

# Influence of invasive *Spartina* growth stages on associated macrofaunal communities

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**Abstract** In coastal wetlands, invasive plants often act as ecosystem engineers altering flow, light and sediments which, in turn, can affect benthic animal communities. However, the degree of influence of the engineer will vary significantly as it grows, matures and senesces, and surprisingly little is known about how the influence of an ecosystem engineer varies with ontogeny. We address this issue on the tidal flats of San Francisco Bay where hybrid *Spartina* (*foliosa* × *alterniflora*) invaded 30 years ago. The invasion has altered the physico-chemical properties of the sediment habitat, which we predicted should cause changes in macrofaunal community structure and function. Through mensurative and manipulative approaches we investigated the influence of different growth stages of hybrid *Spartina* on macrobenthos and the underlying mechanisms. Cross-elevation sampling transects were established covering 5 zones (or stages) of the invasion, running from the tidal

flat (pre-invasion) to an unvegetated dieback zone. Additionally, we experimentally removed aboveground plant structure in the mature (inner) marsh to mimic the 'unvegetated areas'. Our results revealed four distinct faunal assemblages, which reflected *Spartina*-induced changes in the corresponding habitat properties along an elevation gradient: a pre-invaded tidal flat, a leading edge of immature invasion, a center of mature invasion, and a senescing dieback area. These stages of hybrid *Spartina* invasion were accompanied by a substantial reduction in macrofaunal species richness and an increase in dominance, as well as a strong shift in feeding modes, from surface microalgal feeders to subsurface detritus/*Spartina* feeders (mainly tubificid oligochaetes and capitellid polychaetes). Knowledge of the varying influence of plant invaders on the sediment ecosystem during different phases of invasion is critical for management of coastal wetlands.

**Keywords** *Spartina* dieback · Macrofauna · Plant invasion · Plant–sediment–animal interaction · Wetlands · San Francisco Bay

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## Introduction

Ecosystem engineers are species able to create, maintain, modify, or destroy their habitat,

thereby strongly influencing community composition and structure (Jones et al. 1994). Examples of ecosystem engineers have been reported for both plants and animals within a broad spectrum of ecosystems, including coral reefs and estuaries (Bruno and Bertness 2001), woodlands (Vitousek et al. 1987), grasslands (Vivrette et al. 1977), and freshwater systems (Steenkamp and Chown 1996). In wetlands, when an invasive plant that is an ecosystem engineer colonizes a habitat, it can modify the community structure and the entire ecosystem by altering nutrient cycling, productivity, hydrology, particle flux, and habitat availability (Talley and Levin 2001; Crooks 2002). Rarely have the influences of an invasive ecosystem engineer been documented throughout the course of invasion as the invading engineer grows, matures and senesces. Understanding which physico-chemical properties are associated with each phase of plant invasion is essential for understanding invasion-induced changes in macrofaunal communities and associated marsh functions.

*Spartina* (cordgrass) is readily identified as a key ecosystem engineer within salt marshes (Pennings and Bertness 2001; Brusati and Grosholz 2006), and many species are known to be highly invasive (Daehler and Strong 1996). Comparisons of animal communities in *Spartina*-vegetated sediments versus unvegetated tidal flats have yielded disparate trends by marsh. In some marshes dominated by *S. alterniflora* (Zipperer 1996; O'Connell 2002), *S. anglica* (Jackson 1985), *S. foliosa* (Levin et al. 1998), and a hybrid of *Spartina alterniflora* × *S. foliosa* (hereafter referred to as “hybrid *Spartina*”) (Neira et al. 2005), macrobenthic communities exhibit lower densities and fewer species relative to adjacent tidal flats. These differ from existing paradigms that predict positive vegetation effects on macrofaunal abundance and diversity (e.g., Netto and Lana 1999; Hedge and Kriwoken 2000; Pennings and Bertness 2001; Brusati and Grosholz 2006).

*Spartina* stands are not static but rather appear to undergo different stages and dieback, particularly associated with invasion. Dieback of invasive hybrid *Spartina*, *S. anglica* and *S. townsendii* was noted as early as the mid-1920s in Britain (Gray et al. 1991 and references therein). Dieback zones

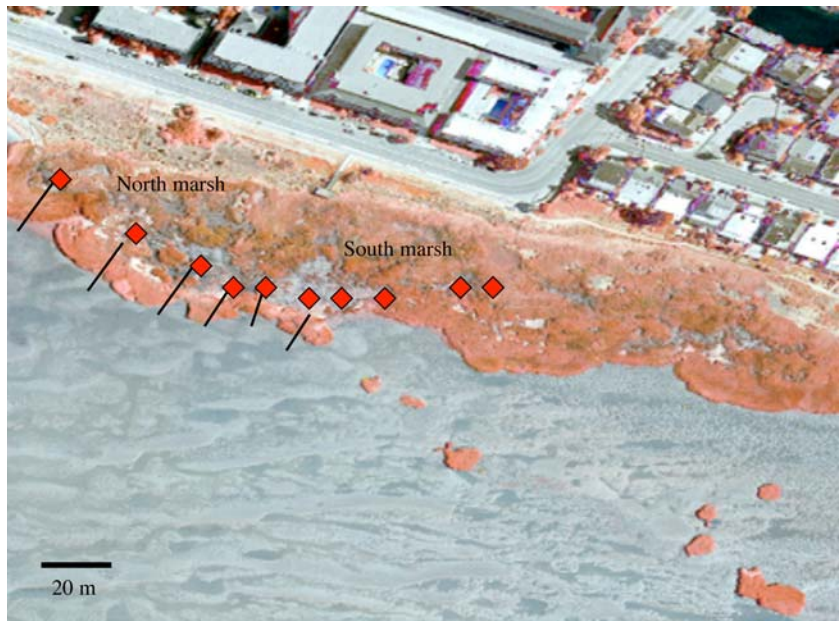
have also been observed in mature *S. alterniflora* meadows in North Carolina (Linthurst and Seneca 1980), Louisiana (Webb et al. 1995; McKee et al. 2004), New York (Hartig et al. 2002), and recently in Georgia, New England, and Virginia (GCRC 2004). Recent studies provide evidence that the interplay between physicochemical stressors and trophic interactions have an important role in dieback of coastal salt marshes (Silliman and Bertness 2002; Silliman et al. 2005).

At our site, a 30-year old tidal flat invasion by hybrid *Spartina* has generated a “continuous meadow” covering ~10 ha punctuated by “dieback areas” of different sizes that are scattered within the meadow (Fig. 1). These dieback areas reflect senescence of hybrid *Spartina* as revealed by the presence of standing dead culms (about 2–10 cm) (Neira pers. obs., Fig. 2A). Assessment of aerial photographs taken in August 2002 indicates that dieback areas devoid of live plants covered about 4% of the meadow at that time.

We hypothesize that hybrid *Spartina* undergoes a sequence of stages following invasion that generates sediment modifications and that infaunal communities should respond accordingly. Within the meadow, the invading edge contains a lower root and shoot density of plants. Plants within the central meadow attain more below ground biomass with greater stem heights and densities, which decrease flow energy by increasing frictional effects. In later, senescing stages (at the upper edge of the meadow), plant densities decline again, leaving high amounts of decaying root material, mixed with trapped sediments and organic matter. We do not know how dieback areas are formed at our study site in Elsie Roemer. Our in situ observations suggest that increasing buildup of H<sub>2</sub>S, reaching levels beyond the resistance threshold of healthy plants, is the most probable cause. Among the contributing factors are increasing deposition of fine-grained particles (including organic matter), decomposition and smothering plants as the result of wrack from both senesced plants and macroalgae (Neira pers. obs., Fig. 2B). These can create dieback areas rich in mud and organic matter at higher elevations.

This study examines the hypotheses that (1) changes in the environmental conditions associated with a spatial (from unvegetated tidal flat to

**Fig. 1** Color infrared aerial photograph (courtesy of P. Rosso) of the study location in Elsie Roemer, San Francisco Bay, California, USA. Dieback areas are seen distributed within the 'continuous meadow' of invasive hybrid *Spartina*. Lines represent the sampling transects from uninvaded tidal flat to dieback areas in Experiment 3. Diamonds represent dieback sites sampled in Experiment 1



dieback areas) and temporal (from early to late invasion) gradient of hybrid *Spartina* invasion will be mirrored in changes in abundance and diversity of benthic macrofaunal communities, (2) the geochemical environment will shift towards one that is highly sulfidic, and (3) the most sulfidic areas, within areas with the oldest *Spartina* zone, and in dieback areas, will be dominated by a few infaunal species highly adapted to sulfidic sediments.

## Materials and methods

### Study site

The study was conducted along the shoreline within the Elsie Roemer Bird Sanctuary (37° 45'35"N; 122° 28'48"W) in San Francisco Bay adjacent to Alameda, California, USA. Hybrid *Spartina alterniflora* (*S. alterniflora* × *S. foliosa*) invaded this area within the last 30 years (Ayres et al. 2003); native *S. foliosa* has not been present in this area since 1992 (Ayres pers. comm.). Tidal amplitude during spring tides is typically 2.5 m with an annual maximum of nearly 3.0 m. Detailed descriptions of the study site are found in Neira et al. (2005) and Neira et al. (2006).

### Sampling design and methods

To investigate both the magnitude and the mechanism of influence of hybrid *Spartina* stages on soils and macrobenthos, we adopted both mensurative and manipulative approaches outlined in three experiments. Our initial observations consisted of paired sampling of high marsh dieback areas and adjacent mature *Spartina* hybrid stands (Experiment 1). Additionally, we experimentally removed the *Spartina* canopy in the mature marsh and sampled the areas as mimics of 'dieback areas' after 90 days (Experiment 2). Once we recognized the dieback areas as a late stage in the invasion process, we then initiated transect sampling spanning 5 zones (or stages) of invasion, running from the tidal flat (pre-invasion) to the dieback areas (post invasion) (Experiment 3). Taken together the resulting data on sediments and macrofauna provide a mechanistic look at changes induced by early invasion, maturation, senescence and loss of invasive *Spartina*.

#### *Experiment 1: A preliminary dieback-area study*

A pair-wise sampling design was used to compare sediment and biotic properties of dieback areas



**Fig. 2** Photographs of: (A) a typical dieback area at Elsie Roemer showing the soft muddy characteristics of the soil. Several short standing dead culms of hybrid *Spartina*, now covered by barnacles, are seen in the foreground, (B) section of the upper marsh at Elsie Roemer covered by wrack composed mainly of green algae (*Ulva* spp.), which is smothering the underlying hybrid *Spartina* plants. Photo credit: C. Weiga

and adjacent hybrid-invaded patches in the upper regions of the hybrid *Spartina* meadow (Fig. 1). In April 2003, 10 replicate blocks, separated by about 10 to 20 m, were established. Each encompassed a dieback-area (i.e., corresponding to Zone 5 in experiment 3) and an adjacent hybrid-*Spartina* vegetated area (later determined to be senescent or Zone 4 in experiment 3). We established 50 × 50 cm quadrats for sampling within each habitat in each block.

Within each quadrat, we made measurements of porewater salinity (S), temperature (T), redox potential (Eh), percent open space, light penetration, and total stem density (in *Spartina* invaded habitat). Sediment cores (18.1 cm<sup>2</sup>, 6 cm deep) were collected for analyses of (a) infauna and belowground plant biomass (from the same sed-

iment core) and (b) sediment properties including percent mud (particles <63 μm), total organic matter (TOM) content. Small cores (1.13 cm<sup>2</sup> × 5 mm deep) were collected for determination of sediment chlorophyll *a* (chl *a*) and water content (WC). Sample collection, preservation and processing are described in Neira et al. (2006).

#### *Experiment 2: Canopy removal experiment*

In order to experimentally create dieback areas, on April 2002 we removed the above-ground portion of the *Spartina* canopy, clipping (and removing) the stems near the sediment surface in 2 × 2 m plots (n = 10). For this experiment we used previously studied areas (for details see Neira et al. 2006) located about 10 m inside hybrid *Spartina* habitat from the tidal flat edge, i.e., the zone 3 (or mature invasion) in Experiment 3 below. After 90 days, we compared the macrofauna and sediment properties of these above-ground removal treatments with those of unmanipulated control areas (corresponding to mature invasion or Zone 3 in experiment 3). Short-term sediment deposition rates were measured in clipped and control plots by deploying Petri-dish sediment traps (Reed 1992) as described by Neira et al. (2006). Fine particle (<63 μm) and organic matter deposition rates were determined from the sediment traps.

#### *Experiment 3: Transects across plant invasion stages*

We established six parallel replicate transects, each of them with 5 areas (i.e., 5 stages × 6 transects, 30 areas in total), to test the hypothesis that changes in the sediment conditions associated with different stages in hybrid *Spartina* invasion at Elsie Roemer are reflected in a response by infauna communities. These transects were arranged in parallel and spanned a gradient of invasion and elevation, from open tidal flat across the *Spartina* meadow to the unvegetated dieback areas (Fig. 1). Along each transect we delimited 5 zones (each with 50 × 50 cm plots): zone 1 = tidal flat, zone 2 = hybrid leading edge (immature invasion), zone 3 = hybrid center (mature invasion), zone 4 = innermost hybrid-vegetated



sediments adjacent to dieback areas (senescing invasion), zone 5 = dieback area.

In each zone (1 to 5) along each of the six replicate transects, we measured sediment properties including porewater S, Eh, T, WC, TOM, porewater sulfide concentration, percent mud content, chl *a*, and pigment composition. Sediment redox potential was measured in the upper 1 cm of sediment (all 3 experiments) and at 1 cm intervals down to 8 cm depth (Experiment 1 only). Sulfide was determined according to Cline (1969) from porewater collected at 4 cm depth with a porewater sampler (Berg and McGlathery 2001). Analytical and infauna analysis methods are described in Neira et al. (2005, 2006).

#### Data analysis

Paired *t*-tests (Table 1 and Table 3) were used to test for significant differences in macrofauna,

sediment properties, and environmental variables between (a) unvegetated dieback areas versus adjacent hybrid *Spartina* patches ( $n = 10$ , Exp. 1), and (b) clipped treatments versus unclipped controls ( $n = 10$ , Exp. 2). One-way ANOVA with a-posteriori Tukey's HSD tests were used to examine among-zone differences in sediment properties and macrofauna along the transects (Exp. 3, Table 4). Data were tested for normality and heteroscedasticity and, when necessary, square root transformed. The non-parametric Wilcoxon test was used when transformed data failed to meet parametric assumptions. All statistical analyses were conducted using JMP 4.0 statistical software. One standard error about the mean is presented unless otherwise indicated. Data shown as proportions were arcsin square-root transformed. Linear regressions (Excel 2003) were used to test relationships among sediment variables, diversity, total macrofaunal density and

**Table 1** Sediment and environmental properties, total density, density of main higher taxa, and diversity indices in dieback areas and adjacent hybrid *Spartina* sediments of Elsie Roemer

|  | Habitat      |       |                         |       |          |
|--|--------------|-------|-------------------------|-------|----------|
|  | Dieback Area |       | Adjacent Hybrid Invaded |       |          |
|  | Mean         | 1 SE  | Mean                    | 1 SE  | <i>P</i> |
| <b>Environmental variables</b>                             |              |       |                         |       |          |
| Salinity (ppt)   | 34.9         | 0.3   | 31.9                    | 0.5   | 0.0004   |
| Temperature (°C)   | 17           | 0.2   | 15.3                    | 0.5   | 0.003    |
| Water content (%)  | 67.4         | 2.4   | 60.2                    | 1.4   | 0.002    |
| Redox potential (mV) top 1 cm                              | -143.7       | 21.1  | -65.0                   | 22.7  | 0.004    |
| TOM (% DW)   | 9.7          | 0.5   | 8.4                     | 0.5   | 0.032    |
| Chl <i>a</i> ( $\mu\text{g g}^{-1}$ )                      | 117.9        | 22.6  | 46.6                    | 6.6   | 0.016    |
| Mud content (%)  | 89.4         | 1.86  | 77.3                    | 3.1   | 0.003    |
| Light penetration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) | 1292.1       | 112.8 | 146                     | 48.5  | < 0.0001 |
| Below-ground plant biomass ( $\text{g m}^{-2}$ )           | 533.7        | 54.7  | 526.0                   | 124.6 | 0.959    |
| Open space (%)   | 99.7         | 0.3   | 28.5                    | 4.7   | < 0.0001 |
| <b>Macrofaunal variables</b>                               |              |       |                         |       |          |
| Total density (No ind core <sup>-1</sup> )                 | 267.4        | 57.91 | 260.8                   | 57.98 | 0.929    |
| Oligochaeta  | 217.7        | 66.6  | 210.7                   | 63.6  | 0.021    |
| Polychaeta   | 42.3         | 13.9  | 37.7                    | 26.4  | 0.206    |
| Bivalvia   | 3.3          | 1.4   | 2.6                     | 2     | 0.234    |
| Crustacea  | 0.5          | 0.4   | 3.3                     | 2.2   | 0.253    |
| Insecta  | 0.5          | 0.5   | 4.6                     | 3.2   | 0.245    |
| Others (Anthozoa + Turbellaria)                            | 2.9          | 1.3   | 1.8                     | 0.8   | 0.269    |
| <b>Diversity Indices</b>                                   |              |       |                         |       |          |
| Taxon richness (No species core <sup>-1</sup> )            | 6.7          | 0.75  | 7.6                     | 1.54  | 0.579    |
| Shanon H' log <sub>10</sub>                                | 0.33         | 0.07  | 0.34                    | 0.10  | 0.938    |
| Evenness J'  | 0.4          | 0.07  | 0.40                    | 0.08  | 0.987    |
| R1 Dominance (%)   | 72.8         | 7.7   | 75.5                    | 8.6   | 0.752    |

Samples were collected in April 2003. *P* are significance values from paired *t* tests ( $n = 10$ ). Core area =  $18.1 \text{ cm}^2$  ( $\times 6 \text{ cm}$  deep). Significance level set at  $\alpha = 0.05$

selected species. Macrofaunal diversity was examined using taxon richness per core, as well as the Shannon–Weiner diversity index ( $H'$ ;  $\log_{10}$ ), Pielou's evenness ( $J'$ ), and Rank 1 Dominance (%), using PRIMER 5.2.2 (Clarke and Warwick 2001) and Biodiversity Pro (McAleece et al. 1999) software.

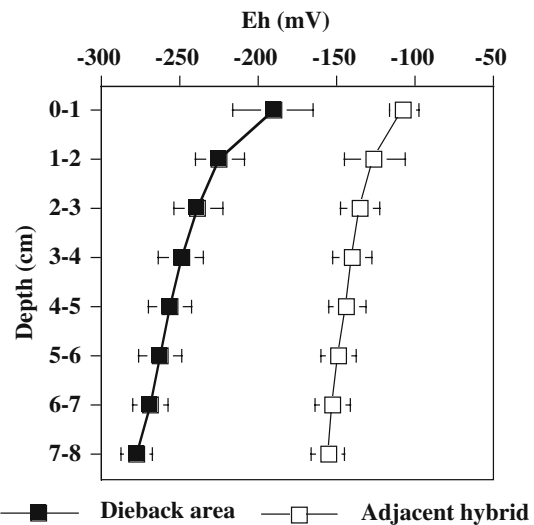
Similarities and differences in macrofaunal assemblages of various experimental treatments were explored using three multivariate methods: 1) non-metric multidimensional scaling (MDS), 2) analysis of similarity (ANOSIM) and 3) similarity percentage (SIMPER) using PRIMER 5.2.2 (Plymouth Marine Laboratory, Clarke and Warwick 2001) on square root transformed, unstandardized data.

## Results

### Experiment 1: Unvegetated dieback areas and adjacent hybrid *Spartina* patches

All environmental variables in dieback area sediments differed significantly from those in adjacent vegetated habitats, except below-ground plant detritus biomass, which was similar in both habitats ( $P = 0.959$ ) (Table 1), suggesting slow root degradation. Light penetration and open space were higher in the dieback areas than in the adjacent vegetated patches. Dieback areas were finer-grained, with higher OM content and chl *a* concentration. Relative to adjacent, invaded patches, dieback area sediments had higher salinity, temperature, and water content. Sediments exhibited reduced conditions in both settings (i.e.,  $Eh < +100$  mV, Meyer-Reil 1983), but values were significantly lower in dieback areas than in vegetated patches (Table 1, Fig. 3).

The environmental differences between dieback and adjacent invaded areas were reflected in species differences. Oligochaetes were slightly but significantly more abundant within the dieback areas relative to adjacent hybrid patches ( $P = 0.021$ ) (Table 1). From a total of 25 species recorded in these habitats, the tubificid oligochaetes *Monopylephorus evertus* and *Tubificoides* spp. dominated the infaunal community, contrib-



**Fig. 3** Depth profiles of redox potential measured at 1 cm intervals in dieback and adjacent hybrid *Spartina* areas at Elsie Roemer (San Francisco Bay). Values are mean  $\pm$  SE

uting over 80% of the individuals in both settings (Fig. 5). The carnivorous polychaete *Eteone californica* was more abundant in the dieback areas than in adjacent *Spartina* patches ( $P = 0.033$ ) (Table 2). However, no differences in mean total macrofaunal density (Fig. 4A), taxon richness (Fig. 4B), or diversity indices were observed (Table 1).

### Experiment 2: Plant canopy removal experiment

Ninety days after canopy removal, most of the sediment and environmental properties of the clipped areas differed from those of the unclipped controls (Table 3, Fig 7A). Clipped sediments were finer-grained, had higher salinity, temperature, total organic matter and chl *a* content than unclipped control sediments. Clipped sediments exhibited more reduced conditions (Table 3), with a very thin oxidized surface layer dominated by benthic diatoms as revealed by high concentrations of fucoxanthin. In contrast, concentrations of zeaxanthin (a proxy for cyanobacteria biomass) did not differ between clipped and unclipped habitats (Table 3). Ninety days after canopy removal, harsh sediment conditions were

**Table 2** Mean densities of macrofauna (>0.3 mm) collected in three experiments in Elsie Roemer, San Francisco Bay, Experiment 1: AH = adjacent hybrid *Spartina* patches versus D = dieback areas (sampled in April 2003), Experiment 2: C = clipped areas versus U = unclipped control (sampled after 90 d of canopy removal in July 2002), and Experiment 3: Zone 1 = pre-invaded tidal flat, Zone 2 = hybrid leading edge (immature invasion), Zone 3 = hybrid center (mature invasion), Zone 4 = innermost hybrid-vegetated sediments adjacent to dieback areas (senescing invasion), and Zone 5 = dieback area (sampled in June 2004)

| Species                             | Exp 1        |             |             | Exp 2       |              |             | Exp 3        |              |               |           |  |  |
|-------------------------------------|--------------|-------------|-------------|-------------|--------------|-------------|--------------|--------------|---------------|-----------|--|--|
|                                     | AH           | D           | U           | C           | U            | Z1          | Z2           | Z3           | Z4            | Z5        |  |  |
| <b>Annelida</b>                     |              |             |             |             |              |             |              |              |               |           |  |  |
| <i>Oligochaeta</i>                  |              |             |             |             |              |             |              |              |               |           |  |  |
| <i>Tubificoides</i> spp.            | 9.6 (3.8)    | 14.7 (11.7) | 20.0 (11.4) | 27.6 (13.0) | 68.8 (18.6)  | 55.2 (32.7) | 10.3 (8.4)   | 197 (74.0)   | 303.2 (239.9) |           |  |  |
| <i>Tectidrilus diversus</i>         | 0.0 (0.0)    | 0.0 (0.0)   | 0.1 (0.1)   | 0.3 (0.3)   | 107.2 (17.1) | 1.0 (0.8)   | 0.0 (0.0)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Monopylephorus evertus</i>       | 201.1 (59.7) | 203 (54.9)  | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0)    | 0.0 (0.0)   | 0.3 (0.3)    | 135.7 (22.1) | 230.5 (43.2)  |           |  |  |
| <i>Enchytraeidae</i> spp.           | 0.0 (0.0)    | 0.0 (0.0)   | 8.2 (6.6)   | 48.1 (34.5) | 0.0 (0.0)    | 3.3 (2.8)   | 9.0 (3.4)    | 0.0 (0.0)    | 1.0 (0.8)     |           |  |  |
| <b>Polychaeta</b>                   |              |             |             |             |              |             |              |              |               |           |  |  |
| <i>Pseudopolydora kempfi</i>        | 0.0 (0.0)    | 0.0 (0.0)   | 0.0 (0.0)   | 0.2 (0.1)   | 4.2 (0.7)    | 0.2 (0.2)   | 0.0 (0.0)    | 0.2 (0.2)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Polydora nuchalis</i>            | 0.2 (0.1)    | 0.0 (0.0)   | 0.0 (0.0)   | 0.5 (0.3)   | 9.8 (2.4)    | 2.7 (1.1)   | 0.5 (0.3)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Polydora cornuta</i>             | 0.0 (0.0)    | 0.0 (0.0)   | 0.1 (0.1)   | 0.1 (0.1)   | 0.0 (0.0)    | 0.0 (0.0)   | 0.0 (0.0)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Sireblosipio benedicti</i>       | 10.8 (6.3)   | 17.8 (7.2)  | 21.4 (9.5)  | 58.5 (24.0) | 103.2 (40.5) | 6.7 (3.1)   | 7.2 (5.6)    | 17.3 (11.9)  | 5.3 (4.9)     |           |  |  |
| <i>Pygospio elegans</i>             | 0.0 (0.0)    | 0.0 (0.0)   | 0.0 (0.0)   | 1.0 (0.7)   | 16.8 (9.9)   | 0.3 (0.3)   | 1.8 (1.3)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Boccardia proboscidea</i>        | 0.0 (0.0)    | 0.0 (0.0)   | 0.3 (0.2)   | 0.3 (0.2)   | 0.0 (0.0)    | 3.8 (1.4)   | 0.3 (0.3)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Heteromastus filiformis</i>      | 3.7 (2.4)    | 1.1 (0.7)   | 3.0 (2.1)   | 3.1 (1.3)   | 25.7 (3.7)   | 2.7 (1.2)   | 0.8 (0.8)    | 0.8 (0.5)    | 0.2 (0.2)     |           |  |  |
| <i>Capitella</i> spp.               | 1.0 (0.5)    | 0.5 (0.2)   | 0.1 (0.1)   | 0.2 (0.1)   | 6.5 (2.1)    | 13.7 (10.1) | 1.3 (1.3)    | 9.2 (7.0)    | 18.5 (14.3)   |           |  |  |
| <i>Eteone californica</i>           | 9.8 (4.9)    | 22.9 (5.8)  | 0.0 (0.0)   | 1.6 (0.8)   | 10.2 (1.7)   | 7.0 (4.0)   | 3.2 (1.9)    | 0.3 (0.2)    | 0.0 (0.0)     |           |  |  |
| <i>Eteone dilatata</i>              | 0.0 (0.0)    | 0.0 (0.0)   | 0.5 (0.5)   | 2.4 (1.1)   | 12.3 (2.1)   | 0.8 (0.5)   | 0.0 (0.0)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Sphaerosyllis californiensis</i> | 4.5 (4.5)    | 0.0 (0.0)   | 0.3 (0.3)   | 1.4 (0.7)   | 22.8 (8.7)   | 3.2 (2.2)   | 0.0 (0.0)    | 0.0 (0.0)    | 0.2 (0.2)     |           |  |  |
| <i>Exogone lourei</i>               | 3.1 (3.0)    | 0.0 (0.0)   | 0.0 (0.0)   | 0.2 (0.2)   | 7.5 (2.3)    | 55.0 (27.3) | 3.8 (2.0)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Fabricia</i> spp.                | 2.8 (2.8)    | 0.0 (0.0)   | 1.7 (1.6)   | 57.1 (40.2) | 0.0 (0.0)    | 0.0 (0.0)   | 101.0 (53.5) | 0.5 (0.2)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Nereis succinea</i>              | 1.8 (1.8)    | 0.0 (0.0)   | 0.3 (0.2)   | 1.9 (0.8)   | 1.2 (0.4)    | 0.2 (0.2)   | 0.0 (0.0)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Tharyx</i> sp.                   | 0.0 (0.0)    | 0.0 (0.0)   | 0.1 (0.1)   | 0.6 (0.4)   | 9.8 (6.3)    | 0.0 (0.0)   | 0.0 (0.0)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Goniadidae</i> sp.               | 0.0 (0.0)    | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0)   | 0.2 (0.2)    | 0.0 (0.0)   | 0.0 (0.0)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Dorvillea</i> sp.                | 0.1 (0.1)    | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0)    | 0.0 (0.0)   | 0.0 (0.0)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <b>Mollusca</b>                     |              |             |             |             |              |             |              |              |               |           |  |  |
| <i>Bivalvia</i>                     |              |             |             |             |              |             |              |              |               |           |  |  |
| <i>Mya arenaria</i>                 | 0.6 (0.4)    | 0.0 (0.0)   | 0.2 (0.1)   | 0.0 (0.0)   | 0.3 (0.2)    | 0.0 (0.0)   | 0.0 (0.0)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Macoma petaluma</i>              | 2.0 (1.6)    | 3.3 (1.4)   | 0.0 (0.0)   | 0.4 (0.3)   | 5.7 (2.0)    | 1.5 (0.7)   | 0.2 (0.2)    | 0.7 (0.5)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Gemma gemma</i>                  | 0.0 (0.0)    | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0)   | 145.2 (27.4) | 4.7 (4.3)   | 0.5 (0.5)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Venerupis philippinarum</i>      | 0.0 (0.0)    | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0)   | 0.3 (0.2)    | 0.2 (0.2)   | 0.0 (0.0)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Musculista senhousia</i>         | 0.0 (0.0)    | 0.0 (0.0)   | 0.1 (0.1)   | 0.0 (0.0)   | 0.0 (0.0)    | 1.7 (1.1)   | 0.2 (0.2)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <b>Arthropoda</b>                   |              |             |             |             |              |             |              |              |               |           |  |  |
| <b>Peracarid crustacea</b>          |              |             |             |             |              |             |              |              |               |           |  |  |
| <i>Corophium</i> spp.               | 1.9 (1.5)    | 0.6 (0.4)   | 3.7 (2.2)   | 25.9 (15.2) | 263.2 (67.1) | 50.7 (19.1) | 7.2 (5.3)    | 0.2 (0.2)    | 0.7 (0.5)     | 0.0 (0.0) |  |  |
| <i>Ampithoe lacertosa</i>           | 0.0 (0.0)    | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0)    | 0.3 (0.3)   | 0.0 (0.0)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |
| <i>Ampithoe valida</i>              | 0.0 (0.0)    | 0.0 (0.0)   | 0.0 (0.0)   | 0.1 (0.1)   | 0.0 (0.0)    | 0.0 (0.0)   | 0.0 (0.0)    | 0.0 (0.0)    | 0.0 (0.0)     | 0.0 (0.0) |  |  |

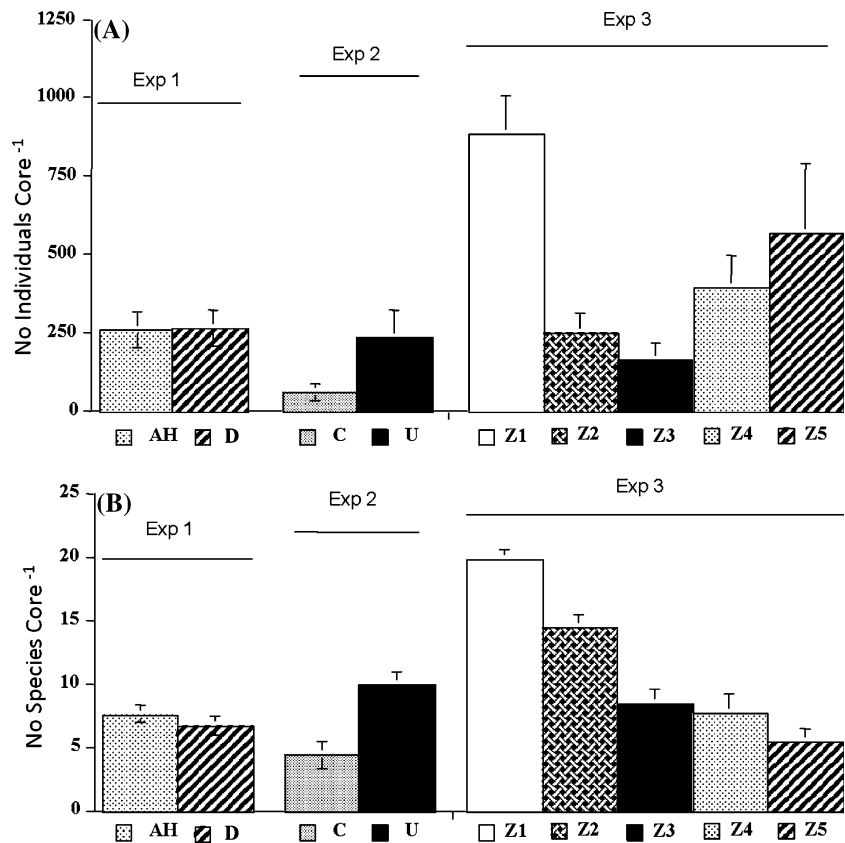
Table 2 continued

| Species                         | Exp 1     |           | Exp 2     |           | Exp 3       |             |           |             |           |
|---------------------------------|-----------|-----------|-----------|-----------|-------------|-------------|-----------|-------------|-----------|
|                                 | AH        | D         | C         | U         | Z1          | Z2          | Z3        | Z4          | Z5        |
| <i>Granditierella japonica</i>  | 0.0 (0.0) | 0.0 (0.0) | 1.9 (1.9) | 5.0 (2.2) | 60.5 (16.6) | 4.7 (2.1)   | 0.0 (0.0) | 0.0 (0.0)   | 0.0 (0.0) |
| <i>Hyale</i> sp.                | 1.2 (0.5) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0)   | 27.3 (13.5) | 5.3 (3.2) | 1.2 (0.6)   | 0.2 (0.2) |
| <i>Traskorchestia traskiana</i> | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.4 (0.3) | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0) | 0.0 (0.0)   | 0.0 (0.0) |
| <i>Ampelisca</i> sp.            | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.2 (0.2)   | 0.0 (0.0)   | 0.0 (0.0) | 0.0 (0.0)   | 0.0 (0.0) |
| <i>Exosphaeroma inornata</i>    | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.1 (0.1) | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0) | 0.0 (0.0)   | 0.0 (0.0) |
| Tanaidacea                      | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.9 (0.5) | 0.0 (0.0)   | 0.8 (0.8)   | 4.2 (4.2) | 0.0 (0.0)   | 0.0 (0.0) |
| Cumacea                         | 0.2 (0.2) | 0.0 (0.0) | 0.4 (0.4) | 0.4 (0.3) | 0.2 (0.2)   | 0.0 (0.0)   | 0.0 (0.0) | 0.0 (0.0)   | 0.0 (0.0) |
| Insecta                         |           |           |           |           |             |             |           |             |           |
| Dolichopodidae larvae           | 0.0 (0.0) | 0.3 (0.2) |           |           | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0) | 0.3 (0.3)   | 0.0 (0.0) |
| Chironomidae larvae             | 0.3 (0.2) | 0.1 (0.1) |           |           | 0.0 (0.0)   | 0.2 (0.2)   | 0.5 (0.3) | 0.0 (0.0)   | 0.0 (0.0) |
| Ceratopogonidae pupae           | 1.7 (1.0) | 0.0 (0.0) | 0.0 (0.0) | 0.1 (0.1) | 0.0 (0.0)   | 0.0 (0.0)   | 0.3 (0.2) | 1.2 (0.7)   | 0.3 (0.2) |
| Poduridae                       | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.3 (0.2) | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0) | 1.8 (1.6)   | 0.0 (0.0) |
| Psychodidae larvae              | 1.4 (0.8) | 0.2 (0.1) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0)   | 0.2 (0.2)   | 4.2 (4.2) | 28.3 (10.1) | 8.5 (4.1) |
| Canacidae larvae                | 1.0 (1.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0) | 0.0 (0.0)   | 0.0 (0.0) |
| Muscidae larvae                 | 0.2 (0.1) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0) | 0.0 (0.0)   | 0.0 (0.0) |
| “Other taxa”                    |           |           |           |           |             |             |           |             |           |
| Anthozoa                        | 0.1 (0.1) | 0.6 (0.5) | 0.0 (0.0) | 0.2 (0.1) | 2.5 (1.0)   | 3.5 (1.5)   | 0.5 (0.3) | 0.2 (0.2)   | 0.8 (0.8) |
| Turbellaria                     | 1.7 (0.7) | 2.3 (0.8) | 0.0 (0.0) | 0.2 (0.1) | 3.2 (1.4)   | 0.2 (0.2)   | 0.0 (0.0) | 0.0 (0.0)   | 0.0 (0.0) |

Values are mean number of individuals per 18.1 cm<sup>2</sup> × 6 cm deep core (± 1SE) of 10 replicate cores (Exp 1 and 2); 6 replicate cores (Exp 3)



**Fig. 4** Macrofaunal density (A) and taxon richness (B) of Experiment 1: adjacent hybrid *Spartina* (AH) versus dieback areas (D), sampled in April 2003, Experiment 2: clipped areas (C, removed after 90 d) versus unclipped (U) control areas, sampled in July 2002, Experiment 3: stages transect, including Zone 1 = tidal flat, Zone 2 = hybrid leading edge (immature invasion), Zone 3 = hybrid center (mature invasion), Zone 4 = innermost hybrid-vegetated habitat adjacent to dieback areas (senescing invasion), Zone 5 = dieback area, sampled in June 2004 at Elsie Roemer (San Francisco Bay). Values are mean  $\pm$  1 SE. Core area = 18.1 cm<sup>2</sup> ( $\times$  6 cm deep)



observed; there was increased input of fine particles and associated OM from the water column and decaying below ground plant material (over 530 g m<sup>-2</sup>) (Table 3), which produced high levels of porewater sulfide. Typically porewater sulfide concentrations were between 300–1800  $\mu$ M in clipped sediments and between 200  $\mu$ M and 900  $\mu$ M in unclipped controls (A.C. Tyler, pers. comm.).

Total macrofaunal density was one quarter and species richness was one half those in unclipped control sediments (Fig. 4A, B). Diversity ( $H'$ ), evenness ( $J'$ ), and R1 dominance did not differ between habitats (Table 3). Abundances of polychaetes, crustaceans, insects, enchytraeid oligochaetes, and 'others' (anthozoans + turbellarians) decreased in clipped areas relative to unclipped controls, while tubificid oligochaete densities were not affected (Table 3). Among the species whose densities declined with clipping were the polychaetes *Streblospio benedicti* ( $t_9 = 2.3$ ,  $P = 0.044$ ), *Eteone dilatata* ( $t_9 = 2.3$ ,  $P = 0.044$ ),

and *Nereis succinea* ( $t_9 = 2.2$ ,  $P = 0.037$ ), and the amphipod *Grandidierella japonica* ( $t_9 = 2.7$ ,  $P = 0.024$ ) (Table 2).

#### Experiment 3: Stages of *Spartina* invasion

As hybrid *Spartina* grows and expands, it undergoes different invasion stages whose sediment and environmental properties change accordingly. There was a slight progressive increase in porewater salinity across zones 1 to 5 (Wilcoxon  $\chi^2 = 16.8$ ,  $P = 0.002$ ), temperature ( $F_{4,25} = 3.1$ ,  $P = 0.033$ ), and water content ( $F_{4,25} = 35.7$ ,  $P = < 0.0001$ ), from tidal flats up to the dieback areas. The dieback areas acted as a sink for particle deposition as revealed by the high mud content. Although there were no significant differences in elevation among zones 3, 4, and 5 ( $P > 0.05$ ), these zones were 86 and 47 cm higher than zones 1 (tidal flat) and zone 2 (immature hybrid), respectively ( $F_{4,25} = 159.3$ ,  $P < 0.0001$ ) (Table 4).

**Table 3** Sediment and environmental properties, total density, density of main higher taxa, and diversity indices in clipped plot areas and unclipped (control) hybrid *Spartina* habitat of Elsie Roemer

|   | Habitat |       |                     |       | <i>P</i> |
|---|---------|-------|---------------------|-------|----------|
|   | Clipped |       | Unclipped (control) |       |          |
|   | Mean    | 1 SE  | Mean                | 1 SE  |          |
| Environmental variables   |         |       |                     |       |          |
| Salinity (ppt)  | 37.8    | 0.6   | 36.6                | 0.3   | 0.021    |
| Temperature (°C)  | 19.9    | 1.1   | 18.2                | 0.4   | 0.040    |
| Water content (%)   | 49.3    | 3.9   | 43.1                | 3.6   | 0.062    |
| Redox potential (mV) top 1 cm   | -161.6  | 23.9  | -27.5               | 25.4  | <0.0001  |
| TOM (% DW)  | 5.7     | 0.6   | 3.7                 | 0.5   | 0.0002   |
| Chl <i>a</i> (µg g <sup>-1</sup> )                                      | 69.4    | 16.9  | 28.8                | 4.4   | 0.050    |
| Mud content (%)   | 66.9    | 4.6   | 48.6                | 5.5   | 0.004    |
| Light penetration (µmol m <sup>-2</sup> s <sup>-1</sup> )               | 567.6   | 150.2 | 73.3                | 20.7  | 0.009    |
| Below-ground plant biomass (g m <sup>-2</sup> )                         | 537.6   | 127.3 | 806.6               | 154.5 | 0.225    |
| Fucoxanthin (mg m <sup>-2</sup> )                                       | 83.4    | 13.2  | 40.1                | 9.9   | 0.022    |
| Zeaxanthin (mg m <sup>-2</sup> )  | 2.5     | 0.5   | 2.6                 | 0.6   | 0.387    |
| Deposition rates  |         |       |                     |       |          |
| Sediment deposition (mg cm <sup>-2</sup> d <sup>-1</sup> )              | 19.5    | 0.9   | 20.4                | 1.1   | 0.511    |
| Fine particle deposition (<63µm) (mg cm <sup>-2</sup> d <sup>-1</sup> ) | 13.1    | 1.5   | 9.3                 | 1.3   | 0.002    |
| Organic matter deposition (mg cm <sup>-2</sup> d <sup>-1</sup> )        | 3.9     | 0.3   | 3.2                 | 0.2   | 0.036    |
| Macrofaunal variables   |         |       |                     |       |          |
| Total density (No ind core <sup>-1</sup> )                              | 62.4    | 25.2  | 239.4               | 82.8  | 0.043    |
| Tubificidae   | 20.1    | 11.5  | 27.9                | 13.3  | 0.638    |
| Enchytraeidae   | 8.2     | 6.6   | 48.1                | 34.5  | 0.032    |
| Polychaeta  | 27.7    | 11.3  | 129.1               | 38.5  | 0.006    |
| Bivalvia  | 0.3     | 0.2   | 0.4                 | 0.3   | 0.726    |
| Crustacea   | 5.0     | 3.5   | 32.8                | 16.1  | 0.035    |
| Insecta   | 0.0     | 0.0   | 0.6                 | 0.3   | 0.040    |
| Others (Anthozoa + Turbellaria)   | 0.0     | 0.0   | 0.4                 | 0.2   | 0.037    |
| Diversity Indices   |         |       |                     |       |          |
| Taxon richness (No species core <sup>-1</sup> )                         | 4.4     | 1.1   | 10.0                | 1.0   | 0.0002   |
| Shanon H' log <sub>10</sub>   | 0.36    | 0.07  | 0.55                | 0.10  | 0.083    |
| Evenness J'   | 0.6     | 0.11  | 0.57                | 0.04  | 0.805    |
| R1 Dominance (%)  | 54.9    | 8.8   | 59.0                | 33.7  | 0.744    |

Samples were collected in July 2002, after 90 days plant removal. *P* are significance values from paired *t* tests. (*n* = 10). Core area = 18.1 cm<sup>2</sup> (× 6 cm deep). Significance level set at  $\alpha$  = 0.05

Sediments were more reduced ( $F_{4,25} = 7.2$ ,  $P = 0.0005$ ) and more sulfidic (Wilcoxon  $\chi^2 = 24.9$ ,  $P < 0.0001$ ) towards dieback areas; sulfide concentrations increased consistently from zones 1 to 5, reaching a maximum in the dieback areas, with an average of  $5727 \pm 712.4 \mu\text{M}$  (absolute maximum  $\sim 8330 \mu\text{M}$ ). At the same time there was an increase in fine particles (Wilcoxon  $\chi^2 = 26.3$ ,  $P < 0.0001$ ), organic matter (Wilcoxon  $\chi^2 = 25.8$ ,  $P < 0.0001$ ) and chl *a* ( $F_{4,25} = 23.3$ ,  $P < 0.0001$ ) from zones 1 to 5 (Table 4). Among the environmental parameters considered, sulfide, organic matter, mud content and chl *a*, all were positively correlated with each other, while

sediment Eh was negatively correlated with all of them (Fig. 6). In contrast, no relationship was found between below-ground plant biomass and either sediment organic matter or pore-water sulfide (Fig. 6).

The microalgal community of all blocks was composed mainly of diatoms as indicated by the high concentrations of fucoxanthin, ranging from  $25.7 \text{ mg m}^{-2}$  to  $73.3 \text{ mg m}^{-2}$ . There was considerable variability in the concentration of fucoxanthin in sediments of immature *Spartina* close to the tidal flat edge, indicating highly patchy distributions of diatoms, probably a result of resuspension. Concentrations of zeaxanthin increased significantly from tidal flats

**Table 4** Sediment and environmental properties, total density, density of main higher taxa, diversity indices, and contribution of feeding mode to total abundance along a transect of progressive invasion by hybrid *Spartina* at Elsie Roemer, San Francisco Bay. Sampling and measure-

ments were made in June 2004. Values are mean ( $\pm$  1SE). Zones: 1 = tidal flat, 2 = hybrid leading edge (immature invasion), 3 = hybrid inner (mature invasion), 4 = dieback area- adjacent hybrid (senescing invasion), 5 = dieback area

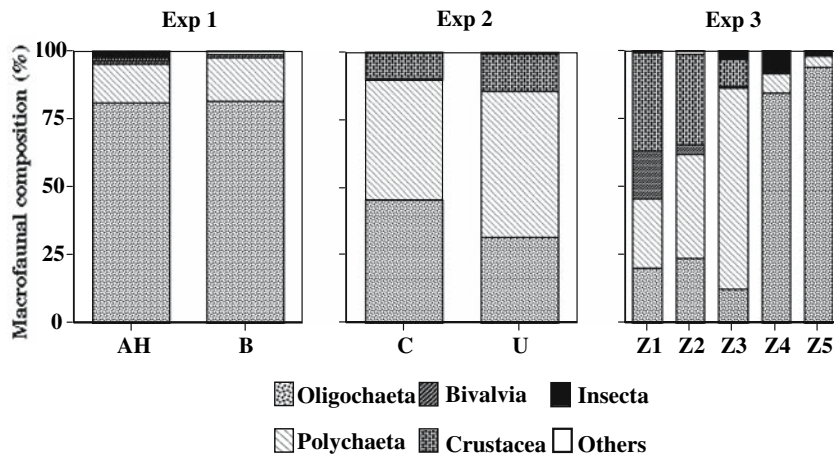
|   | Zone                       |                             |                              |                                       |                             |
|---|----------------------------|-----------------------------|------------------------------|---------------------------------------|-----------------------------|
|   | 1<br>Tidal flat            | 2<br>Hybrid<br>leading edge | 3<br>Hybrid<br>inner         | 4<br>Dieback area-<br>adjacent hybrid | 5<br>Dieback<br>area        |
| <b>Environmental variables</b>                            |                            |                             |                              |                                       |                             |
| Salinity (ppt)  | 33.3 (0.4) <sup>b</sup>    | 33.3 (0.4) <sup>b</sup>     | 34.0 (0.3) <sup>b</sup>      | 34.7 (0.5) <sup>b</sup>               | 39.3 (0.9) <sup>a</sup>     |
| Temperature (°C)  | 16.6 (0.2) <sup>ab</sup>   | 16.0 (0.1) <sup>b</sup>     | 16.1 (0.3) <sup>ab</sup>     | 16.7 (0.1) <sup>ab</sup>              | 17.2 (0.2) <sup>a</sup>     |
| Water content (%)   | 33.8 (1.7) <sup>c</sup>    | 31.8 (2.0) <sup>c</sup>     | 54.0 (2.0) <sup>b</sup>      | 56.2 (2.2) <sup>b</sup>               | 71.5 (2.7) <sup>a</sup>     |
| Bulk density (g cm <sup>-3</sup> )                        | 2.33 (0.17) <sup>a</sup>   | 2.53 (0.20) <sup>a</sup>    | 1.05 (0.09) <sup>b</sup>     | 0.98 (0.09) <sup>bc</sup>             | 0.55 (0.05) <sup>a</sup>    |
| Mud content (%)   | 10.9 (2.2) <sup>c</sup>    | 25.5 (4.6) <sup>c</sup>     | 52.9 (5.1) <sup>b</sup>      | 86.1 (4.0) <sup>a</sup>               | 92.3 (2.9) <sup>a</sup>     |
| TOM (% DW)  | 1.4 (0.2) <sup>c</sup>     | 2.9 (0.6) <sup>bc</sup>     | 5.4 (0.9) <sup>b</sup>       | 10.1 (0.7) <sup>a</sup>               | 10.9 (0.7) <sup>a</sup>     |
| Sulfide (μM)  | 19.6 (5.2) <sup>c</sup>    | 252.8 (61.5) <sup>bc</sup>  | 410.8 (69.8) <sup>bc</sup>   | 1779.8 (499.9) <sup>b</sup>           | 5727.8 (712.4) <sup>a</sup> |
| Redox potential (top 1 cm) (mV)                           | +51.2 (38.5) <sup>a</sup>  | -102.0 (47.0) <sup>ab</sup> | -172.2 (40.8) <sup>abc</sup> | -222.2 (30.0) <sup>bc</sup>           | -302.5 (32.8) <sup>c</sup>  |
| Light penetration (mmol m <sup>-2</sup> s <sup>-1</sup> ) | 382.5 (28.1) <sup>a</sup>  | 10.8 (0.9) <sup>b</sup>     | 12.8 (3.0) <sup>b</sup>      | 42.8 (9.6) <sup>b</sup>               | 381.2 (29.5) <sup>a</sup>   |
| Chl <i>a</i> (μg g <sup>-1</sup> )                        | 11.2 (0.6) <sup>d</sup>    | 91.4 (16) <sup>cd</sup>     | 224.9 (42.2) <sup>bc</sup>   | 289.8 (29.6) <sup>ab</sup>            | 454.9 (64.4) <sup>a</sup>   |
| Fucoxanthin (mg m <sup>-2</sup> )                         | 25.7 (19.6) <sup>a</sup>   | 55.0 (37.8) <sup>a</sup>    | 73.3 (5.6) <sup>a</sup>      | 50.9 (8.5) <sup>a</sup>               | 32.4 (8.9) <sup>a</sup>     |
| Zeaxanthin (mg m <sup>-2</sup> )                          | 0.4 (0.04) <sup>b</sup>    | 0.9 (0.2) <sup>b</sup>      | 1.1 (0.4) <sup>b</sup>       | 1.3 (0.1) <sup>b</sup>                | 7.3 (0.2) <sup>a</sup>      |
| Below-ground plant biomass (g m <sup>-2</sup> )           | 47.9 (13.2) <sup>b</sup>   | 346.2 (88.9) <sup>a</sup>   | 719.2 (287.5) <sup>a</sup>   | 335.2 (60.6) <sup>a</sup>             | 255.1 (46.7) <sup>ab</sup>  |
| Plant density (No stems m <sup>-2</sup> )                 | 0 <sup>c</sup>             | 163 (16.4) <sup>a</sup>     | 172.8 (12.4) <sup>a</sup>    | 100 (12.4) <sup>b</sup>               | 0 <sup>c</sup>              |
| Plant height (cm)   | 0 <sup>b</sup>             | 87.3 <sup>ab</sup>          | 125.4 <sup>a</sup>           | 86.2 <sup>ab</sup>                    | 0 <sup>ab</sup>             |
| Elevation (cm)  | 51 (1.3) <sup>c</sup>      | 90 (2.5) <sup>b</sup>       | 137 (3.4) <sup>a</sup>       | 140 (4.1) <sup>a</sup>                | 137 (3.6) <sup>a</sup>      |
| <b>Macrofaunal variables</b>                              |                            |                             |                              |                                       |                             |
| Total density (No ind core <sup>-1</sup> )                | 887.3 (120.3) <sup>a</sup> | 251.5 (61.1) <sup>b</sup>   | 162.7 (54.6) <sup>b</sup>    | 395.3 (101.6) <sup>ab</sup>           | 569.3 (219.0) <sup>ab</sup> |
| Oligochaeta   | 176.0 (35.7) <sup>ab</sup> | 59.5 (35.5) <sup>b</sup>    | 19.7 (12.1) <sup>b</sup>     | 333.2 (96.1) <sup>ab</sup>            | 534.7 (283.9) <sup>a</sup>  |
| Polychaeta  | 230.2 (81.0) <sup>a</sup>  | 96.2 (51.6) <sup>ab</sup>   | 120 (67.0) <sup>ab</sup>     | 28.3 (20.0) <sup>b</sup>              | 24.2 (19.6) <sup>b</sup>    |
| Bivalvia  | 151.5 (29.8) <sup>a</sup>  | 8.0 (6.3) <sup>b</sup>      | 0.8 (0.9) <sup>b</sup>       | 0.7 (0.5) <sup>b</sup>                | 0.0 (0.0) <sup>b</sup>      |
| Crustacea   | 324.0 (84.1) <sup>a</sup>  | 83.8 (35.8) <sup>b</sup>    | 16.7 (12.7) <sup>b</sup>     | 1.3 (0.8) <sup>b</sup>                | 0.8 (0.7) <sup>b</sup>      |
| Insecta   | 0.0 (0.0) <sup>b</sup>     | 0.4 (0.4) <sup>b</sup>      | 5.0 (4.7) <sup>ab</sup>      | 31.7 (12.7) <sup>a</sup>              | 8.8 (4.3) <sup>ab</sup>     |
| Others (Anthozoa + Turbellaria)                           | 5.7 (2.4) <sup>a</sup>     | 3.7 (1.7) <sup>ab</sup>     | 0.5 (0.3) <sup>b</sup>       | 0.2 (0.2) <sup>b</sup>                | 0.8 (0.8) <sup>b</sup>      |
| <b>Diversity indices</b>                                  |                            |                             |                              |                                       |                             |
| Taxon richness (No species core <sup>-1</sup> )           | 19.8 (0.8) <sup>a</sup>    | 14.5 (0.9) <sup>b</sup>     | 8.5 (1.1) <sup>c</sup>       | 7.7 (1.5) <sup>c</sup>                | 5.5 (0.9) <sup>c</sup>      |
| Shanon H' log <sub>10</sub>                               | 0.91 (0.02)                | 0.81 (0.05)                 | 0.55 (0.09)                  | 0.44 (0.05)                           | 0.25 (0.06)                 |
| Evenness J'   | 0.70 (0.02)                | 0.70 (0.05)                 | 0.61 (0.10)                  | 0.54 (0.04)                           | 0.36 (0.06)                 |
| R1 Dominance %  | 31.9 (3.8)                 | 37.3 (4.9)                  | 55.3 (10.2)                  | 59.3 (3.7)                            | 80.6 (6.5)                  |
| <b>Contribution by feeding mode (%)</b>                   |                            |                             |                              |                                       |                             |
| Surface feeders   | 69.8 (4.0) <sup>a</sup>    | 41.7 (6.3) <sup>b</sup>     | 78.9 (6.5) <sup>a</sup>      | 12.2 (3.9) <sup>c</sup>               | 2.5 (0.8) <sup>c</sup>      |
| Subsurface deposit feeders                                | 23.5 (4.4) <sup>a</sup>    | 30.0 (10.9) <sup>c</sup>    | 13.4 (7.1) <sup>bc</sup>     | 86.8 (4.0) <sup>c</sup>               | 97.2 (0.8) <sup>b</sup>     |
| Carnivory/Omnivory  | 6.7 (0.8) <sup>b</sup>     | 28.2 (7.2) <sup>a</sup>     | 7.4 (2.8) <sup>b</sup>       | 0.7 (0.6) <sup>b</sup>                | 0.2 (0.1) <sup>b</sup>      |

Core area = 18.1 cm<sup>2</sup> (× 6 cm deep). Contrasts made using *a posteriori* Tukey HSD tests are indicated with letters

towards later stages of invasion and ultimately the dieback areas (Wilcoxon  $\chi^2 = 10.6$ ,  $P = 0.031$ ), where the ratio zeaxanthin/fucoxanthin, 0.273 (=cyanobacteria/diatoms) was one order of magnitude higher than in tidal flats (zone 1) (0.045) or the immature invasion (zone 2) (0.032) (Table 4).

### Macrofaunal assemblage changes

The distinct stages of the hybrid *Spartina* invasion were paralleled by differences in faunal community composition, with a more diverse faunal assemblage in the uninvaded tidal flat (Zone 1) and a less diverse community in the dieback areas



**Fig. 5** Percent composition of major macrofaunal taxa ( $\geq 0.3$  mm) at Elsie Roemer, San Francisco Bay in Experiments 1, 2, and 3, as described in Fig. 4. 'Others' include anthozoans + turbellarians

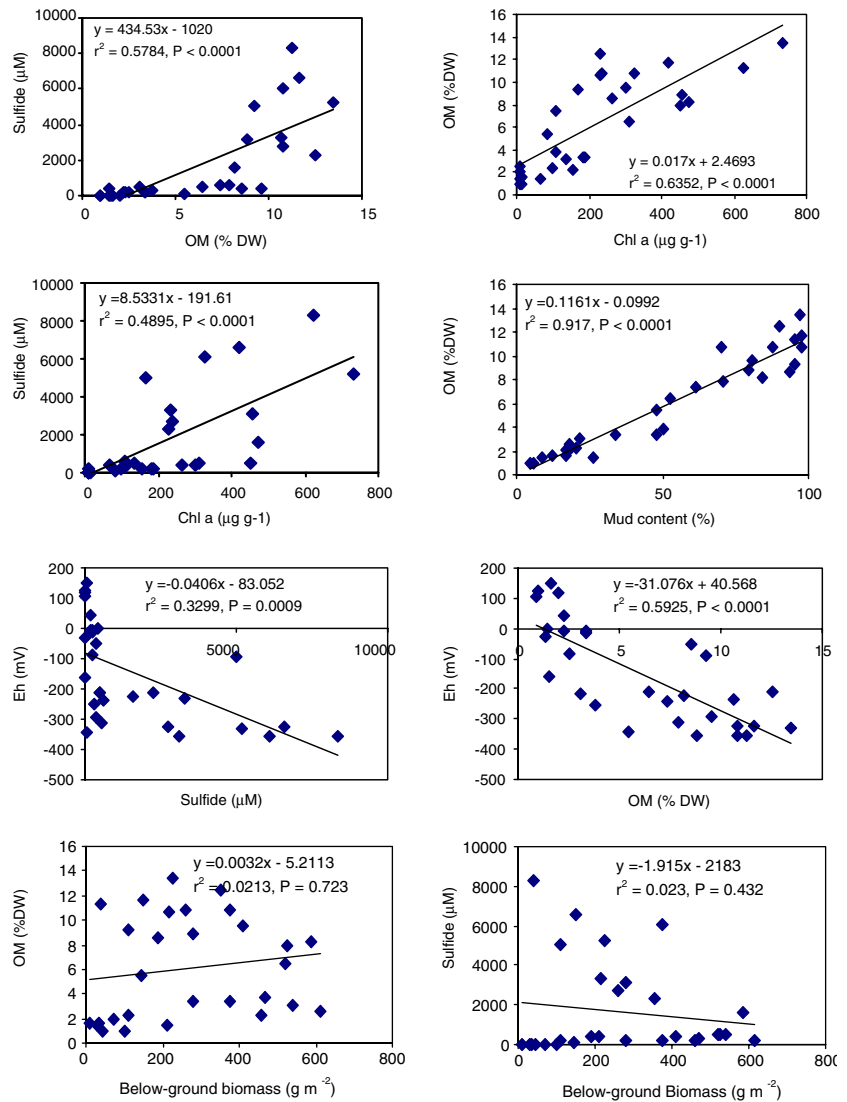
(Fig. 5). Macrofaunal total density was highest in the tidal flats (Zone 1), decreased drastically to a minimum in the dense, mature stand (Zone 3), and increased again in the dieback areas (Zone 5) (Fig. 4A, Table 4). Taxon richness declined uniformly across the meadow; uninvaded tidal flats (Zone 1) were associated with highest species richness (Fig. 4), while dieback areas were associated with the lowest richness, low Shannon diversity index ( $H'$ ), low evenness ( $J'$ ), and highest Rank 1 dominance (Table 4). The tidal flats contained a high proportion of polychaetes (25.9%), amphipods (36.5%), bivalves (17.1%), as well as oligochaetes (19.8%). Within the immature (Zone 2) and mature (Zone 3) *Spartina* invasion sites, there was an increased representation of polychaetes (38.2 and 73.8%, respectively). In Zone 3, polychaetes had the highest proportional contribution (73.8%), and psychodid insect larvae and enchytraeid oligochaetes also became more important, while amphipods and bivalves were drastically reduced. In the senescing *Spartina* invasion (Zone 4) and dieback area (Zone 5), oligochaetes comprised approximately 90% of the total fauna (Fig. 5, Table 2).

Taxon richness and diversity indices ( $H'$ ,  $J'$ ) across the meadow were negatively correlated with sediment organic matter content and pore-water sulfide concentration, and positively correlated with sediment Eh, while R1 dominance was positively correlated with organic matter and

sulfide (Appendix A). Sediment organic matter, sulfide, mud content, temperature and salinity were positively associated with densities of the tubificid oligochaete *M. evertus*. High sulfide concentrations were positively associated with densities of *Tubificoides* sp. and *Capitella* sp.; increased OM and fine-grained sediments and reduced conditions favored Psychodidae larvae (Appendix A). In contrast, sediment organic matter, sulfide, lower Eh and mud content were negatively associated with densities of spionid polychaetes *Polydora nuchalis* and *Pygospio elegans*, the phyllodocid *E. californica*, the syllid *Spharrosyllis californiensis*, and the bivalve *Macoma petalum*. Anthozoan densities tended to be negatively associated with Chl *a* concentrations (Appendix A).

Surface feeding was the most common feeding mode observed among macrofauna from tidal flat to mature *Spartina* stands (Zone 1 to 3), while subsurface-deposit feeding was the dominant feeding mode in the senescing and dieback areas (Zone 4 and 5). Carnivory and omnivory were best represented in the immature invasion stage (Zone 2) (Table 4). Herbivorous grazing, represented by chironomid larvae, was negligible and was observed only in Zone 2 (0.1%) and Zone 3 (< 0.3%). In the uninvaded tidal flat, bivalves (*G. gemma*), amphipods (*Corophium* spp. and *G. japonica*), and spionid polychaetes (e.g., *Streblospio benedicti*) were the primary

**Fig. 6** Experiment 3. Regression plots showing relationships between selected soil variables along the stages transect at Elsie Roemer, San Francisco Bay, sampled in June 2004. Variables include porewater sulfide, organic matter, chl *a*, redox potential, and belowground biomass

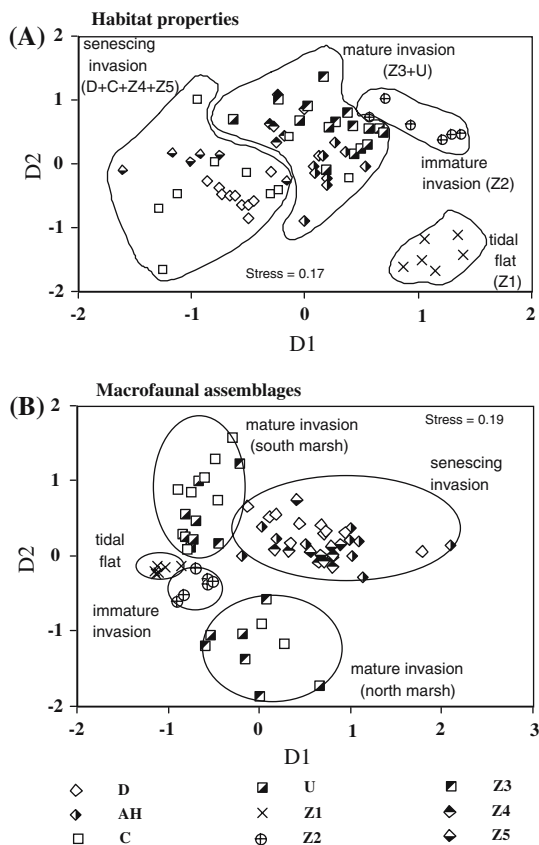


surface feeders, while the oligochaetes *T. diversus*, *Tubificoides* cf. *fraseri*) along with *Heteromastus filiformis*, were the main subsurface-deposit feeders. Within the immature stands (Zone 2) surface feeders, represented by *Hyale* sp. and some corophiids and *S. benedicti*, were reduced in general. Subsurface feeders in Zone 2 included *T. cf. fraseri*, *Capitella* spp. and *H. filiformis*, while carnivores/omnivores (*Exogone lourei* and *E. californica*) become more important than in Zone 1. High representation of surface feeders in Zone 3 (mature invasion), was due to the occasional

high abundance of the sabellid polychaete, *Fabricia* spp. In Zone 4 (senescing invasion) and Zone 5 (dieback), subsurface-deposit feeding was overwhelmingly represented by two tubificid species, *Monopylephorus evertus* and *Tubificoides* cf. *brownae* and to a lesser extent by *Capitella* spp. The surface-feeding habit in Zone 4 and 5 was limited largely to Psychodidae larvae (Table 2).

Non-metric multidimensional scaling (MDS) of macrofaunal assemblages, including data from all three experiments, produced five distinct faunal assemblages: (1) pre-invasion tidal flats,





**Fig. 7** Multidimensional scaling (MDS) plots of **(A)** environmental variables and **(B)** macrofaunal communities considering all three experiments sampled at Elsie Roemer, San Francisco Bay. Each point represents data from one core. Environmental variables include percent organic matter content, percent mud content, water content, chl *a*, redox potential, salinity, temperature, light penetration, and belowground biomass. The stress value measures how well the two-dimensional plot represents the multidimensional distances among the data. D = dieback areas, AH = adjacent hybrid *Spartina*, C = clipped areas, U = unclipped control areas, Zone 1 = tidal flat, Zone 2 = hybrid leading edge (immature invasion), Zone 3 = hybrid center (mature invasion), Zone 4 = innermost hybrid-vegetated habitat adjacent to dieback areas (senescing invasion), Zone 5 = dieback area

(2) immature invasion, (3) south marsh mature invasion, (4) north marsh mature invasion, and (5) senescing and dieback areas (Fig. 7B). These mirrored the corresponding habitat properties (Fig. 7A). The mature invasion was characterized by a wide range of *Spartina*-related sediment properties, generating two distinct faunal assemblages, both patchily distributed. The difference

between the north and south mature marsh assemblages was attributed to the dominant presence of *Fabricia* spp. (over 62% of fauna). *Fabricia* was more numerous in the north marsh, while in the south marsh, the spionid polychaete, *S. benedicti* comprised over 34% of the fauna. In this zone, within-habitat percent similarity was only 31% (SIMPER, Appendix B).

## Discussion

This analysis of how hybrid *Spartina*, as an ecosystem engineer, affects below-ground species abundance and diversity, supports the hypothesis that a sequence of changes in macrofaunal community structure occur in response to different stages of wetland plant invasion. We have documented how different phases ranging from early growth of newly colonizing plants to senescent adult plants affect physico-chemical processes, sediment edaphic factors as well as correlated changes in benthic animal communities. Our results showing reduced diversity and habitat quality associated with later invasion stages are consistent with other studies that have shown declines in sediment microbial activity (Wardle and Ghani 1995), supply rates of nutrients (Chapin et al. 1994) and plant litter decomposition rates (Crews et al. 1995) in mature plant invasions. The results of this study indicate that the plant stages sequence involves progressive physico-chemical alteration of the sediment conditions, where factors like sediment organic matter, anoxia, grain size, along with porewater sulfide appear closely associated with changes in macrofaunal communities. At this point we infer a causal relationship, but a definitive demonstration of these relationships awaits future experiments.

Many mechanisms have been shown to influence soft-bottom benthos including pollution, organic enrichment, anoxia/hypoxia, predation, competition and physical disturbance (e.g., Pearson and Rosenberg 1978; Zajac et al. 1982; Harkantra and Rodrigues 2003), with dynamic shifts occurring in both composition and the nature of animal–sediment interactions (Rhoads and Boyer 1982).

The patterns of benthic macrofaunal distribution observed in this and other studies (i.e., Neira et al. 2005, 2006; Grosholz et al. in press) reflect complex plant–animal interactions. For example, hybrid *Spartina* has facilitated the presence of several non-indigenous invertebrate species, creating areas of greater abundance in the recently colonized *Spartina* edge areas not present on the open mudflat (Grosholz et al. in press). Hybrid *Spartina* appears to facilitate the colonization of oligochaetes at higher elevation and at the same time to inhibit other taxa such as crustacean and bivalves. Recruitment of barnacles (*Balanus glandula*) is inhibited by hybrid *Spartina* when compared with adjacent mudflats (Neira et al. 2006). Hybrid *Spartina* also facilitates the European green crab *Carcinus maenas* in terms of abundance (particularly smaller size classes) as compared with the adjacent mudflat (Grosholz et al. in press). But, in turn, this predator inhibits the establishment of crustaceans and bivalves, reinforcing the changes brought about by this plant invasion (Neira et al. 2006). The changes of benthic macrofaunal structure observed also reflect trophic forcing (Levin et al. 2006). Hybrid *Spartina* invasion has substantially shifted the tidal flat infaunal invertebrate community from one dominated by surface microalgae feeders to one dominated by below-ground plant detritus consumers (Levin et al. 2006). In addition to direct changes in availability of detritus and algae, indirect changes in food supply for benthos may be mediated by hybrid *Spartina* reduction of flow speed affecting flux of suspended particles (Neira et al. 2006).

In our study we found five distinct faunal assemblages (Fig. 7B), which reflect *Spartina*-induced changes in the corresponding habitat properties (Fig. 7A). Flow rates might be the potential environmental driver responsible for the difference between north and south mature marshes. The significant negative correlation between fauna diversity (as taxon richness,  $H'$ ,  $J'$ ) and positive correlation of R1 dominance with sediment organic matter and porewater sulfide (Appendix A) suggest that the main factor responsible for these changes is sulfide which is toxic to a number of plant and animal species (Lee et al. 1999). Increased sulfide concentrations

and reduced faunal abundances and taxon richness occurred in our clipping experiments, and persisted far longer than the 90 days presented here (Neira, unpublished data, A. C. Tyler, pers. comm.). However, correlation does not necessarily indicate causality, and therefore further studies involving sulfide manipulation are needed to clarify the role of sulfide as a factor underlying changes in the macrofaunal community.

Because a strong correlation was observed between diversity and sediment organic matter content, it is likely that hypoxia was also involved in the macrofauna diversity decline in senescing-dieback habitats. Dieback of hybrid *Spartina* occurs during the late stage in which the plant species itself modifies sediment physico-chemical conditions. The plants, through effects on flow and detritus, create toxic, anaerobic, and waterlogged conditions that can result in self-destruction (Gray et al. 1991—for *S. anglica*). Beyond a threshold of environmental conditions created in the dieback area, increased fine-grained particles and sulfide lead to senescence and destruction of adjacent plants. At this point internal processes rather external forcing such as wrack deposition may expand the dieback areas. This problem follows the model proposed by Van de Koppel et al. (2005), in which positive feedback allows the system to buffer the effects of variation in physical conditions inducing self-organization (represented here by the mature invasion). However, as the system develops, it can be more susceptible to disturbances (e.g., smashing plants, wrack deposition), which may result in the self-destruction (dieback). It is likely that as this occurs, facilitative animal activities (burrowing, oxygenation) diminish as well, contributing to the formation of a high-stress, low-diversity ecosystem.

To summarize, we identify a sequence of stages, from tidal flat to dieback, in the invasion by hybrid *Spartina*. There are cascading changes in sediment conditions that lead to a substantial reduction in taxon richness, increased dominance, and a shift in feeding modes. At the Elsie Roemer site, this trophic shift, along a gradient from pre-invasion, immature, and mature invasion to post-invasion, is manifested as a shift from surface microalgal feeders to subsurface detritus/*Spartina* feeders. While we have attributed this shift to

plant-induced changes in toxic sulfide (and hypoxia), organic matter, and redox potential, other factors such as food availability (Levin et al. 2006), predation, and flow (Neira et al. 2006) may also be implicated. The extent to which biotic interactions drive the trajectories is unknown. Negative interactions between infaunal species, such as *M. evertus*, and *S. benedicti* (McCann and Levin 1989), could also account for disjunct species distributions associated with different invasion stages.

Understanding each stage of hybrid *Spartina* invasion may allow us to determine when and how long it will take a system (including sediment and animals) to recover after *Spartina* has been removed. Our findings provide the basis for potential use of macrofaunal species as indicators of system recovery after eradication. Understanding the general causes of different phases of

invasion, the processes responsible, and factors that can modify those processes, is critical for managing plant invasions and restoring disturbed ecosystems.

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**Appendix A** Relationships among sediment variables, diversity, total macrofaunal density, and selected macrofaunal species, whose densities significantly changed within a transect of different stages of hybrid *Spartina* invasion in Elsie Roemer, San Francisco Bay

| B. Relationships between sediment variables and macrofauna | Independent variable | R <sup>2</sup> | ± | df   | F    | P        |
|--|----------------------|----------------|---|------|------|----------|
| Taxon richness   | Sulfide              | 0.27           | – | 1,28 | 10.2 | 0.003    |
|  | Organic matter       | 0.53           | – | 1,28 | 30.9 | < 0.0001 |
|  | Eh                   | 0.43           | + | 1,28 | 20.7 | < 0.0001 |
| Shannon index (H')   | Sulfide              | 0.38           | – | 1,28 | 17.4 | 0.0002   |
|  | Organic matter       | 0.56           | – | 1,28 | 36.3 | < 0.0001 |
| Evenness (J')  | Sulfide              | 0.31           | – | 1,28 | 12.4 | 0.001    |
|  | Organic matter       | 0.32           | – | 1,28 | 13.3 | 0.001    |
| R1 Dominance   | Sulfide              | 0.32           | + | 1,28 | 13.0 | 0.001    |
|  | Organic matter       | 0.43           | + | 1,28 | 20.8 | < 0.0001 |
| Total density  | Sulfide              |                |   |      |      | NS       |
|  | Organic matter       |                |   |      |      | NS       |
| <i>Monopylephorus evertus</i>                              | Sulfide              | 0.69           | + | 1,28 | 62.9 | < 0.0001 |
|  | Organic matter       | 0.59           | + | 1,28 | 41.2 | < 0.0001 |
|  | Mud content          | 0.51           | + | 1,28 | 29.7 | < 0.0001 |
|  | Salinity             | 0.52           | + | 1,28 | 30.5 | < 0.0001 |
|  | Temperature          | 0.14           | + | 1,28 | 4.8  | 0.036    |
| <i>Tubificoides</i> spp.                                   | Sulfide              | 0.12           | + | 1,28 | 3.9  | 0.050    |
| <i>Polydora nuchalis</i>                                   | Sulfide              | 0.14           | – | 1,28 | 4.9  | 0.035    |
|  | Organic matter       | 0.32           | – | 1,28 | 13.1 | 0.001    |
| <i>Pygospio elegans</i>                                    | Organic matter       | 0.14           | – | 1,28 | 4.4  | 0.044    |
|  | Eh                   | 0.21           | + | 1,28 | 7.7  | 0.009    |
| <i>Capitella</i> spp.                                      | Sulfide              | 0.15           | + | 1,28 | 4.81 | 0.036    |
| <i>Eteone californica</i>                                  | Sulfide              | 0.17           | – | 1,28 | 5.8  | 0.032    |
|  | Organic matter       | 0.32           | – | 1,28 | 13.2 | 0.001    |
| <i>Sphaerosyllis californiensis</i>                        | Organic matter       | 0.19           | – | 1,28 | 6.6  | 0.016    |
|  | Mud content          | 0.22           | – | 1,28 | 7.9  | 0.008    |

**Appendix A** continued

| B. Relationships between sediment variables and macrofauna | Independent variable | R <sup>2</sup> | ± | df   | F    | P      |
|--|----------------------|----------------|---|------|------|--------|
| <i>Macoma petalum</i>                                      | Organic matter       | 0.23           | – | 1,28 | 8.5  | 0.007  |
|  | Chl <i>a</i>         | 0.21           | – | 1,28 | 7.5  | 0.010  |
|  | Organic matter       | 0.29           | – | 1,28 | 11.9 | 0.001  |
|  | Chl <i>a</i>         | 0.28           | – | 1,28 | 10.9 | 0.002  |
|  | Eh                   | 0.34           | + | 1,28 | 14.3 | 0.0007 |
| <i>Grandidierella japonica</i>                             | Mud content          | 0.35           | – | 1,28 | 15.0 | 0.0005 |
|  | Organic matter       | 0.26           | – | 1,28 | 9.7  | 0.004  |
| Anthozoa   | Eh                   | 0.22           | + | 1,28 | 7.8  | 0.009  |
|  | Chl <i>a</i>         | 0.213          | – | 1,28 | 7.6  | 0.010  |
| Psychodidae larvae   | Organic matter       | 0.31           | + | 1,28 | 12.7 | 0.001  |
|  | Mud content          | 0.25           | + | 1,28 | 9.5  | 0.004  |
|  | Eh                   | 0.16           | – | 1,28 | 5.3  | 0.029  |

Sampling was made in June 2004. NS = not significant, + = positive and – = negative relationships. Df = degrees of freedom

**Appendix B** Comparisons of macrofaunal assemblages of dieback area, dieback-area adjacent hybrid (Exp 1), sampled in April 2003, clipped and unclipped habitats (Exp 2), sampled after 90 d plant removal in July 2002, and five zones representing hybrid *Spartina* invasion stages (Exp 3), sampled in June 2004 in Elsie Roemer (San Francisco Bay). Pairwise Analysis of Similarity (ANOSIM) tests for macrofaunal similarities between habitats are given above the diagonal. Values on the diagonal are percent similarity within habitat (SIMPER); values below

the diagonal are percent dissimilarity between habitats (SIMPER). Significance was set at  $\alpha = 0.05$ . Experiment 1 includes: D = dieback area and AH = adjacent hybrid *Spartina*, Experiment 2 includes: C = clipped area and U = unclipped control, and Experiment 3 includes: Z1 = pre-invaded tidal flat, Z2 = hybrid leading edge (immature invasion), Z3 = hybrid inner (mature invasion), Z4 = dieback area-adjacent hybrid (senescing invasion), and Z5 = dieback area

| Habitat | Exp 1 |        | Exp 2  |        | Exp 3  |        |        |        |        |        |
|---------|-------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
|         | D     | AH     | C      | U      | Z1     | Z2     | Z3     | Z4     | Z5     |        |
| Exp 1   | D     | 52.59% | 0.322  | 0.001  | 0.001  | 0.001  | 0.003  | 0.002  | 0.002  | 0.001  |
|         | AH    | 53.71% | 40.88% | 0.001  | 0.001  | 0.024  | 0.069  | 0.033  | 0.001  | 0.002  |
| Exp 2   | C     | 84.12% | 87.95% | 33.40% | 0.002  | 0.001  | 0.001  | 0.001  | 0.002  | 0.023  |
|         | U     | 82.13% | 85.78% | 71.07% | 32.40% | 0.002  | 0.001  | 0.001  | 0.138  | 0.314  |
| Exp 3   | Z1    | 82.69% | 85.49% | 83.15% | 70.54% | 75.69% | 0.002  | 0.002  | 0.002  | 0.002  |
|         | Z2    | 81.88% | 82.89% | 77.31% | 69.93% | 61.43% | 50.96% | 0.006  | 0.002  | 0.002  |
|         | Z3    | 86.71% | 85.75% | 81.55% | 77.25% | 84.39% | 72.86% | 31.02% | 0.002  | 0.002  |
|         | Z4    | 59.99% | 58.29% | 82.86% | 82.34% | 82.57% | 78.16% | 84.80% | 61.85% | 0.201  |
|         | Z5    | 55.67% | 55.19% | 83.42% | 84.61% | 86.24% | 80.45% | 87.09% | 39.93% | 60.85% |

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