

Benthic macrofaunal communities of three sites in San Francisco Bay invaded by hybrid *Spartina*, with comparison to uninvaded habitats

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ABSTRACT: A hybrid cordgrass, formed from a cross between *Spartina alterniflora* (Atlantic cordgrass) and *S. foliosa* (Pacific cordgrass), has recently spread within the intertidal zone of south San Francisco Bay. Sediment properties and macroinfaunal community structure were compared in patches invaded by *Spartina* hybrid and adjacent uninvaded patches at 3 sites in San Francisco Bay (2 tidal flats and 1 *Salicornia* marsh). We hypothesized that (1) sediments vegetated by *Spartina* hybrid would have reduced sediment grain size, higher organic matter content, lower redox potential, lower salinity and reduced microalgal biomass relative to adjacent unvegetated tidal flat sediments, and (2) that differences in the sediment environment would correspond to changes in the infaunal invertebrate community structure and feeding modes. We observed 75% lower total macrofaunal density and lower species richness in *Spartina*-vegetated sediments at Elsie Roemer (30 yr old invasion) than in an adjacent unvegetated tidal flat. This was due to lower densities of surface-feeding amphipods, bivalves, cirratulid and spionid polychaetes. The proportional representation of subsurface-deposit feeders was greater in *Spartina* patches than in unvegetated sediments. At a more recently invaded site (Roberts Landing; 15 yr invasion), *Spartina* patches differed from tidal flat sediments in composition, but not in abundance. Native (*Salicornia*) and *Spartina* patches exhibited similar sediment properties at San Mateo, where the *Spartina* hybrid invaded 8 to 10 yr earlier. No differences were detected in densities or proportions of surface- or subsurface-deposit feeders, but the proportion of carnivores/omnivores and grazers increased in the hybrid-invaded patches. These studies suggest that the invasive *Spartina* hybrid in south San Francisco Bay can have differing effects on sediment ecosystems, possibly depending on the location, age, or type of habitats involved.

KEY WORDS: Benthos · Biodiversity · Cordgrass · Deposit feeding · Infauna · Macrobenthos · Plant invasion · Salt marsh · Redox potential

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INTRODUCTION

The presence of plants in tidal settings affects ecosystem-level processes such as nutrient cycling and productivity by altering hydrographic properties, disturbance frequency and sedimentation rates (Bertness 1988, De la Cruz et al. 1989, Leonard & Luther 1995). The sediments, microbes, infaunal invertebrates and marsh macrophytes of coastal wetlands form a highly integrated system whose ecological functions (e.g. decomposition, nutrient cycling, trophic support, baffling) provide key ecosystem services such as nursery support, water filtration, and

storm protection (Snelgrove 1999, Snelgrove et al. 1997, 2000). The ability of vascular plant presence, cover, density and composition to influence the structure and function of wetlands has been widely recognized (Leonard & Luther 1995, Levin & Talley 2000). Plant effects on salt marsh sediments and biota have been elucidated through investigations of newly restored ecosystems (Levin et al. 1996, Craft & Sacco 2003, Stanczak & Keiper 2004) and by tracking changes following plant invasion (Posey 1988, Posey et al. 1993, Talley & Levin 2001).

Introduction of non-indigenous plant species into tidal wetlands has occurred worldwide (Ruiz et al. 1997,

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Adam 2002). By controlling, space and food resources available to other organisms through alterations in biotic, physical and biogeochemical sedimentary properties (e.g. Levin & Talley 2000, Talley & Levin 2001), vascular plants invading tidal habitats typically act as ecosystem engineers (Jones et al. 1994, Crooks 2002).

Plant invasions of tidal habitats are widespread on the east and west coasts of North America and in Europe. The purple loosestrife *Lythrum salicaria* has replaced native species in wetlands of Canada and Washington State (Thompson et al. 1987). The reed grass *Phragmites australis* has invaded large areas of mid-Atlantic tidal *Spartina alterniflora* marsh (Leonard et al. 2002), and the Japanese eelgrass *Zostera japonica* has invaded extensive mudflat areas of Oregon and Washington (Posey 1988). On the west coast of North America, there are 4 non-native species of *Spartina* (*S. alterniflora*, *S. anglica*, *S. patens*, and *S. densiflora*) and 1 native species, *S. foliosa* (Daehler & Strong 1996, Ayres et al. 2004). The smooth cordgrass *S. alterniflora*, native to the east coast of North America and the Gulf of Mexico, is found in Willapa Bay, Washington State and in San Francisco Bay, California (Spicher & Josselyn 1985, Daehler & Strong 1997) as well as Tasmania (Australia) (Hedge & Kriwoken 2000) and China (Chung 1990).

Spartina alterniflora was first introduced into San Francisco Bay, California, USA as part of experimental marsh restoration projects by the US Army Corps of Engineers (USACE) in the early 1970s. Early on, Callaway & Josselyn (1992) recognized the competitive superiority and greater ecological range of the exotic *Spartina* relative to the native (*S. foliosa*) and predicted the native *S. foliosa* would be outcompeted and eliminated. Soon after its introduction, *S. alterniflora* hybridized naturally with the native cordgrass *S. foliosa* (Daehler & Strong 1997), producing a more vigorous plant, which has since invaded numerous marshes in south San Francisco Bay (Ayres et al. 1999). Compared with their parental species, the hybrids are taller, grow at a greater stem density, and have a denser root system (Ayres et al. 2003). At the time of writing, *S. alterniflora* and its hybrids covered ca. 190 ha of tidal flat and salt marsh in San Francisco Bay, mainly in south Bay.

Effects of plant invasion on sediment properties, plant and macrofaunal composition are not consistent among sites. Marsh sediments invaded by *Phragmites australis* along the lower Connecticut River estuary, exhibited much lower organic matter content, greater litter accumulation and higher chlorophyll *a* concentrations than the uninvaded areas (Talley & Levin 2001). Also, macro-infaunal densities were lower and the assemblage shifted from dominance by burrowing oligochaetes and midges to tube-building and surface-feeding forms. In *Spartina anglica* and *S. foliosa* marshes, lower diversity or density and different

macrofaunal composition have been reported relative to unvegetated areas (Frid & James 1989, Jackson 1985, Levin et al. 1998). However, in SE Brazil, higher macrofaunal density and species richness were observed in *S. alterniflora* habitats relative to unvegetated areas (Lana & Guiss 1991). *S. alterniflora*-invaded mudflats of Willapa Bay, Washington State, USA exhibited higher macrofaunal densities than uninvaded areas, and an increase in subsurface, deposit-feeding taxa (e.g. *Capitella*) occurred in older meadows of *S. alterniflora* (Zipperer 1996).

In this study we compare sediment properties and macroinfaunal community structure in 3 paired *Spartina* hybrid-invaded and adjacent uninvaded habitats of south San Francisco Bay. In 2 locations, unvegetated tidal flats are being invaded by *Spartina* hybrid. In a third, a *Salicornia virginica* marsh is being invaded by *Spartina* hybrid. Our general understanding of how macrophytes influence salt marsh sediments and infauna (reviewed in Levin & Talley 2000) guided the sampling. We hypothesized that (1) *Spartina* hybrid-vegetated sediments would have finer sediment grain size, higher organic matter content, lower redox potential, lower salinity and reduced microalgal biomass, relative to adjacent unvegetated tidal flat sediments, and (2) that differences in the sediment environment would correspond to changes in the macroinfaunal community structure and feeding modes. Observations of sediment and faunal differences associated with *Spartina* hybrid habitat of San Francisco Bay may provide valuable information about the role of vascular plants in structuring marsh ecosystems, as well as baseline data against which to document further change. We focused on the macroinfaunal community because it represents an important trophic link between primary production derived from the marsh and higher consumers (Currin et al. 1995, Kreeger & Newell 2000). Changes in abundance, composition, and lifestyles of infaunal organisms, and hence their accessibility to consumers, reflect the extent and efficiency of trophic functions in coastal wetlands.

MATERIALS AND METHODS

Study locations. Sampling was conducted in June 2001 at 3 sites in south San Francisco Bay, California, USA (Fig. 1). The northernmost site, Elsie Roemer, lies in the city of Alameda along the shoreline adjacent to Elsie Roemer Bird Sanctuary (37°45'35" N, 122°28'48" W). *Spartina*-hybrid first invaded the tidal flat here about 30 yr ago. The invaded area forms a continuous meadow of *Spartina* hybrid which borders the open tidal flat (Fig. 1). In addition, there are some islands of *Spartina* hybrid scattered 20 to 50 m from the

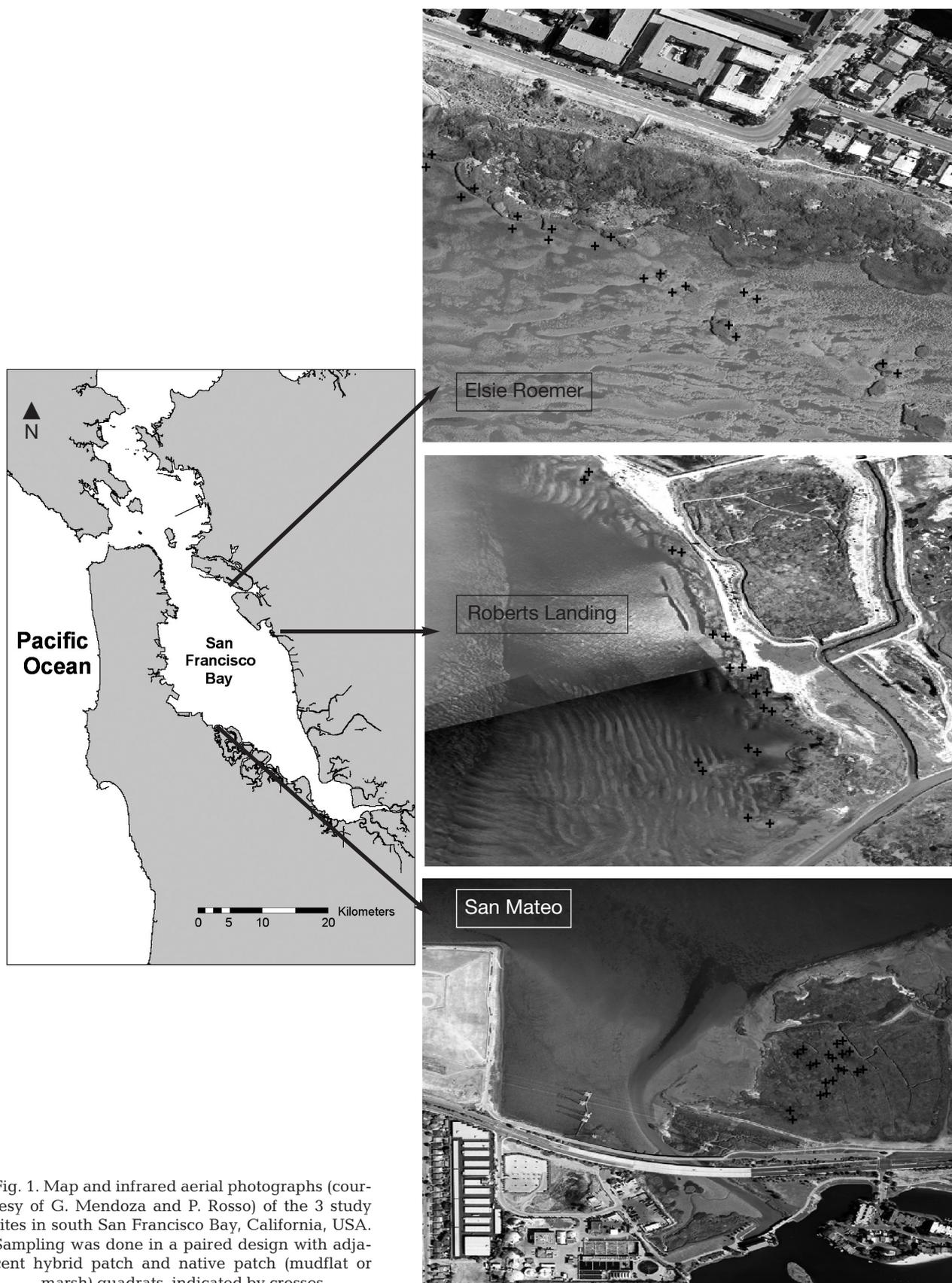


Fig. 1. Map and infrared aerial photographs (courtesy of G. Mendoza and P. Rosso) of the 3 study sites in south San Francisco Bay, California, USA. Sampling was done in a paired design with adjacent hybrid patch and native patch (mudflat or marsh) quadrats, indicated by crosses

edge of the meadow (Fig. 1). Both meadows and islands were sampled.

Approximately 12 km to the south, we sampled Roberts Landing (37° 40' 13" N, 122° 09' 42" W), a long exposed shoreline, situated north of Hayward Regional Shoreline, near San Lorenzo Creek. The invasion involves 10 to 15 yr old *Spartina* patches of various heights and densities scattered along the shoreline within the tidal flat. Genetic characterization of *Spartina* from this site using RAPD markers (Random Amplified Polymorphic DNA; D. Strong, D. Ayres pers. comm.) revealed the presence of *Spartina* hybrids and the native *S. foliosa* co-existing side by side. Sampling included both tall (*Spartina* hybrid) and short (native *S. foliosa*) vegetated patches.

We sampled San Mateo marsh, a vegetated site on the western side of south San Francisco Bay (37° 41' 11" N, 122° 17' 06" W) (Fig. 1) where the perennial *Salicornia virginica* is the dominant vascular plant. At higher tidal elevations, the macrophytes *Distichlis spicata*, *Frankenia salina*, *Triglochin maritima*, and *Grindelia* sp. are also present. The invasion of *Salicornia*-dominated areas by *Spartina* hybrid in San Mateo is estimated to be relatively recent (8 to 10 yr ago). Large round patches (40 to 240 m²) have been converted from *Salicornia*-inhabited areas into monotypic swards of *Spartina* hybrid, with about 50% cover by *Spartina* hybrids in 1999 (Ayres et al. 2004).

Sampling design and field methods. A pair-wise sampling design was used to compare sediment and biotic properties of hybrid-invaded patches to adjacent tidal flats (Elsie Roemer, Roberts Landing) and to *Salicornia* marsh (San Mateo). A total of 10 replicate blocks separated by about 20 to 50 m from one another were established along the shoreline (Elsie Roemer and Roberts Landing) or in the marsh (San Mateo). Within each block, we sampled 1 hybrid-invaded quadrat (0.5 × 0.5 m) and 1 control patch in the adjacent (ca. 5 m away) open tidal flat (Elsie Roemer, Roberts Landing) or *Salicornia* meadow (San Mateo). At Elsie Roemer, the blocks included continuous meadow and islands of *Spartina* hybrid (5 each) (Fig. 1). At Roberts Landing, 6 blocks were established along the shoreline, and an additional 4 were *Spartina* islands (Fig. 1). One 0.25 m² quadrat was designated haphazardly within the plant-invaded area and within the open tidal flat of the corresponding block.

Within each quadrat, measurements were made of total *Spartina* (or *Salicornia*) stem density, average stem height (n = 15) for *Spartina* hybrid plants, percent open space (space between culms), percent cover for each plant species, and percent cover of green algae and/or microalgae mat. Light penetration was measured above and below the hybrid canopy or at the sediment surface

in unvegetated quadrats using a LICOR spherical sensor (LI-192SA) with a LI-1400 data logger.

Pore water salinity was measured in each quadrat from the top 3 cm of sediment. The sediment was squeezed against a Whatman filter paper inside a 10 cm³ syringe and the salinity was measured with a hand-held salinity refractometer. Small cores were collected within each quadrat for determination of benthic chlorophyll a (1.13 cm² × 5 mm depth) and of pigment composition (0.56 cm² × 5 mm) using high performance liquid chromatography (HPLC). An additional core (1.13 cm² × 1 cm) was used to determine water content and porosity. Cores (18.1 cm², 0 to 6 cm) were collected for analyses of macrofauna and belowground plant biomass (from the same sediment core) and sediment properties including particle size and organic matter content. Macrofaunal cores were preserved in 8% buffered formalin with rose bengal. Samples for HPLC were put in glass vials and kept at -80°C; the remaining sediment samples were kept frozen at -20°C until further analysis. Sediment redox potential was measured at the 3 study sites at 1 and 5 cm depth in the sediment column with a portable Mettler Toledo mV-meter. In order to better examine redox depth gradients at the *Spartina*-vegetated and tidal flat habitats of Elsie Roemer, a more detailed redox depth profile was generated by gradually inserting a single electrode (Mettler Toledo InLab®) at 1 cm intervals through the sediment. The mV readings were corrected to the standard hydrogen electrode by adding +207 mV (Giere et al. 1988).

Information about below-ground sediment structure of vegetated and unvegetated sediments in Elsie Roemer and Roberts Landing was obtained by X-raying 2 replicate slabs of sediments collected with a plexi-glass corer (3 × 12 × 18 cm deep). X-radiography was performed using ACOMA's model PX-20N portable X-ray unit.

Tidal elevations for each block at each location in vegetation and on mudflats were surveyed with a Topcon Total Station (Model GTS-603). Tidal elevations for all field sites were referenced to NOAA tidal benchmarks (using NAVD 88) that had been resurveyed within the last 15 yr. At least 2 tidal benchmarks were located within the vicinity of each site and we surveyed benchmarks relative to each other to check for accuracy.

Laboratory methods. Sediment cores for analysis of macrofauna and below ground plant material were washed through a 0.3 mm mesh. Animals retained on the sieve were sorted, counted and identified to the lowest taxonomic level possible using a dissecting microscope and, when necessary, compound microscope. Feeding modes were assigned based on Fauchald & Jumars (1979). Below-ground plant detritus material (≥0.3 mm) was removed from the macrofaunal cores (upper 6 cm), dried at 60°C and weighed on an analytical balance. Because in San Mateo the

Spartina hybrid was already established as mono-specific patches inside the *Salicornia* meadow, all root material within the core was assumed to be from *Spartina* plants. Sediment samples for grain size and organic matter content analysis were homogenized and wet-sieved through a 2 mm mesh to remove large shells and roots. A portion of sediment was digested with hydrogen peroxide and wet sieved through a 63 μm mesh for particle size analysis. Both fractions of the sample (≥ 63 and < 63 μm) were dried at 60°C and weighed to determine percent sand. Total organic matter content was determined by weight loss of dried sediment after ignition at 500°C for 4 h. Water content and porosity were determined by weight loss after drying a known volume of sediment and assuming a sediment and water density of 2.65 g cm⁻³ (quartz) and 1.025 g cm⁻³, respectively (Buchanan 1984).

Chlorophyll *a* concentration was determined spectrophotometrically from sediment samples extracted with 90% acetone according to Plante-Cuny (1973). Because our study system was limited to the sediment ecosystem, the chlorophyll *a* is an estimate of living microalgal biomass from the sediment not including algae attached to plant stems. More detailed pigment composition was analyzed using HPLC techniques (Brotas & Plante-Cuny 1998) following extraction with 90% acetone. Pigments were identified based on comparisons of their retention times with single species standards. Analysis for differences in microphytobenthos composition was based on the abundances of chlorophyll *a* (all oxygenic photoautotrophs), zeaxanthin (cyanobacteria), and lutein (green algae and vascular plants). Fucoxanthin was used as an indicator of diatoms because microscopic observations revealed the absence or very low amounts of brown algae and dinoflagellates, the other algae containing this pigment. Changes in microbial mat community composition was estimated by the ratio of zeaxanthin to fucoxanthin, which reflects the abundance of cyanobacteria relative to diatoms (Pinckney et al. 1995).

Statistical analysis. Matched-pairs *t*-tests (using JMP 4.0 statistical software) were used to test for significant differences in macrofauna, sediment properties, and environmental variables between invaded and uninvaded habitats. One-way ANOVA with an *a posteriori* Tukey's HSD test was used to examine between-site differences in sediment and faunal properties. One standard error (SE) about the mean is presented with mean data unless otherwise indicated. All proportion data were arcsin-square-root transformed prior to ANOVA and then back-transformed for presentation in graphs.

Similarities and differences in macrofaunal communities were explored using non-metric multidimensional scaling (MDS), based on Bray-Curtis similarity indices. Stress values indicate how well the solution (2-dimensional MDS plot) reflect the similarities among cores. Values < 0.1 are good and < 0.2 are useful (Clarke 1993). Pair-wise comparisons for significant differences in macrofaunal composition between habitats (and sites) were made using Analysis of Similarity (ANOSIM) (Clarke 1993). Similarity Percentage (SIMPER) analyses were used to determine the percent of dissimilarity (or similarity) of samples and the particular taxa responsible for differences between groups (Clarke 1993). These multivariate analyses (MDS, ANOSIM, SIMPER) were run using PRIMER (Plymouth Marine Laboratory, Clarke 1993, Clarke & Warwick 1994) on square-root-transformed, unstandardized data.

RESULTS

Vegetation and algae characteristics

The former open tidal flat sediments of Elsie Roemer and Roberts Landing were converted to a grass landscape by the invasive *Spartina* hybrid (Fig. 1). The invaded tidal flat habitats had higher shoot density at Roberts Landing (450 ± 60 plants m⁻²) than Elsie Roemer (292 ± 19 plants m⁻²) ($t_{18} = 2.4$, $p = 0.025$). At both sites tall stems formed a compact below-ground root matrix and a dense canopy (Fig. 2). The shoot density of *Spartina*-hybrid patches growing in San Mateo (269 ± 35 plants m⁻²) was significantly lower than shoot density in the native *Salicornia virginica* habitat (698 ± 115 plants m⁻²) ($t_{18} = 3.6$, $p = 0.002$), but no differences were observed in plant height, percent cover and below-ground plant biomass between the *Spartina*-invaded and *Salicornia*-vegetated sediments (Fig. 3).



Fig. 2. Compact below-ground root matrix formed by *Spartina* hybrid at Elsie Roemer. (Photo by C.N., June 2001)

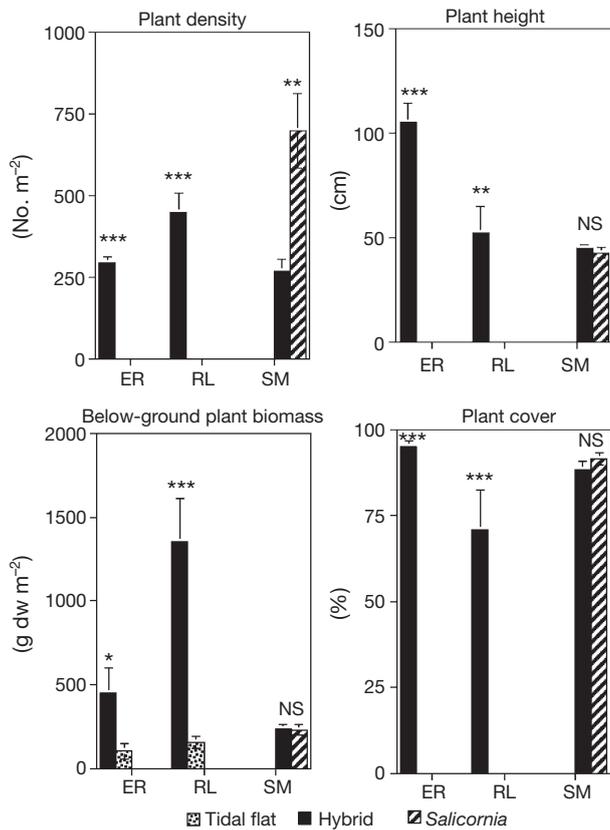


Fig. 3. *Spartina* properties at Elsie Roemer (ER), Roberts Landing (RL) and San Mateo (SM) in south San Francisco Bay. Values are mean \pm 1 SE. Asterisks indicate significant differences based on paired *t*-tests comparing invaded patches (*Spartina* hybrid) and uninvaded patches (tidal flat or *Salicornia* marsh). * $0.01 \leq p < 0.05$, ** $0.001 \leq p < 0.01$, *** $p < 0.001$

Microphytobenthos

There were no significant differences in sediment microalgal biomass, as reflected by chlorophyll *a* concentration, between *Spartina*-invaded and uninvaded sediments at any of the 3 sites (Fig. 4). However, at Elsie Roemer we found higher chlorophyll *a* concentrations in sediments of the *Spartina* hybrid islands relative to the meadow ($p = 0.022$). At Roberts Landing, the diatom biomass, as indicated by the concentration of fucoxanthin, was significantly reduced in the hybrid-invaded habitat ($7.97 \pm 1.04 \mu\text{g cm}^{-2}$) relative to the tidal flat ($13.34 \pm 1.33 \mu\text{g cm}^{-2}$) ($t_{3,2} = 18$, $p = 0.005$). Concentrations of lutein (green algae and vascular plants) and zeaxanthin (cyanobacteria) did not differ between invaded and uninvaded habitats. There was considerable variability in the ratios of zeaxanthin to fucoxanthin among samples, indicating a highly patchy distribution of the microphytobenthos groups, but no differences in this ratio were detected between *Spartina*-invaded and uninvaded sediments at any site.

Environmental and sediment properties

Sediment properties in *Spartina* hybrid-invaded habitats differed relative to those of the adjacent uninvaded tidal flat sediments. *Spartina*-invaded patches in Roberts Landing were finer-grained ($t_9 = 2.4$, $p = 0.042$), with higher organic matter content relative to uninvaded patches ($t_9 = 2.4$, $p = 0.05$). However, in Elsie Roemer and San Mateo, these properties did not vary significantly among patch types (Fig. 4). Invaded sediments exhibited lower porewater salinities ($t_9 = 3.4$, $p = 0.008$) at Elsie Roemer and Roberts Landing, but no major changes were observed in porosity (Fig. 4).

Spartina hybrid-invaded patches occurred 0.3 m higher in the intertidal than the adjacent tidal flats both at Elsie Roemer and Roberts Landing (Fig. 4). At Elsie Roemer, mean elevations (\pm SE) of the vegetated area and tidal flat were 0.98 ± 0.05 m and 0.64 ± 0.06 m above mean lower low water (MLLW), respectively ($t_{18} = 4.3$, $p = 0.0005$) while at Roberts Landing, mean elevations of the vegetated area and tidal flat were 2.81 ± 0.10 m and 2.54 ± 0.03 m above MLLW, respectively ($t_{18} = 4.4$, $p = 0.0003$). Also, hybrid island sites at both Elsie Roemer (Fig. 2) and Roberts Landing showed higher elevations than the meadow. This may have been caused by erosion of surrounding tidal flat sediments (E.D.G. pers. obs.). At San Mateo, no significant difference in elevation was found between the hybrid-vegetated area (1.99 ± 0.02 m above MLLW) and the *Salicornia* meadow (2.02 ± 0.02 m above MLLW) ($t_{18} = 1.3$, $p = 0.203$).

Light penetration was significantly lower (83 and 71%, respectively, $p < 0.001$) as was open space ($p < 0.001$) at the *Spartina* hybrid-vegetated sites (Elsie Roemer, Roberts Landing) relative to the unvegetated tidal flat sites. At San Mateo, the high number of plants as well as the dense canopy (about 90% cover) (Fig. 3) led to low light penetration and open space in both *Spartina*-invaded and *Salicornia* habitats (Fig. 4).

Redox potential, which is often used to quantify the degree of reduction or oxidation, and hence availability of nutrients, of wetland sediments (Gambrell & Patrick 1978), differed slightly in *Spartina* hybrid-invaded sediments relative to uninvaded sediment patches. In general, most sediments exhibited reduced conditions ($E_h < +100$ mV, Meyer-Reil 1983) in the top 1 and 5 cm (Fig. 5A,B). Depth profiles of E_h made in Elsie Roemer revealed that sediments underlying stands of *Spartina* hybrid were more oxidized than uninvaded tidal flat habitats (Fig. 5C) ($t_{14} = 6.4$, $p < 0.0001$). Our E_h measurements down to 8 cm covered most of the root-matrix zone and suggest that *Spartina* hybrid oxidizes the sediments around the roots and rhizomes.

X-radiographs of sediments in Elsie Roemer and Roberts Landing (tidal flat invasions) revealed dif-

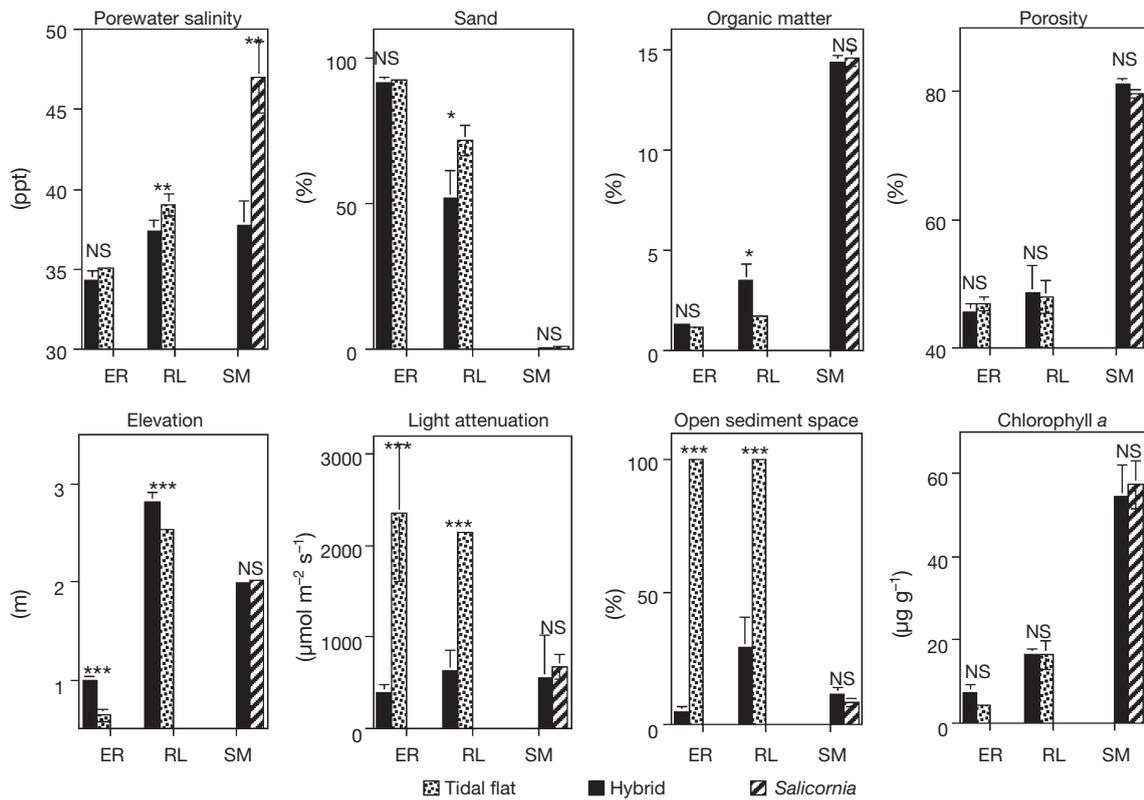


Fig. 4. Sediment properties and microalgal biomass (chl a) at Elsie Roemer (ER), Roberts Landing (RL) and San Mateo (SM) in south San Francisco Bay. Values are mean \pm 1 SE. Asterisks indicate significant differences based on paired *t*-tests comparing invaded patches (*Spartina* hybrid) and uninvaded patches (tidal flat or *Salicornia* marsh). * $0.01 \leq p < 0.05$, ** $0.001 \leq p < 0.01$, *** $p < 0.001$

ferences in below-ground structure between the *Spartina* hybrid-invaded habitat and open tidal flats (Fig. 6). At Elsie Roemer, hybrid-invaded sediments had a compact root matrix with no apparent lamination and bivalves and polychaete tubes were scarce (Fig. 6A). In contrast, the uninvaded tidal flat sediments were bioturbated, especially the top 2 cm layer, with visible tubes of spionid (e.g. *Pygospio elegans*, *Streblospio benedicti*) and capitellid polychaetes (*Heteromastus filiformis*, *Capitella* spp.) and bivalve shells (*Gemma gemma*) (Fig. 6B).

At Roberts Landing, the plant-invaded sediment had characteristics similar to Elsie Roemer, with a dense network of tiny rhizomes, 2 imperfect laminations (Fig. 6C) and the top few mm bioturbated by worm burrows. However, the adjacent tidal flat showed a conspicuously structured sediment profile (Fig. 6D). The uppermost 5 cm were relatively homogeneous with active feeding voids and

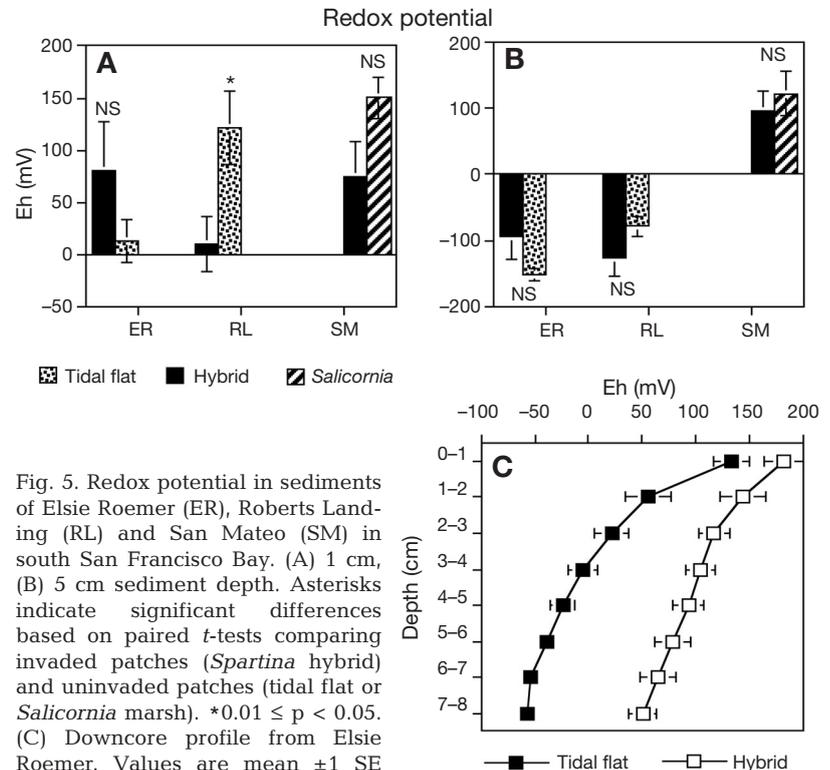


Fig. 5. Redox potential in sediments of Elsie Roemer (ER), Roberts Landing (RL) and San Mateo (SM) in south San Francisco Bay. (A) 1 cm, (B) 5 cm sediment depth. Asterisks indicate significant differences based on paired *t*-tests comparing invaded patches (*Spartina* hybrid) and uninvaded patches (tidal flat or *Salicornia* marsh). * $0.01 \leq p < 0.05$. (C) Downcore profile from Elsie Roemer. Values are mean \pm 1 SE

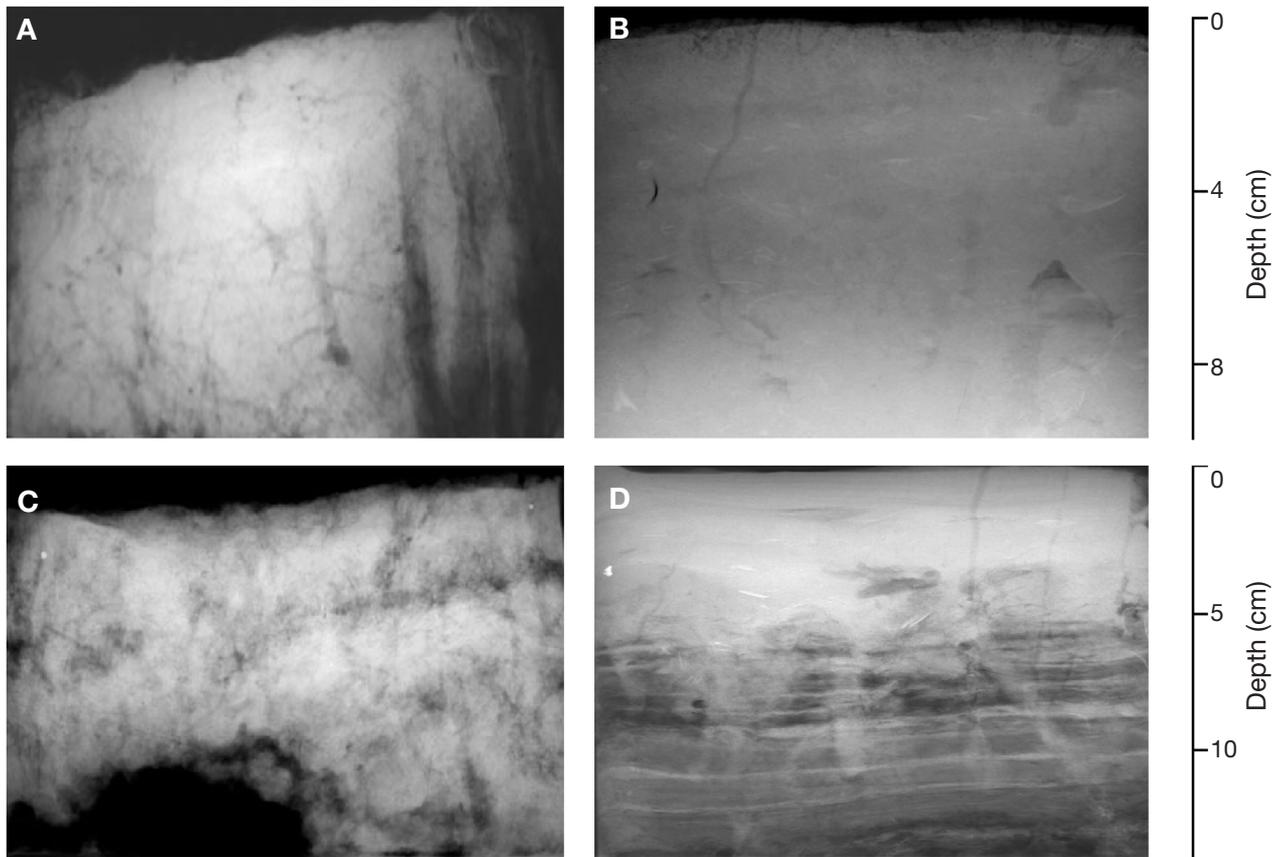


Fig. 6. X-radiographs of sediments from (A) Elsie Roemer hybrid *Spartina* marsh, (B) Elsie Roemer tidal flat, (C) Roberts Landing hybrid *Spartina* marsh, (D) Roberts Landing tidal flat. Note laminated sediments beneath a bioturbated zone in (D)

bivalve shells, with sediments crossed by capitellid burrows. Underneath this layer, the sediment displayed distinct laminae crossed by old roots and rhizomes, suggesting earlier vegetation at the site (Fig. 6D). The very thin lamination intervals indicated a rapid, short-term sediment accumulation in this formerly vegetated habitat. The presence of rooted vegetation disrupts the sediment layers and may have resulted in addition of organic material to greater depth.

Macrofaunal abundance, composition and diversity

Macrofaunal community structure differed in each system studied. At Elsie Roemer total density was 75% lower ($p < 0.001$) in *Spartina* hybrid sediments ($10.9 \text{ ind. cm}^{-2}$) than on tidal flats ($41.3 \text{ ind. cm}^{-2}$), but sediments of Roberts Landing and San Mateo exhibited no density differences between *Spartina* and reference sites (Fig. 7). *Spartina* hybrid areas were associated with lower species richness (evaluated as the number of species per core) and different macrofaunal community composition than the unvegetated

tidal flat sites (Fig. 7). Significantly lower densities of amphipods (*Grandidierella japonica*, corophiid spp.), bivalves (*Gemma gemma*), and cirratulid polychaetes (*Tharyx* spp.) were recorded (Table 1). Densities of capitellid polychaetes (*Heteromastus filiformis*, *Capitella* spp.) and tubificid oligochaetes (*Tubificoides brownae*, *T. fraseri*) were similar in *Spartina* hybrid and tidal flat sediments (Table 1). No differences were recorded in faunal parameters or diversity indices between *Spartina* island and *Spartina* meadow sites at Elsie Roemer and Roberts Landing.

In the naturally vegetated marsh (San Mateo), *Spartina* hybrid- and *Salicornia*-dominated sediments exhibited few faunal differences (Fig. 7). Total macrofaunal densities were similar and only 5 of 32 species exhibited density differences in invaded and uninvaded patches. Two tubificid oligochaetes (*Tubificoides brownae* and *Tubificoides* sp. A) and a gastropod (*Myosotella myosotis*) were more abundant in hybrid-invaded sediments, while the tubificid oligochaete *Tubificoides heterochaetus* and 1 spionid polychaete (*Pygospio elegans*) were more abundant in *Salicornia*-vegetated sediments (Table 1). Species richness

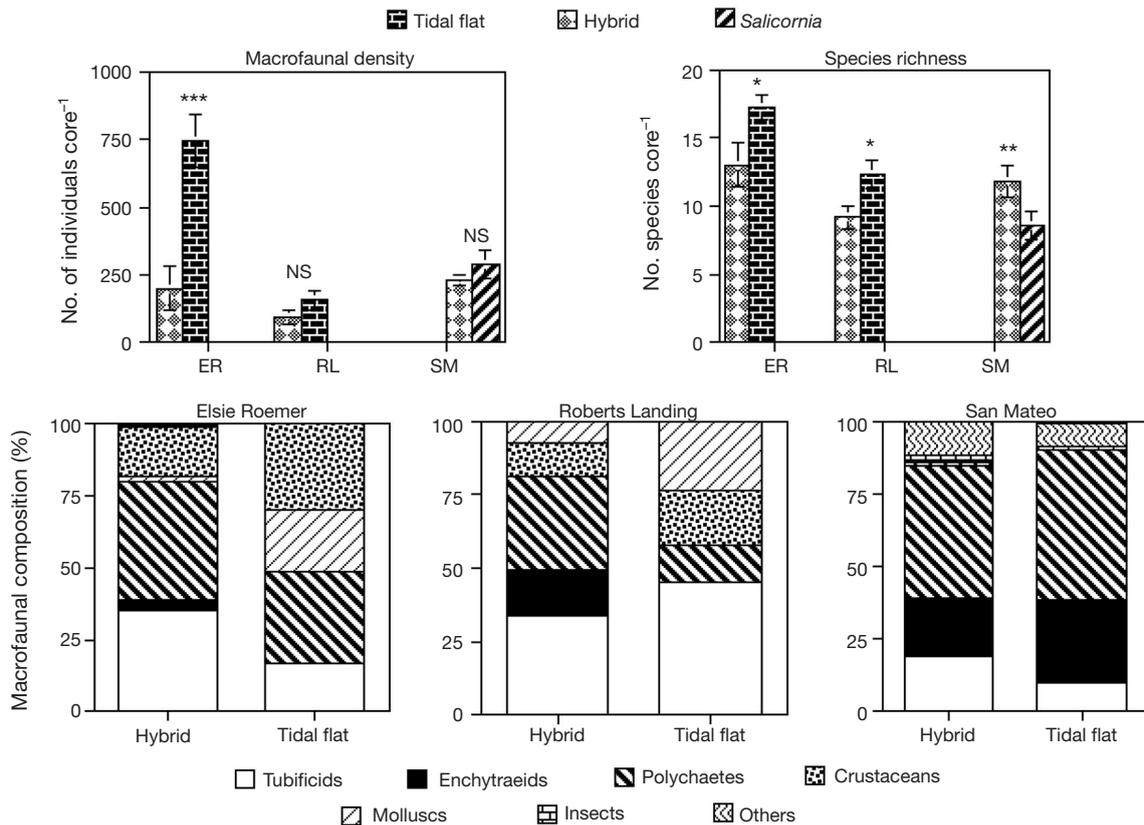


Fig. 7. Macrofaunal density, species richness and composition at Elsie Roemer (ER), Roberts Landing (RL) and San Mateo (SM) in south San Francisco Bay. Values are mean \pm 1 SE. Asterisks indicate significant differences based on paired *t*-tests comparing invaded patches (*Spartina* hybrid) and uninvaded patches (tidal flat or *Salicornia* marsh). * $0.01 \leq p < 0.05$, ** $0.001 \leq p < 0.01$, *** $p < 0.001$

was 30% higher ($t_{18} = 2.7, p = 0.013$) in the *Spartina* hybrid patches relative to the *Salicornia* meadow, which we attributed to the presence of podurid, ephidrid, aphidid, saldid, and formicid larval insect species. However, in terms of density there were no differences between habitats (Table 1).

Multivariate analyses (MDS) of macrofaunal assemblages (Fig. 8) indicate community differences between *Spartina*-invaded and uninvaded sediment (ANOSIM, $p = 0.001$ and $p = 0.003$, for Elsie Roemer and Roberts Landing, respectively). The extent of community similarity between *Spartina*-invaded and uninvaded habitats was similar in Elsie Roemer and in Roberts Landing (SIMPER, both 31% similarity, ANOSIM, $p < 0.005$) (Table 2). For our analysis we considered tall and short *Spartina* patches as a single entity in Roberts Landing because (1) they exhibited no difference in total macrofaunal density ($t_8 = 0.3, p = 0.805$), (2) multivariate analyses indicated the macrofaunal assemblage was not different (ANOSIM, $p = 0.754$), and (3) densities of all 29 species present did not show significant differences (each $p > 0.05$) between tall and short plant habitat. At San Mateo, macrofaunal communities in the *Salicornia*-vegetated

(uninvaded) sediment differed from those patches invaded by *Spartina* hybrid (ANOSIM, $p = 0.014$), with only 50% similarity (SIMPER) (Fig. 8, Table 2).

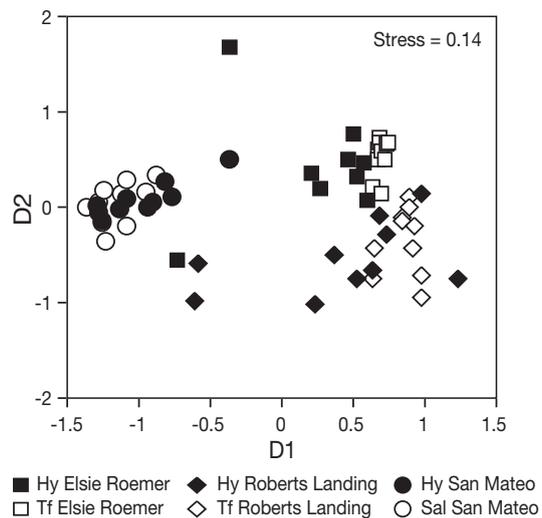


Fig. 8. Multidimensional scaling (MDS) plot of macrofaunal assemblages (≤ 0.3 mm) in hybrid-invaded sediments (Hy) and tidal flat sediments (Tf) at Elsie Roemer, Roberts Landing, and San Mateo in south San Francisco Bay

Table 1. Mean densities of macrofauna (>0.3 mm) in *Spartina hybrid*-invaded and uninvaded tidal flats and *Salicornia*-dominated marshes of south San Francisco Bay. Values are average number of individuals per 18.1 cm² × 6 cm deep core (1 SE), n = 10. Samples were collected in May/June 2001. p-values are given for paired *t*-tests comparing *Spartina*-invaded and uninvaded sediments at each site. 'Other Diptera' include Psychodidae larvae, Dolichopodidae pupae, Ceratopogonidae larvae, Ephidridae larvae

Taxon	Elsie Roemer			Roberts Landing			San Mateo		
	<i>Spartina hybrid</i>	Tidal flat	p	<i>Spartina hybrid</i>	Tidal flat	p	<i>Spartina hybrid</i>	<i>Salicornia</i>	p
Annelida									
Oligochaeta									
<i>Tubificoides brownae</i>	68.6 (32.6)	72.6 (12.9)	0.923	14.2 (11.1)	35.8 (15.2)	0.330	6.3 (2.3)	0	0.025
<i>Tubificoides fraseri</i>	0.7 (0.5)	11.5 (8.7)	0.249	14.3 (10)	30.9 (12.4)	0.362	0.7 (0.7)	0	0.343
<i>Tubificoides heterochaetus</i>	0	0		0	0		0.3 (0.3)	8 (3)	0.035
<i>Tubificoides inops</i>	0	0		0	1.9 (1.3)	0.198	0	0	
<i>Tubificoides</i> sp. A	0	0		0	0		4.4 (1.5)	1.4 (1.3)	0.054
<i>Tubificid</i> sp.	0	0		0	0		1.5 (0.9)	0.8 (0.5)	0.535
<i>Tectidrilus diversus</i>	0	42 (15.1)	0.022	0	0		0	0	
<i>Limnodriloides barnardi</i>	0	0		2.3 (1.3)	1.1 (0.6)	0.140	0	0	
<i>Monopylephorus rubroniveus</i>	0	0		0	0		1.6 (1)	0	0.148
Naididae	0	0		0	0		27.6 (5.6)	17 (8.9)	0.237
Enchytraeidae	7.1 (5.1)	0	0.197	13.6 (12.7)	0	0.312	45.9 (14)	84.1 (41)	0.420
Polychaeta									
<i>Pseudopolydora paucibranchiata</i>	0	0.3 (0.2)	0.081	0	0		0	0	
<i>Pseudopolydora kempii</i>	3.9 (2.8)	8.1 (8.1)	0.221	0.3 (0.3)	0	0.193	0	0	
<i>Polydora cornuta</i>	0.5 (0.4)	3.9 (3.9)	0.097	4.5 (2.3)	0.4 (0.2)	0.097	0	0.1	0.343
<i>Boccardia proboscidea</i>	34.8 (20.4)	0.3 (0.3)	0.127	0	0		0	0	
<i>Streblospio benedicti</i>	9.5 (8.4)	34.1 (11.3)	0.112	7.6 (3.6)	5.5 (2.3)	0.669	0.2 (0.1)	0.1 (0.1)	0.343
<i>Pygospio elegans</i>	5 (3.3)	117 (45.8)	0.034	1.2 (0.7)	0.5 (0.3)	0.321	4.8 (3)	17.5 (5.8)	0.037
<i>Heteromastus filiformis</i>	5.5 (2.2)	3.5 (0.7)	0.400	3.4 (1.5)	1.5 (0.2)	0.269	2.8 (1.3)	35.2 (21)	0.147
<i>Capitella</i> spp.	7.6 (3.1)	5.7 (1.2)	0.490	0	0		0.7 (0.7)	0.5 (0.5)	0.829
<i>Mediomastus</i> sp.	0	0		0	0		2.7 (1.6)	3 (2.1)	0.917
<i>Eteone californica</i>	7.1 (3.2)	7.3 (1.9)	0.963	2.2 (1.3)	4.8 (2.8)	0.419	0.8 (0.4)	0.1 (0.1)	0.066
<i>Eteone dilatatae</i>	1.3 (0.7)	9 (1.1)	<0.0001	3.3 (1.3)	7 (2.4)	0.052	0	0.1 (0.1)	0.343
<i>Sphaerosyllis californiensis</i>	3.6 (3.3)	6.7 (1.6)	0.312	0	0		0	0	
<i>Fabricia limnicola</i>	0.4 (0.4)	0	0.343	3.2 (3.2)	0.1 (0.1)	0.359	91.4 (15.6)	94.3 (23.9)	0.903
<i>Nereis succinea</i>	0.4 (0.2)	0.5 (0.2)	0.726	2.9 (1)	0.1 (0.1)	0.026	0.1 (0.1)	0.1 (0.1)	1.000
<i>Tharyx</i> sp.	1.2 (0.5)	40.7 (11.3)	0.007	0.1 (0.1)	0	0.343	2.4 (2.4)	0	0.343
<i>Dorvillea</i> sp.	0.1 (0.1)	0	0.343	0	0		0	0	
Goniadidae	0	0.1 (0.1)	0.343	0	0		0	0	
Mollusca									
Bivalvia									
<i>Musculista senhousia</i>	0.4 (0.3)	0	0.223	0	0		0	0	
<i>Mya</i> sp.	0.5 (0.3)	1.4 (0.8)	0.193	2 (1.4)	0.2 (0.1)	0.196	0	0	
<i>Mya arenaria</i>	0	0		0.1 (0.1)	0.2 (0.1)	0.591	0	0	
<i>Tellina</i> sp.	0.1 (0.1)	0	0.343	0	0		0	0	
<i>Macoma petalum</i>	0	0		3.4 (1.8)	6.8 (2.3)	0.346	0	0	
<i>Gemma gemma</i>	0.5 (0.3)	159.5 (43.7)	0.006	4.9 (2.2)	16.7 (2.9)	0.014	0	0	
<i>Nutricola confusa</i>	0	0		0	4.4 (1.2)	0.006	0	0	
<i>Venerupis philippinarum</i>	1.6 (0.5)	1.5 (0.6)	0.899	0	0		0	0	
Gastropoda									
<i>Myosotella myosotis</i>	0	0		0	0		1.6 (0.4)	0	0.004
Arthropoda									
Peracarid crustacea									
Corophiid spp.	27.4 (9.8)	176.5 (37.8)	0.002	2.8 (1.4)	2.7 (1.5)	0.935	1.8 (1.8)	0.2 (0.1)	0.199
<i>Grandidierella japonica</i>	5.2 (3.5)	36.9 (13.1)	0.048	2.3 (1.5)	14.5 (9.8)	0.251	0	0	
<i>Hyale</i> sp.	0.5 (0.4)	0	0.244	0	2 (1)	0.073	0	0	
Gammarid sp. EE	0	0		1.2 (1.2)	15.9 (11.7)	0.196	0	0	
Gammarid sp. XX	0	0		0	0.8 (0.5)	0.136	0	0	
<i>Amphitoe valida</i>	0.8 (0.4)	0.6 (0.5)	0.785	0	0		0	0	
<i>Orchestia traskiana</i>	0.2 (0.1)	0	0.168	0	0		0.5 (0.2)	0.3 (0.2)	0.343
Ampeliscidae	0	0		0	0.1 (0.1)	0.343	0	0	
Caprellidae	0.1 (0.1)	0	0.343	0	0		0	0	
<i>Exosphaeroma inornata</i>	0.2 (0.1)	0	0.168	0	0		0	0	
<i>Gnorimosphaeroma</i> sp.	0.1 (0.1)	0	0.43	0	0		0	0	
Tanaidacea	0.1 (0.1)	5.4 (3.6)	0.171	0	0		0	0	
Cumacea	0.1 (0.1)	0.4 (0.2)	0.279	0	0.4 (0.2)	0.036	0	0	

Table 1 (continued)

Taxon	Elsie Roemer			Roberts Landing			San Mateo		
	<i>Spartina</i> hybrid	Tidal flat	p	<i>Spartina</i> hybrid	Tidal flat	p	<i>Spartina</i> hybrid	<i>Salicornia</i>	p
Insecta									
Diptera									
Poduridae	0.8 (0.7)	0	0.280	0.2 (0.1)	0		0.6 (0.3)	0	
Chironomidae larvae	0	0		0.2 (0.2)	0		0	0	
<i>Ormosia</i> sp. (Tipulidae)	0	0		0	0		3.3 (1)	1.8 (0.9)	0.329
'Other Diptera'	0	0		0	0		0.6 (0.4)	0.6 (0.4)	0.433
Homoptera									
Aphidae	0	0		0	0		0.1 (0.1)	0	0.343
Hemiptera									
Saldidae	0	0		0	0		0.1 (0.1)	0	0.343
Hymenoptera									
Formicidae	0	0		0	0		0.1 (0.01)	0	
Arachnida									
Acari	0.1 (0.1)	0	0.343	0	0		0.5 (0.3)	1.2 (1.1)	0.568
Cnidaria									
Hydrozoa	0	0		0	0		26 (7)	23.1 (8.2)	0.797
Anthozoa									
<i>Nematostella vectensis</i>	0.3 (0.2)	0.5 (0.3)	0.443	0	0		0	0	
Platyhelminthes									
Turbellaria	0.1 (0.1)	0.4 (0.3)	0.394	0	0		0	0	
Nemertea	0.3 (0.3)	0.3 (0.3)	1.000	0	0		0	0	
No. ind. per core	196.7 (81.7)	746.7 (99.2)	<.001	90.2 (60.2)	154.3 (69.3)	0.247	229.4 (20.1)	289.5 (53.2)	0.272
No. species per core	13 (4.1)	17.2 (0.9)	0.018	9.2 (0.9)	12.3 (1)	0.049	11.8 (1.2)	8.6 (1)	0.008

Macrofaunal feeding modes

Surface feeding was the most common feeding habit observed among wetland infauna in south San Francisco Bay (46 to 77 %). The second most common was subsurface-deposit feeding (19 to 49 %), followed by carnivory and omnivory (4 to 16 %) and herbivorous grazing (0.3 to 2 %). However, the proportional representation of each feeding mode varied between *Spartina*-invaded and uninvaded habitats. At Elsie Roemer, the proportion of surface feeders was higher in uninvaded tidal flat ($77 \pm 4\%$) than in the hybrid-invaded habitat ($46\% \pm 6\%$) ($t_{18} = 4.7$, $p = 0.0002$). Conversely, the proportion of subsurface-deposit feeders was significantly higher in the invaded habitat ($t_{18} = 3.9$, $p = 0.001$) (Fig. 9). At Roberts Landing there were no differences in feeding mode representation between *Spartina*-invaded and uninvaded tidal flat sediments. At San Mateo, no differences were detected in the representation of surface- ($p = 0.480$) or in subsurface-deposit feeders ($p = 0.941$) in *Spartina*-invaded versus *Salicornia*-dominated sediments. However, the proportion of carnivores/omnivores was 2.5 times higher ($t_{18} = 4.7$, $p = 0.0002$) and the proportion of grazers was 6.6 times higher ($t_{18} = 3.3$, $p = 0.003$) in the hybrid-invaded patches relative to patches dominated by native *Salicornia*. Because the overall representation of carnivores and omnivores among infauna was very small in both patch types (Fig. 9), these trends may have minimal ecological significance.

DISCUSSION

Tidal flat invasion

The 3 benthic systems studied displayed variation in the type and magnitude of differences between *Spartina*-invaded sediments and native (uninvaded) patches. Contributing factors may include local properties which vary among locations, time since invasion, and the type of habitat being invaded. The *Spartina* invasion began much earlier at Elsie Roemer (~30 yr) than at Roberts Landing (10 to 15 yr). In addition, elevations were lower (<1 m vs 2.5 to 2.8 m above MLLW), and the sediments were significantly coarser ($t_{18} = 4.1$, $p = 0.0007$) (Fig. 3) at Elsie Roemer than at Roberts Landing, indicating different flow regimes. The *Spartina* hybrid was taller at Elsie Roemer ($t_{18} = 3.5$, $p = 0.0027$), however, the below-ground biomass (upper 6 cm) was higher in Roberts Landing ($t_{18} = 3.0$, $p = 0.007$). Among the 2 tidal flat invasions, we observed greater vegetation effects on sediment at Roberts Landing (7 of 9 properties, Figs. 4 & 5), but much stronger effects on infaunal community structure at Elsie Roemer (Fig. 7, Table 1). These observations suggest that sediment properties are not driving the faunal differences alone. Rather, the faunal differences may be related to duration of *Spartina* influence, greater susceptibility of sandy faunas to plant influence on flow or detritus availability, or to variation in predation pressure.

Table 2. Comparisons of macrofaunal assemblages of invaded and uninvaded habitats at 3 sites in San Francisco Bay sampled in May/June 2001. Probabilities resulting from pair-wise 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 habitat (SIMPER). Significance was set at $\alpha = 0.05$. H ER = *Spartina* hybrid Elsie Roemer, H RL = *Spartina* hybrid Roberts Landing, H SM = *Spartina* hybrid San Mateo, T ER = tidal flat Elsie Roemer, T RL = tidal flat Roberts Landing, S SM = *Salicornia* San Mateo

SITE/ HABITAT	H ER	H RL	H SM	T ER	T RL	S SM
H ER	32.29%	0.002	0.001	0.001	0.001	0.001
H RL	78.57%	28.73%	0.001	0.001	0.003	0.001
H SM	85.51%	88.27%	57.84%	0.001	0.001	0.014
T ER	68.63%	77.89%	90.37%	62.94%	0.001	0.001
T RL	79.51%	68.86%	91.83%	71.66%	47.03%	0.001
S SM	88.85%	89.39%	49.82%	92.55%	95.72%	51.11%

The low elevation and high-energy regime of Elsie Roemer in June 2001 are associated with exceptionally high faunal densities on the tidal flat ($\approx 400\,000$ ind. m^{-2}). Of the individuals present, 80% belong to 2 taxa (*Gemma gemma* and corophiid amphipod species; Table 1), so much of the apparent invasion effect at Elsie Roemer (75% lower density in *Spartina* patches) may be attributed to declines in these surface-feeding taxa (Fig. 9). This pattern is persistent over seasons and years; total macrofaunal densities were 71% lower in the invaded areas than in tidal flats (E. Brusati pers.

comm.) in October 2001 and 64% lower in July 2003 (C.N. pers. obs.).

Some responses of the Roberts Landing and Elsie Roemer tidal flat ecosystem to *Spartina* invasion were similar. At both sites about half of the species present (51 and 55%) exhibited lower mean densities in the *Spartina*-invaded sediments (Table 1). Furthermore, both locations exhibited a 25% decline in macroinfaunal species richness (Fig. 7).

Our findings of lower density and species richness in tidal flats habitats invaded by *Spartina* hybrid contrast sharply with existing paradigms about positive vegetation effects on marine macrobenthos (Bertness et al. 2000). However, a survey of the literature addressing *Spartina* influence on macrobenthos reveals disparate patterns, depending on the *Spartina* species, habitats and geographic region involved (Table 3). Where *S. alterniflora* is a native (West Atlantic) and mature (natural marshes), it appears to enhance macrofaunal density and species richness relative to mudflats. Presence of vegetation may enhance infaunal densities via increased substrate stability, increased food resources, refuge from predators, and hence greater survivorship (Orth 1977, Orth et al. 1991, Lee & Kneib 1994). Newly planted *Spartina* has little effect on macrobenthos however (Levin et al. 1996, Craft & Sacco 2003).

On the Pacific coast, where *Spartina* is invasive (*S. anglica*, *Spartina* hybrid) or the native is *S. foliosa*, *Spartina*-inhabited sediments seemed to have lower macroinfaunal densities relative to the mudflat (present study, Table 3). Our observation of reduced den-

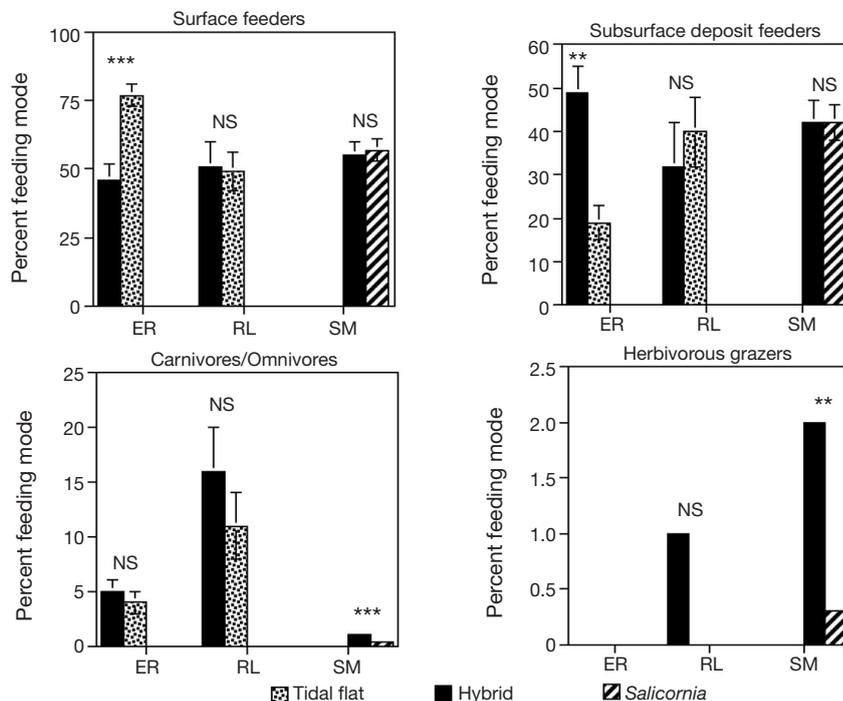


Fig. 9. Mean percent representation of macrofaunal feeding groups within the hybrid-invaded and uninvaded habitats of Elsie Roemer, Roberts Landing and San Mateo during May/June 2001. Data are based on 10 cores from each habitat. ** = $0.001 \leq p < 0.01$, *** = $p < 0.001$

Table 3. *Spartina* spp. Influence on benthic macrofaunal populations and communities

Vegetation type/ location	Taxon studied	Influence on fauna	Source
<i>S. alterniflora</i> Galveston Bay, Texas, USA	Macrofauna/ meiofauna	Higher mean densities of most macrofaunal and meiofaunal species in vegetated sediments than in unvegetated areas	Wardle et al. (2001)
<i>S. alterniflora</i> Paranaguá Bay, Paraná, Brazil	Macrofauna	Higher density, species richness, and greater temporal stability in vegetated areas compared with unvegetated areas	Lana & Guiss (1991)
<i>S. alterniflora</i> Tar Landing Bay, North Carolina, USA	Macrofauna/ meiofauna	Higher macrofauna and meiofauna densities in sediments containing <i>S. alterniflora</i> culms than in unvegetated sediments	Rader (1984)
<i>S. alterniflora</i> Galveston Bay, Texas, USA	Peracarid crustaceans	Higher peracarid density in sediments containing <i>S. alterniflora</i> stems than in bare sediments	Goldberg (1996)
<i>S. alterniflora</i> Paranaguá Bay, Paraná, Brazil	Gastropods	Higher densities of <i>Neritina virginea</i> with increased <i>Spartina</i> density, biomass and height	Bonnet et al. (1994)
<i>S. alterniflora</i> Alabama, USA	Clams	Positive correlation between stem density and <i>Geukensia demissa</i> density	West & Williams (1986)
<i>S. alterniflora</i> Galveston Bay, Texas, USA	Natant macrofauna	<i>Palaemonetes pugio</i> , <i>Penaeus aztecus</i> and <i>Callinectes sapidus</i> more abundant in vegetated than in unvegetated patches	Zimmerman & Minello (1984)
<i>S. alterniflora</i> Galveston Bay, Texas, USA	Natant macrofauna	Macrobenthic, juvenile blue crabs and fiddler crab diversity unaffected by unvegetated channel presence. Oligochaetes present mostly in vegetated patches	Minello et al. (1994)
<i>S. alterniflora</i> Willapa Bay, Washington State, USA	Macrofauna	Higher densities in invaded patches in April and lower densities in August relative to open tidal flat. Increased densities of subsurface-deposit feeders in invaded patches	Zipperer (1996)
<i>S. alterniflora</i> Willapa Bay, Washington State, USA	Clams	Lower <i>Macoma inconspicua</i> density in <i>S. alterniflora</i> patches than in mudflats. <i>Mya arenaria</i> varied from greatest densities along the inside edge of the patches in spring, to higher densities on the mudflat in summer	Ratchford (1995)
<i>S. alterniflora</i> Willapa Bay, Washington State, USA	Clams	Lower densities of <i>Macoma</i> spp. and higher densities of <i>Venerupis philipinarum</i> in <i>Spartina</i> patches than in mudflats	Dumbauld et al. (1997)
<i>S. alterniflora</i> Willapa Bay, Washington State, USA	Macrofauna	Lower densities of crustaceans and bivalves, enhanced densities of dipteran in <i>S. alterniflora</i> -invaded mudflats	O'Connell (2002)
<i>S. alterniflora</i> North Carolina, Louisiana, USA	Macrofauna	Lower diversity in salt marshes relative to adjacent mudflats	Cammen (1979)
<i>S. alterniflora</i> , <i>S. cynosuroides</i> , <i>Juncus roemerianus</i> Cape Fear Estuary, NC, USA	Clams	Lower densities in <i>Spartina</i> than in <i>J. roemerianus</i> marsh	Capehart & Hackney (1989)
<i>S. alterniflora</i> and created marsh Galveston Bay, Texas, USA	Macrofauna	Higher densities and species richness (mainly polychaetes) in natural <i>S. alterniflora</i> patches than in created, vegetated marsh	Minello & Webb (1997)
<i>S. alterniflora</i> and <i>Schoenoplectus robustus</i> North Carolina, USA	Macrofauna	Higher abundances in older-vegetated than in young-vegetated sites. Macrofauna composition differed between the oldest (15 yr) and youngest (4 yr) sites	Posey et al. (1997)
<i>S. alterniflora</i> North Carolina, USA	Macrofauna	No differences in succession of vegetated versus unvegetated plots in a created marsh	Levin et al. (1996)
<i>S. anglica</i> and native marsh Little Swanport, Tasmania, Australia	Macrofauna	Higher species richness and higher total abundance of invertebrates in <i>S. anglica</i> marsh and native salt marsh relative to mudflat	Hedge & Kriwoken (2000)
<i>S. anglica</i> , <i>Salicornia</i> spp. Norfolk, England	Macrofauna	Lower species richness in vegetated areas than in sand and mudflat	Frid & James (1989)
<i>S. anglica</i> Seafeld Bay, Suffolk, England	Macrofauna	Lower densities of bivalves and <i>Corophium</i> , and higher densities of tubificid oligochaetes in vegetated areas relative to mudflat	Jackson (1985)
<i>S. foliosa</i> Mission Bay, California, USA	Macrofauna	Lower density and species richness on salt marsh than mudflat	Levin et al. (1998)
<i>S. foliosa</i> , <i>Salicornia virginica</i> and <i>S. bigelovii</i> Mission and San Diego Bays, California, USA	Macrofauna	Higher tubificid oligochaete densities in <i>S. foliosa</i> , higher insect, nauid oligochaete and peracarid densities in <i>Salicornia</i>	Talley & Levin (1999) Levin & Talley (2000)
<i>S. foliosa</i> , <i>Salicornia bigelovii</i> Tijuana Estuary, California, USA	Macrofauna	Higher density of polychaetes and insects in <i>Spartina foliosa</i> , higher density of gastropods, nauid and enchytraeid oligochaetes and peracarids in <i>S. virginica</i>	Levin et al. (1997)
<i>Spartina</i> hybrid invading tidal flat San Francisco Bay, USA	Macrofauna	Lower total density and species richness in <i>Spartina</i> hybrid-invaded areas than in tidal flats. Loss of surface feeders; increases or no effect on subsurface-deposit feeders in vegetated patches	This study
<i>Spartina</i> hybrid invading <i>Salicornia</i> marsh San Francisco Bay, USA	Macrofauna	Slight difference in faunal composition with higher species richness in hybrid-invaded patches relative to <i>Salicornia</i> marsh, but no differences in total densities	This study

sities of surface-feeding animals (corophiids and bivalves) concur with those reported for invasive *S. anglica* (Jackson 1985), and *S. alterniflora* (Zipperer 1996) (Table 3). In Willapa Bay *S. alterniflora* invasion of tidal flats led to lower abundances of crustaceans and bivalves as well as burrowing polychaetes, and enhanced densities of dipteran larva and pupae (O'Connell 2002). We did not find these trends in polychaetes and insects in the tidal invasions of south San Francisco Bay, although insect species richness was greater in *Spartina* patches relative to *Salicornia* patches in the San Mateo marsh.

Salt marsh invasion

A nearly opposite benthic response to that reported at Elsie Roemer and Roberts Landing was observed in the marsh invasion at San Mateo, where the native habitat is dominated by *Salicornia virginica*. Total faunal densities did not differ between *Spartina* hybrid and *Salicornia* patches, but more individuals were collected in *Spartina* patches for 72% of the species, and species richness per core was 27% greater in the *Spartina*-invaded sediments. Not only was this site vegetated prior to the invasion, but the sediments were more saline ($F_{2,27} = 3.25$, $p = 0.05$), finer-grained ($F_{2,27} = 65.8$, $p < 0.0001$), more porous ($F_{2,27} = 57.5$, $p < 0.0001$) and had higher organic content ($F_{2,27} = 216.5$, $p < 0.0001$) and microalgal biomass ($F_{2,27} = 27.8$, $p < 0.0001$) than the other sites (Fig. 4). The invaded sediments of San Mateo also exhibited higher concentrations of the algal pigments fucoxanthin ($F_{2,27} = 4.772$, $p = 0.017$), zeaxanthin ($F_{3,36} = 4.009$, $p = 0.014$), and lutein ($F_{3,33} = 6.223$, $p = 0.002$) than the *Spartina*-invaded tidal flats of Elsie Roemer and Roberts Landing.

There are few consistent, general trends evident in comparisons of macrobenthos inhabiting *Spartina* versus other forms of marsh vegetation (Table 3). Lower bivalve densities have been noted in *Spartina*-vegetated sediments relative to *Juncus roemerianus* (Capehart & Hackney 1989). In the Tijuana estuary, southern California, there were higher densities of polychaetes and insects in *S. foliosa* habitats, while in *S. virginica* habitats, gastropods, naidid and enchytraeid oligochaetes dominated in density (Levin et al. 1997). In nearby Mission Bay, the *Spartina* zone had higher densities of tubificid oligochaetes and lower densities of insects, peracarid crustaceans and naidid oligochaetes than the *Salicornia* zone (Talley & Levin 1999, Levin & Talley 2000). At San Mateo we observed higher species richness and increased densities of several tubificid species and a gastropod, as well as greater insect richness in the *Spartina*-invaded than *Salicornia* habitat (Table 1). As the invaded habitat is transformed into

a monospecific *Spartina* hybrid stand, the sediments at San Mateo become less densely vegetated, possibly facilitating some macrobenthic species showing enhancement (Table 1).

Mechanisms of change, trophic implications and possible consequences

Across the range of locations and habitats studied, we observed varied macrofaunal responses to *Spartina* invasion, ranging from density reduction (Elsie Roemer), to composition change (Roberts Landing), to species enhancements (insects—San Mateo). A full mechanistic understanding of the sources of this variation would entail detailed, experimental studies of *Spartina* hybrid effects on flow, substrate, elevation, light, algal production, predation pressure, and other possible factors. Successional studies that track changes in single invasions over time, at a number of different sites with different substrata and in different vegetation regimes, will help distinguish the relative importance of invasion duration from various environmental factors.

Many of the species shown to have lowered density in tidal flat habitats invaded by hybrid *Spartina* are surface-feeding forms such as *Gemma gemma*, *Corophium* spp., *Grandidierella japonica*, *Tharyx* spp., *Streblospio benedicti*, and *Pygospio elegans*. These are more readily consumed by predatory fish and birds (Green & Hobson 1970, Whitlatch 1977, Thompson 1982, Nichols & Thompson 1985a,b) than invasion-tolerant, subsurface-deposit feeders such as capitellid polychaetes and oligochaetes that live deeper in the sediment column and are less accessible to epibenthic predators. Thus, where *Spartina* has invaded open tidal flat for several decades, the foraging area and food base for shorebirds and epibenthic fish has probably declined. In contrast, *Spartina* invasion of *Salicornia* marsh could provide a more rich and diverse food base for other kinds of wetland consumers. In both types of invasion, *Spartina* has created additional habitat for the endangered California clapper rail in south San Francisco Bay (J. C. Nordby pers. comm.), adding complexity to already difficult decision-making concerning control measures. The present studies illustrate the heterogeneous, context-dependent effects of an invasive plant on benthos in tidal wetlands. They also suggest, but do not confirm, time dependence.

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