due to a mediterranean climate, our studies emphasized the importance of the light reduction function of plants. Halophytes generally occur at higher tidal elevations in the southern California marshes compared to Atlantic marshes. Although the exact mechanisms behind observed macrobenthos changes may differ, comparison with studies in the high marshes/salt pans of Georgia and Argentina reveals complementary mechanisms behind changes in plant–animal interactions. Studies by Nomann and Pennings (1998) and Bortolus et al. (2002) demonstrated the ability of plants to buffer harsh physical conditions (high temperature, soil hardness, organism heat stress, and dehydration) via shading and provision of predation refugia. We predict that these salt marsh plant effects on the benthic ecosystem should be especially strong at lower latitudes, higher temperatures, and in arid regions, such as southern California.

Our experiments demonstrate that the light reduction function provided by the vascular plant canopy is crucial to maintaining the natural biotic community of southern California salt marsh sediments. Although the connection has been made between light intensity and associated consumers (Nomann and Pennings 1998, Franken et al. 2005), this research isolates the strong relationship between plant-mediated light regime and sediment-dwelling organisms in coastal wetlands. These results highlight the probability that any anthropogenic change influencing plant density, cover, height, or growing season will alter salt marsh algal and animal assemblages via light regulation.

Acknowledgments

We thank field assistants and laboratory helpers, especially P. McMillan, C. Neira, G. Mendoza, J. Gonzalez, J. Fodrie, J. Leddick, G. Checkley, L. Pierotti, N. Ben-Aderat, L. Guzman, and J. Pompa. Special thanks go to Chris Janousek for his assistance in developing methods for HPLC analysis, to Maria Vernet for providing facilities for pigment analysis, and to David Harris (Stable Isotope Facility, UC Davis) for stable isotope analysis. Thanks also to M. Newman, C. Currin, E. Sala, J. Leichter, D. Holway, P. Dayton, and three anonymous reviewers for helpful comments. This publication was supported by the National Sea Grant College Program of the U.S. Department of Commerce's NOAA Grants R/CZ 173 and R/CZ 190C through the CA Sea Grant College Program and by the California State Resources Agency. The views expressed herein do not necessarily reflect the views of any of those organizations. This material is also based upon work supported by the California Department of Boating and Waterways, the UC Marine Sciences Council CEQI (UCMARINE 32114), and the National Science Foundation (DEB 0333444). Access to the study site was granted by the UC Natural Reserve System.

Literature Cited

Beardall, J., A. Johnston, and J. Raven. 1998. Environmental regulation of CO_2-concentrating mechanisms in microalgae. Canadian Journal of Botany 76:1010–1017.

Bertness, M. D. 1988. Peat accumulation and success of marsh plants. Ecology 69:703–713.

Bertness, M. D. 1991*a*. Interspecific interactions among high marsh perennials in a New England salt marsh. Ecology 72: 125–137.

Bertness, M. D. 1991*b*. Zonation of *Spartina patens* and *Spartina alterniflora* in New England salt marsh. Ecology 72:138–148.

Bertness, M. D. 1992. The ecology of a New England salt marsh. American Scientist 80:260–268.

Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191–193.

Bertness, M. D., and S. D. Hacker. 1994. Physical stress and positive associations among marsh plants. American Naturalist 144:363–372.

Bickel, D. J., and C. E. Dyte. 1989. Family Dolichopodidae. Pages 398–418 *in* E. J. Brill, editor. A catalog of Australasian and Oceanian Diptera. Bishop Museum Press, Leiden, The Netherlands.

Bortolus, A., E. Schwindt, and O. Iribane. 2002. Positive plant–animal interactions in the high marsh of an Argentinean coastal lagoon. Ecology 83:733–742.

Bruno, J. F., and M. D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. Pages 201–221 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer, Sunderland, Massachusetts, USA.

Brusati, E. D., and E. D. Grosholz. 2006. Native and introduced ecosystem engineers produce contrasting effects on estuarine infaunal communities. Biological Invasions 8: 683–695.

Buchanan, J. B. 1984. Methods for the study of marine benthos. IBP Hand Book 16:41–65.

Cariou-LeGall, V., and G. F. Blanchard. 1995. Monthly HPLC measurement of pigment concentration from an intertidal muddy sediment of Marennes-Oleron Bay, France. Marine Ecology Progress Series 121:171–179.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143.

Clarke, K. R., and R. M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council,UK, and Plymouth Marine Laboratory, Plymouth, UK.

Clements, F. E. 1991. Nature and structure of the climax. Pages 252–284 *in* L. A. Real and J. H. Brown, editors. The foundations of ecology: classic papers with commentaries. University of Chicago Press, Chicago, Illinois, USA.

Currin, C. A., S. Y. Newell, and H. W. Paerl. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. Marine Ecology Progress Series 121: 99–116.

Currin, C., S. Wainright, K. Able, M. Weinstein, and C. Fuller. 2003. Determination of food web support and trophic position of the mummichog, *Fundulus heteroclitus*, in New Jersey smooth cordgrass (*Spartina alterniflora*), common reed (*Phragmites australis*) and restored salt marshes. Estuaries 26:495–510.

Dash, M. C., and J. B. Cragg. 1972. Selection of microfungi by Enchytraidae (Oilgochaeta) and other members of the soil fauna. Pedobiologia 12:282–286.

de Szalay, F. A., D. P. Batzer, and V. H. Resh. 1996. Mesocosm and macrocosm experiments to examine effects of mowing emergent vegetation on wetland invertebrates. Environmental Entomology 25:303–309.

Franken, R., B. Waluto, E. Peeters, J. Gardeniers, J. Beijer, and M. Scheffer. 2005. Growth of shredders on leaf litter biofilms: the effect of light intensity. Freshwater Biology 50:459–466.

Gallagher, J. L. 1971. Algal productivity and some aspects of the ecological physiology of the edaphic communities of Canary creek tidal marsh. Dissertation. University of Delaware, Newark, Delaware, USA.

Gambrell, R. P., and W. H. Patrick. 1978. Chemical and microbiological properties of anaerobic soils and sediments. Pages 375–423 *in* D. D. Hook and R. M. M. Crawford, editors. Plant life in anaerobic environments. Ann Arbor Scientific, Ann Arbor, Michigan, USA.

Giere, O., A. Eleftheriou, and D. J. Murison. 1988. Abiotic factors. Pages 61–78 *in* R. P. Higgens and H. Thiel, editors. Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, D.C., USA.

Gleason, M. L., D. A. Elmer, N. C. Pien, and J. S. Fisher. 1979. Effects of stem density upon sediment retention by salt marsh cordgrass. Estuaries 2:271–273.

Hooper, D. U., et al. 2000. Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. BioScience 50:1049–1061.

Janousek, C. N. 2005. Functional composition and diversity in assemblages of marine wetland microalgae and photosynthetic bacteria: succession, spatial variation, and influence on productivity. Dissertation. University of California, San Diego, California, USA.

Kwak, T. J., and J. B. Zedler. 1997. Food web analysis of southern California coastal wetlands using multiple stable isotopes. Oecologia 110:262–277.

Lamberti, G., S. Gregory, L. Ashkenas, A. Steinman, and C. McIntire. 1989. Productive capacity of periphyton as a determinant of plant–herbivore interactions in streams. Ecology 70:1840–1856.

Lana, P. C., and C. Guiss. 1992. Macrofauna–plant–biomass interactions in a euhaline salt marsh in Paranagua Bay (SE Brazil). Marine Ecology Progress Series 80:57–64.

Leonard, L. A., and M. E. Luther. 1995. Flow dynamics in tidal marsh canopies. Limnology and Oceanography 40:1474–1484.

Levin, L. A., and C. A. Currin. 2005. Recovery of trophic function in restored Pacific wetlands. California Sea Grant College Program Research Completion Report. Paper Coastal 04-04. University of California, San Diego, California, USA.

Levin, L. A., C. Neira, and E. D. Grosholz. 2006. Invasive cordgrass modifies wetland trophic function. Ecology 87: 419–432.

Levin, L. A., and T. S. Talley. 2000. Influences of vegetation and abiotic environmental factors on salt marsh benthos. Pages 661–708 *in* M. P. Weinstein and D. A. Kreeger, editors. Concepts and controversies in tidal marsh ecology. Kluwer, Amsterdam, The Netherlands.

Levin, L. A., and T. S. Talley. 2002. Natural and manipulated sources of heterogeneity controlling early faunal development of a salt marsh. Ecological Applications 12:1785–1802.

Levin, L. A., T. S. Talley, and J. Hewitt. 1998. Macrobenthos of *Spartina foliosa* (Pacific cordgrass) salt marshes in Southern California: community structure and comparison to a Pacific mudflat and a *Spartina alterniflora* (Atlantic smooth cordgrass) marsh. Estuaries 21:129–144.

Lovell, C. R. 2002. Plant–microbe interactions in the marine environment. Pages 2539–2554 *in* G. Bitton, editor. Encyclopedia of environmental microbiology. Wiley, New York, New York, USA.

Lüning, K. 1980. Critical levels of light and temperature regulating the gametogenesis of three *Laminaria* species (Phaeophyceae). Journal of Phycology 16:1–15.

Moseman, S. M., L. A. Levin, C. A. Currin, and C. Forder. 2004. Colonization, succession, and nutrition of macrobenthic assemblages in a restored wetland at Tijuana Estuary, California. Estuarine Coastal and Shelf Science 60: 755–770.

Moy, L. D., and L. A. Levin. 1991. Are *Spartina* marshes a replaceable resource? A functional approach to evaluation of marsh creation efforts. Estuaries 14:1–16.

Neira, C., E. D. Grosholz, L. A. Levin, and R. Blake. 2006. Mechanisms generating modification of benthos following tidal flat invasion by a *Spartina hybrid*. Ecological Applications 16:1391–1404.

Neira, C., L. A. Levin, and E. D. Grosholz. 2005. Benthic macrofaunal communities of three sites in San Francisco Bay invaded by hybrid *Spartina*, with comparison to uninvaded habitats. Marine Ecology Progress Series 292:111–126.

Nomann, B., and S. Pennings. 1998. Fiddler crab-vegetation interactions in hypersaline habitats. Journal of Experimental Marine Biology and Ecology 225:53–68.

Pagliosa, P. R., and P. C. Lana. 2005. Impact of plant cover removal on macrobenthic community structure of a subtidal salt marsh. Bulletin of Marine Science 77:1–17.

Pennings, S. C., M. B. Grant, and M. D. Bertness. 2005. Plant zonation in low-latitude salt marshes: disentangling roles of flooding, salinity, and competition. Journal of Ecology 93: 159–167.

Peterson, B. J., R. E. Howarth, and R. H. Garritt. 1985. Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. Science 227:1361–1363.

Plante-Cuny, M. R. 1973. Reserches sur la production primaire bentique en milieu marin tropical. I. Variations de la production primaire et des teneurs en pigments photosynthetiques sur quelques fonds sableux: valeur des résultats obtenus par lab méthode due ^{14}C. Cahiers Office de la Recherche Scientifique et Technique de Outre-Mer, Serie Océanogra 11:317–348.

Raven, J., A. Johnston, J. Kübler, R. Korb, S. McInroy, L. Handley, C. Scrimgeour, M. Vanderklift, S. Fredricksen, and K. Dunton. 2002. Seaweeds in cold seas: evolution and carbon acquisition. Annals of Botany 90:525–536.

Seliskar, D. M., J. L. Gallagher, D. M. Burdick, and L. A. Mutz. 2002. The regulation of ecosystem functions by ecotypic variation in the dominant plant: a *Spartina alterniflora* salt-marsh case study. Journal of Ecology 90:1–11.

Smith, C. R., M. C. Austen, G. Boucher, C. Heip, P. A. Hutchings, G. M. King, I. Koike, J. D. Lambshead, and P. R. Snelgrove. 2000. Global change and biodiversity linkages across the sediment–water interface. BioScience 50: 1108–1120.

Snelgrove, P. V. R., M. C. Austen, G. Boucher, C. Heip, P. A. Hutchings, G. M. King, I. Koike, J. D. Lambshead, and C. R. Smith. 2000. Linking biodiversity above and below the marine sediment–water interface. BioScience 50:1076–1088.

Swift, M. J., and J. M. Anderson. 1993. Biodiversity and ecosystem function in agricultural systems. Pages 15–43 *in* E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer, Berlin, Germany.

Talley, T. S., and L. A. Levin. 1999. Macrofaunal succession and community structure in *Salicornia* marshes of southern California. Estuarine Coastal and Shelf Science 49:713–741.

Warren, R. S., and W. A. Neiring. 1993. Vegetation change on a northeast tidal marsh: interaction of sea-level rise and marsh accretion. Ecology 74:96–103.

Wavre, M., and B. O. Brinkhurst. 1971. Interactions between some tubificid oligochaetes and bacteria found in the sediments of Toronto Harbor. Journal of Fisheries Research Board Canada 28:335–341.

Zedler, J. B., C. S. Nordby, and B. E. Kus. 1992. The ecology of Tijuana Estuary, a National Research Reserve. National Oceanic and Atmospheric Administration, Coastal Resource Management, Washington, D.C., USA.

APPENDIX

A table showing macrofaunal density at two sampling points and in two habitats (*Ecological Archives* E088-056-A1).