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MECHANISMS GENERATING MODIFICATION OF BENTHOS FOLLOWING TIDAL FLAT INVASION BY A *SPARTINA* HYBRID

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Abstract. Many coastal habitats are being substantially altered by introduced plants. In San Francisco Bay, California, USA, a hybrid form of the eastern cordgrass *Spartina alterniflora* is rapidly invading open mudflats in southern and central sections of the Bay, altering habitat, reducing macrofaunal densities, and shifting species composition. The invasion has resulted in significant losses of surface-feeding amphipods, bivalves, and cirratulid polychaetes, while subsurface feeding groups such as tubificid oligochaetes and capitellid polychaetes have been unaffected. In the present paper, we document the causes and mechanisms underlying the changes observed. Through a series of in situ manipulative experiments we examined the influence of hybrid *Spartina* canopy on a range of physical, chemical, and biological properties. The hybrid *Spartina* canopy exerted a strong influence on the hydrodynamic regime, triggering a series of physical, chemical, and biological changes in the benthic system. Relative to tidal flats, water velocity was reduced in hybrid patches, promoting deposition of fine-grained, organic-rich particles. The resulting changes in the sediment environment included increased porewater sulfide concentrations and anoxia, which led to poor survivorship of surface feeders such as bivalves, amphipods, and polychaetes. These are key taxa that support higher trophic levels including migratory shorebirds that feed on tidal flats. Altered flow in the *Spartina* canopy further contributed to changes in barnacle recruitment and resuspension of adult benthic invertebrates. Increased crab-induced predation pressure associated with *Spartina* invasion also contributed to changes in benthic invertebrate communities. Our results suggest that multiple physical, chemical, biotic, and trophic impacts of the *Spartina* invasion have resulted in substantial changes in benthic communities that are likely to have important effects on the entire ecosystem.

Key words: hybrid *Spartina*; larval recruitment; macrobenthos; plant–animal interaction; plant invasion; predation; San Francisco Bay; sediment deposition; *Spartina alterniflora*; trophic shift; water flow; wetlands.

INTRODUCTION

Among the most serious threats to natural ecosystems has been the introduction of nonnative plants now rapidly occurring on a global scale (Drake et al. 1989, Thompson 1991, Vitousek et al. 1997, Chapin et al. 2000). Many of these plant introductions have caused substantial changes including alteration of habitat structure, extinction of native species, reduced ecosystem productivity, and changes in nutrient cycling that may have profound ecological and economic consequences (Vitousek 1986, 1990, Pimentel et al. 2000, Ayres et al. 2003). Introduced plants may cause these changes through either direct effects, for instance through alteration of habitat structure (Peterson et al. 1984, Talley and Levin 2001), or indirect effects through reductions in light levels, wind and water velocities, or alteration in nutrient availability, erosional, or depositional regimes (Fonseca et al. 1982, Eckman 1987, 1990).

Important examples of changes caused by vascular plant invasion include the introduction of *Myrica faya* to nitrogen-limited ecosystems in Hawaii, which resulted in fundamental changes in the functional and structural properties of the native forest (Vitousek et al. 1987). The invasion of *Tamarix* spp. has had similarly substantial effects in the riparian systems of the southwest United States, resulting in increased salinity, productivity, and surface litter, and reduced species diversity (Berry 1970, Gaskin and Schaal 2002). Recent invasions of freshwater plants into estuarine systems (e.g., *Phragmites australis* and *Tamarix* spp. in salt marshes) have raised new issues about plant roles in ecosystem function (Chapin et al. 1997, 2000).

Vascular plants invading coastal wetlands have produced notable ecosystem changes. Major invaders include *Phragmites australis* in the northeast United States (Fell et al. 1998, Talley and Levin 2001, Warren et al. 2001), *Hydrilla verticillata* in the upper reaches of Chesapeake Bay (Posey et al. 1993), *Zostera japonica* in the U.S. Pacific Northwest (Harrison and Bigley 1982, Larned 2003), purple loosestrife, *Lythrum salicaria*, in western North America and Canada (Thompson et al.

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PLATE 1. *Spartina alterniflora* × *foliosa* hybrid invading tidal flats at Elsie Roemer, San Francisco Bay, California, USA. Photo credit: C. Neira.

1987), and *Spartina alterniflora* on the west coast of the United States (Callaway and Josselyn 1992, Daehler and Strong 1996, Feist and Simenstad 2000). Plant invasions have particularly significant impacts when colonizing otherwise unvegetated tidal flats, where they reduce foraging area for shorebirds and fishes, decrease light and water flow, increase sedimentation rates, and reduce production of benthic algae (Posey 1988, Daehler and Strong 1996, Zipperer 1996, Stenzel et al. 2002).

In San Francisco Bay, more than 790 ha of mudflats and marshes have been invaded by *Spartina alterniflora* and its hybrids (see Plate 1; Ayres et al. 2004, Zaremba and McGowan 2004). Reasons for the competitive success of hybrid *Spartina* are still not well understood, although relative to the native *Spartina* (*S. foliosa*), the hybrid produces larger, more vigorous vegetative growth, produces much greater amounts of pollen, and has a greater tidal range (Daehler and Strong 1997, Ayres et al. 1999, 2003).

The specific impacts of hybrid *Spartina* invasion on sediment properties, macrofaunal communities, and ecosystem functioning were poorly known until recently. Mensurative studies conducted at three locations in San Francisco Bay showed variable decline in macrofaunal abundances (up to 75% reduction at one site), as well as important shifts in species composition in the hybrid-invaded patches relative to tidal flats (Neira et al. 2005). Surface-feeding bivalves (*Gemma gemma*), amphipods (*Corophium* spp., *Grandidierella japonica*), and polychaetes (*Tharyx* sp., *Eteone dilatata*) were negatively affected by invasion, while subsurface polychaetes (*Heteromastus filiformis*, *Capitella* spp.) and oligochaetes (Tubificidae) were less affected or unaffected.

Such changes can alter food web function because the generally larger and more accessible surface feeders are most commonly consumed by fishes and birds. The nature and extent of habitat modification by hybrid *Spartina* varies with the ecosystem invaded, the age of invasion, and with hydrodynamic and physicochemical regime (Neira et al. 2005). However, the specific mechanisms underlying the observed changes remain unclear.

The aim of the present study is to evaluate the link between changes induced by hybrid *Spartina* in the physical and chemical environment and changes in benthic communities. We have previously shown that groups of surface-feeding invertebrates, which provide food for higher trophic levels such as migratory shorebirds, decline substantially with the invasion of hybrid *Spartina* (Neira et al. 2005). We hypothesize that canopy structure of *Spartina* modifies water flow and sediment deposition and alters sediment characteristics in ways that will significantly influence recruitment of juvenile invertebrates, transport of adults, and the presence of predators that are ultimately responsible for changes in macrofaunal communities. We performed a series of in situ manipulative experiments to examine the influence of hybrid *Spartina* canopy on water velocity, juvenile recruitment, adult advection and transport, and rates of predation as mediators of change in this benthic community.

MATERIALS AND METHODS

Study site

The study site is in the city of Alameda, California, USA (San Francisco Bay) along the shoreline within the

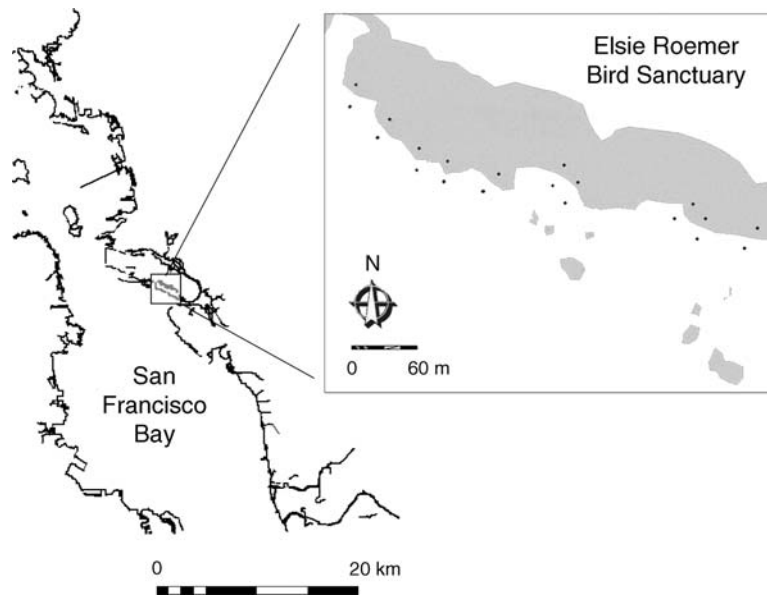


FIG. 1. Location of the study area in San Francisco Bay, California, USA. Dots indicate paired sampling locations (10 blocks) on open tidal flat and hybrid *Spartina* habitat.

Elsie Roemer Bird Sanctuary (37°45'35" N; 122°28'48" W). *Spartina alterniflora* and its hybrids first invaded this area ~30 years ago (Ayres et al. 2003); native *S. foliosa* has not been present in this area since 1992 (D. R. Ayres, *personal communication*). The area vegetated by hybrid *Spartina* forms a rather continuous meadow (~10 ha) that borders the open tidal flat. Sediments are coarse (~90% sand on the tidal flat and ~60% sand in vegetated patches), with organic matter content usually ranging from 1.0% to 1.5% on the tidal flat and from 1.7% to 3.5% in the marsh. Tidal amplitude during spring tides is typically 2.5 m with an annual maximum of nearly 3.0 m. More details of the study site are found in Neira et al. (2005).

Effects of plant canopy structure

In order to test the hypothesis that the aboveground structure of hybrid *Spartina* modifies sediment deposition and water flow in ways that influence macrofaunal community structure, we delimited 10 2 × 2 m plots located ~10 m inside the hybrid *Spartina* meadow (i.e., 5–7 m further into the vegetation than with our previous mensurative studies; Neira et al. 2005). Ten parallel plots were established on the tidal flat adjacent to each of the vegetation plots, ~10 m from the vegetation edge (Fig. 1).

Relative water flow.—The effects of plant structure on relative water circulation were assayed using the gypsum dissolution technique (Doty 1971) simultaneously in all blocks and treatments. We follow the assumptions of others (Doty 1971, Howerton and Boyd 1992, Thompson and Glenn 1994) that as water velocity increases over the gypsum blocks so does turbulence and mass transfer of the gypsum to the water per unit time (g/d).

Preweighed gypsum blocks (9 cm in diameter × 2 cm in height, ~130 g; modified after Doty [1971]) were attached to the underside of inverted L-shaped PVC pipes so that the exposed surface of the blocks faced the substrate ~10 cm above it. We deployed sets of blocks for three-, four-, and six-day intervals during April and June 2002. After each deployment, the gypsum blocks were returned to the lab, dried at 60°C, and reweighed to determine mass lost since deployment.

We also made single point measurements of actual water velocities using paired measurements of flow with a Marsh-McBirney Flow Meter 2000 (Marsh-McBirney, Frederick, Maryland, USA) inside the vegetated area and on the open mudflat (at least 5 m from the edge). We measured flow ~1 m from the vegetation edge (inside the meadow), because this was sufficient to represent the conditions within the canopy due to the high stem density of hybrid *Spartina* in this area. Locating these areas within a short distance of the meadow edge allowed us to avoid disturbing nests and nestlings of the federally endangered California Clapper Rail (*Rallus longirostris obsoletus*). Lastly these areas also coincided with the location of our previous invasion studies (Neira et al. 2005). Velocities were measured ~15 cm above the substratum on several days. This height was great enough to avoid boundary layer effects near the substratum, but low enough to be within a zone of approximate maximum aboveground plant biomass.

In order to understand the influence of hybrid *Spartina* on instantaneous velocity during peak flow, we made flow measurements over intervals of <1 min (three 10-s measurements) during periods of maximum ebb and flow tides. We repeated these measurements

over several dates in paired plots inside and outside *Spartina*.

Sediment deposition.—To quantify the effects of aboveground structure of hybrid *Spartina* on short-term sediment deposition rates, we deployed Petri dish sediment traps (Reed 1992). Traps consisted of 9-cm diameter, GF/F filters (Whatman) placed on Petri dish lids (rim downwards) held flush with the substratum with wire staples. Twenty sediment traps (one replicate per each of 10 blocks in hybrid and tidal flat habitat) were deployed at low tide, and retrieved 24 h later. Deployments were made during two successive days in July 2002. In the laboratory, trapped sediments were gently rinsed with distilled water to remove salts and transferred onto preweighed aluminum dishes, oven-dried at 60°C, and weighed. Sediment deposition rate was calculated as mass deposited per trap and expressed in $\text{mg}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$. Deposited sediment was weighed, combusted (500°C for 4 h), and reweighed to determine organic content. In order to obtain a rough estimate of the particle size deposited on traps, sediment was wet-sieved through a 63 μm mesh. Both fractions of the sample ($\geq 63 \mu\text{m}$ and $< 63 \mu\text{m}$) were dried at 60°C and weighed to determine percentage mud.

Sediment characteristics.—We examined the influence of the hybrid *Spartina* invasion on sediment properties in both invaded and tidal flat habitats (paired replicates in each of 10 blocks). In each block, we made measurements of porewater salinity, redox potential, temperature, porosity, water content, total organic matter (TOM), percentage mud content, and sediment chl *a* (a proxy for microalgal biomass). For analysis of porewater salinity, sediment (0–3 cm deep) was squeezed against Whatman filter paper inside a 10-cm³ syringe and the salinity of water passing through was measured with a hand-held refractometer. Chlorophyll *a* concentration was determined from small sediment cores (1.13 cm² × 5 mm deep) spectrophotometrically according to Plante-Cuny (1973) after extraction with 90% acetone. Total organic matter was determined by mass loss of dried sediment after ignition at 500°C for 4 h. Sediment water content and sediment porosity were determined according to Buchanan (1984). Sediment temperature was recorded at 2 cm depth with a digital thermometer. Sediment redox potential was measured in the top 1 cm with a portable Mettler Toledo mV-meter (Mettler Toledo, Columbus, Ohio, USA). Sediment cores (18.1 cm², 0–6 cm deep), collected for quantification of macrofauna, were preserved in 8% buffered formalin with Rose Bengal stain. In the laboratory, macrofauna cores were sieved through a 300- μm mesh sieve, sorted under a dissecting microscope, and identified to the lowest taxonomic level possible.

Biological effects

Juvenile recruitment.—To examine how the modified flow in hybrid *Spartina* could influence recruitment of benthic invertebrates, we measured recruitment of

barnacles (*Balanus glandula*) on shells of the introduced mussel *Geukensia demissa*, which is the most common mussel at this site and is typically fouled with barnacles. We assumed that the flow effects of hybrid *Spartina* could be manifested as either reductions in the flux of larvae because of reduced horizontal advection rates (Yund et al. 1991) or as reduced survival of settling larvae. Three shells of *G. demissa* glued individually to wooden dowels were placed in each of the 10 blocks in hybrid *Spartina* and on tidal flats (60 dowels total) with mussels positioned ~10–20 cm above the substratum. After four weeks, we counted the total number of barnacles per shell and calculated the median number of barnacles per plot ($n = 10$ per habitat).

Adult advection and/or transport.—To test the hypothesis that hybrid *Spartina* plant structure has altered the transport dynamics of benthic fauna, we deployed passive cylindrical tube traps (Butman 1986, Yund et al. 1991) made of clear polypropylene (2.7 cm wide × 22 cm long; aspect ratio of 8:1). Prior to outplanting, we added 15 mL of 90 g/L saline solution to the tube to prevent escape of trapped organisms, to dampen eddies and resuspension (Lau 1979, Butman 1986), and to avoid contamination concerns associated with formalin. We gently filled the remaining volume with filtered seawater. On the exposed tidal flats, we attached the tubes to PVC pipes above the sediment surface with cable ties. Within the hybrid *Spartina* habitat, tubes were inserted into the substrate leaving the tube mouth ~5 cm above the sediment surface. Previous one-day trials had shown that tubes placed flush with the sediment surface rapidly became filled with sediment. We deployed 10 tubes in both tidal flat and hybrid habitats (one per block) for four days and contents were preserved in 8% buffered formalin until analysis.

Sediment transplant experiment

In order to determine whether (1) changes in invertebrate community composition within hybrid *Spartina* habitat relative to the tidal flat were due to poor survivorship of selected taxa, and (2) whether this was associated with shifts in sediment properties, we transplanted intact tidal flat sediment and associated infauna to *Spartina*-invaded habitat. Experiments were initiated in June 2002 in the original 10 blocks. To make space for transplanted sediment in the hybrid *Spartina* habitat, we inserted a plastic frame into the sediment (10 cm deep) to delimit an area of 25 × 25 cm, and the entire segment including root matrix was removed. In the adjacent open tidal flat (~10 m from the vegetation edge), two plastic frames (25 × 25 cm, 10 cm deep) were inserted into the sediment ~10 cm apart. The sediment contained in one of them was transplanted intact to the hole excavated in the vegetated habitat. The sediment section of the second frame was removed and replaced to serve as a control. After 40 and 155 days, we examined sediment properties. We collected cores (18.1 cm², 0–6 cm deep) for analysis of sediment macrofauna,

percentage mud content ($<63 \mu\text{m}$), total organic matter, and chl *a*.

Predator inclusion or exclusion experiment

We investigated whether the decline of surface feeders observed in tidal flats following invasion by hybrid *Spartina* could be due in part to increased predation pressure. Previous work has shown that densities of the European green crab (*Carcinus maenas*), a generalist predator introduced into San Francisco Bay ~15 years ago (Cohen et al. 1995), were approximately five times higher in hybrid *Spartina* meadows (mean of 3.0 crabs per trap day) than on adjacent unvegetated mudflats (mean of 0.6 crabs per trap day; E. D. Grosholz, unpublished data). To examine the effects of green crab predation on macrofauna following hybrid *Spartina* invasion, we initiated in situ exclusion and inclusion experiments on 14 July 2004. A total of eight replicate blocks were selected within hybrid *Spartina* habitat. We established a total of five treatments per block. Four treatments were distributed randomly in the hybrid *Spartina* habitat blocks, and were separated by at least 1 m from each other: (1) tidal flat sediment transplanted into the hybrid zone with open cages (two sided), (2) tidal flat sediment transplanted into hybrid zone with full cage and no crabs, (3) tidal flat sediment transplanted into the hybrid zone with full cage with one crab, (4) unmanipulated hybrid zone sediment with full cage and no crabs. On the tidal flat we created a fifth treatment in which sediment was removed and replaced with no cage and no crabs.

We predicted that if crab predation was contributing to changes in benthic invertebrates, tidal flat sediment transplanted into the hybrid area, but protected from crab predation (Treatment 2), would retain the invertebrate assemblage typical of the tidal flats. Consistent with this prediction, we would expect that the invertebrate assemblage in Treatment 1, where ambient densities of green crabs and other predators were allowed access ("open" cages), and in Treatment 3, where a fixed density of crabs were maintained, would soon converge on that of the hybrid zone. Treatment 4 was established to test for cage effects and since it involved unmanipulated sediment within hybrid *Spartina*, it was expected to maintain an invertebrate assemblage typical of the hybrid zone. Treatment 5 was established to test for the effects of transplanting, and since it used transplanted tidal flat sediments (picked up and replaced), it was expected to maintain an invertebrate assemblage typical of tidal flat areas.

Cages consisted of galvanized hardware cloth ($30 \times 30 \times 50$ cm) with 6.3-mm mesh supported on PVC pipe (1 cm in diameter) buried in the sediment with the top removable to allow measurements and manipulations. Transplant of intact tidal flat sediment was made as described in the *Materials and Methods: Sediment transplant experiment*. Green crabs (carapace width ~40 mm) were collected in adjacent areas with minnow

traps prior to deployment in cages. The density of one crab per cage (four crabs/m²) was used based on prior studies (Cohen et al. 1995, Grosholz et al. 2000). Background samples for macrofauna and chl *a* were taken one day prior to the establishment of the treatments. After four weeks, we measured sediment temperature, salinity, and redox potential, and collected sediment cores for analysis of macrofauna, total organic matter (TOM), percentage mud content, chl *a*, porosity, and water content.

Data analysis

Paired *t* tests were used to test for differences among paired blocks (1–10) in macrofauna, sediment properties, and environmental variables between (1) tidal flat habitats invaded and uninvaded by hybrid *Spartina*, and (2) transplants and controls. One-way ANOVA with a posteriori Tukey's hsd tests was used to examine among-treatment differences (hybrid, tidal flat habitats, or predator inclusion or exclusion experiment) in sediment properties and macrofauna. Data were tested for normality and homogeneity of variances, and, where necessary, were square-root transformed. The nonparametric Wilcoxon test was used when transformation failed to normalize data. All parametric analyses were conducted using JMP 4.0 statistical software (SAS 2000). One standard error about the mean is presented with mean values unless otherwise indicated. All proportion data were arcsine square-root transformed. Similarities and differences in macrofaunal assemblages of the transplant experiment were explored using non-metric multidimensional scaling (MDS), based on Bray-Curtis similarity indices. Pairwise comparisons for significant differences in macrofaunal composition between habitats were made using analysis of similarity (ANOSIM). Similarity percentage (SIMPER) analyses were used to determine the percentage of dissimilarity (or similarity) within and between habitat assemblages (transplant and controls). MDS, ANOSIM, and SIMPER were run using PRIMER (Plymouth Marine Laboratory, Plymouth, UK; see Clarke 1993, Clarke and Warwick 1994) on square-root transformed, unstandardized data.

RESULTS

Physicochemical effects of plant canopy structure

Relative water flow.—Mass loss from gypsum blocks was approximately two times greater in the open tidal flat than in the areas invaded by hybrid *Spartina* for the three sampling periods (paired *t* test, $t_9 = 7.96$, $P < 0.0001$; Table 1). Flow measurements also indicated that hybrid *Spartina* canopy significantly reduced flow speed. In uninvaded tidal flats, mean water velocity was 3.3 ± 0.8 cm/s (mean \pm SE), while velocity in vegetated areas averaged $\sim 0.8 \pm 0.1$ cm/s.

Bulk sediment deposition into short-term sediment traps was 1.4 times higher in hybrid *Spartina* than on tidal flats (paired *t* test, $t_9 = 3.7$, $P = 0.005$; Table 1). Fine

TABLE 1. Comparison of physicochemical and biological effects (mean \pm SE) induced by hybrid *Spartina* canopy at the Elsie Roemer Bird Sanctuary, California, USA.

Variable	Habitat		P
	Tidal flat	Hybrid-invaded	
Relative water circulation			
Gypsum mass loss (g/d)			
April	13.4 (0.9)	6.7 (0.7)	<0.0001
May	9.9 (0.3)	4.4 (0.4)	<0.001
June	20.1 (1.1)	8.9 (0.9)	<0.0001
Mean pooled	14.5 (0.9)	6.6 (0.5)	<0.0001
Water flow (cm/s)	3.3 (0.8)	0.8 (0.1)	0.007
Deposition rates			
Sediment deposition (mg·cm ⁻² ·d ⁻¹)	14.2 (2.9)	20.4 (1.1)	0.005
Fine particle (<63 μ m) deposition (mg·cm ⁻² ·d ⁻¹)	1.8 (0.6)	9.3 (1.3)	0.0001
Organic matter deposition (mg·cm ⁻² ·d ⁻¹)	0.4 (0.1)	3.2 (0.2)	<0.0001
Biological changes			
Barnacle recruitment (individuals per mussel shell)	32.1 (6.4)	3.6 (1.3)	0.035
Animals trapped (individuals per tube trap)	10.5 (2.0)	19.4 (2.3)	0.019

particles comprised 45% of the sediment deposited on vegetated areas vs. <13% of the sediment deposited on the tidal flat, and were deposited at rates five times higher in vegetated areas than in the tidal flat (paired *t* test, $t_9 = 6.3$, $P = 0.0001$; Table 1). The fine particles deposited on vegetated areas were associated with a higher sediment organic matter content ($13.9\% \pm 0.8\%$) relative to the unvegetated tidal flat ($1.9\% \pm 0.4\%$; paired *t* test, $t_9 = 18.3$, $P < 0.0001$). Short-term organic matter deposition rates derived from sediment traps were eight times higher in the vegetated habitat than in tidal flats (paired *t* test, $t_9 = 18.1$, $P < 0.0001$; Table 1).

Sediment characteristics.—Sediments in hybrid *Spartina* had higher percentage mud than tidal flat sediment ($48.6\% \pm 5.5\%$ and $10.7\% \pm 2.9\%$, respectively; paired *t* test, $t_9 = 7.5$, $P < 0.0001$), as well as higher total organic matter ($3.7\% \pm 0.5\%$ and $1.3\% \pm 0.2\%$, respectively; paired *t* test, $t_9 = 4.8$, $P = 0.001$), chl *a* (28.8 ± 4.4 μ g/g and 6.9 ± 0.5 μ g/g, respectively; paired *t* test, $t_9 = 4.9$, $P = 0.0008$), and porosity ($65.2\% \pm 3.3\%$ and $48.8\% \pm 2.3\%$, respectively; paired *t* test, $t_9 = 5.8$, $P = 0.0002$). Sediment in the hybrid *Spartina* habitat exhibited reduced conditions (redox potential $E_h = -27 \pm 25.4$ mV) when compared with the tidal flat ($E_h = +63.9 \pm 12.1$ mV; paired *t* test, $t_9 = 2.6$, $P = 0.027$). Concurrently, sulfide concentrations ranged between 200 and 900 μ mol/L in the hybrid *Spartina* sediment (0–4 cm) but were <20 μ mol/L in the tidal flat (A. C. Tyler, unpublished data).

Biological changes

We observed significantly reduced recruitment of barnacles onto mussel shells in the hybrid *Spartina* habitat relative to the open tidal flat after eight weeks, with nine times more barnacles per shell on the tidal flat than in the hybrid *Spartina* areas (paired *t* test, $t_9 = 2.3$, $P = 0.035$; Table 1).

In contrast, we found twice as many animals in tube traps placed in hybrid *Spartina* sediments as in the unvegetated tidal flat (paired *t* test, $t_9 = 2.8$, $P = 0.019$; Table 1). About 70% of the animals in the tube traps were adult benthic macrofauna, suggesting passive (and maybe active) dispersal after resuspension. Faunal assemblages in traps differed between hybrid-invaded and tidal flat habitats (analysis of similarity, ANOSIM, $P = 0.013$). There were higher densities of *Eteone californica* (Phyllodocidae) and barnacle cyprids as well as lower densities of ostracods and *Sphaerosyllis californiensis* (Syllidae) in unvegetated tidal flats relative to habitats invaded by hybrid *Spartina* (similarity percentage, SIMPER).

Sediment transplant experiment

After 40 days, environmental conditions and sediment properties of tidal flat sediment transplanted to hybrid *Spartina* habitat exhibited characteristics similar to those observed previously in *Spartina* areas. Mud content was 40% higher in the transplanted sediment ($15.3\% \pm 3.1\%$) than in the control (removed and replaced) tidal flat sediment ($10.2\% \pm 2.6\%$; paired *t* test, $t_9 = 2.7$, $P = 0.024$). Total organic matter was higher in the transplanted sediment ($1.6\% \pm 0.2\%$) than in the tidal flat treatment ($1.3\% \pm 0.1\%$; paired *t* test, $t_9 = 3.1$, $P = 0.013$), as was sediment chl *a* (transplanted 21.8 ± 5.1 μ g/g vs. tidal flat 6.8 ± 0.4 μ g/g; paired *t* test, $t_9 = 2.9$, $P = 0.020$), and porosity (transplanted $58.7 \pm 2.8\%$ vs. tidal flat $50.8 \pm 1.7\%$; paired *t* test, $t_9 = 2.5$, $P = 0.033$). Sediment redox potential became more negative in the transplanted sediment ($E_h = -75.2 \pm 16.4$ mV) than in the tidal flat treatment ($E_h = +49.7 \pm 10.9$ mV; paired *t* test, $t_9 = 2.9$, $P = 0.0002$). Sediment temperature did not differ between transplanted ($18.4^\circ \pm 0.4^\circ\text{C}$) and tidal flat treatments ($18.6^\circ \pm 0.7^\circ\text{C}$; paired *t* test, $t_9 = 0.5$, $P = 0.623$) nor did porewater salinity (36.1 ± 0.2 and 35.9 ± 0.3 g/L, respectively; paired *t* test, $t_9 = 0.5$, $P = 0.619$).

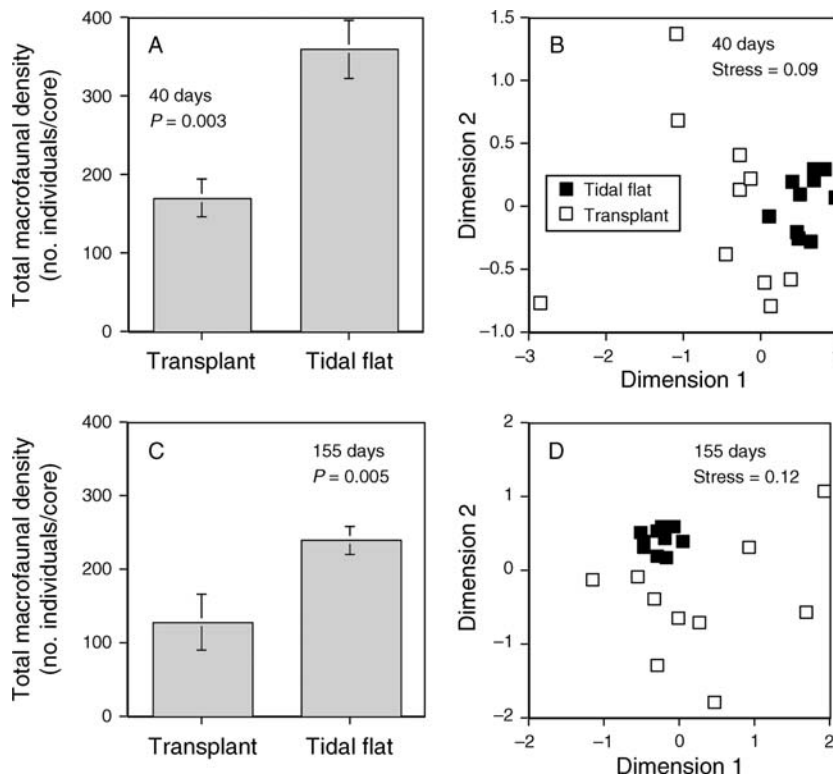


FIG. 2. Transplant experiment. Total macrofaunal density (mean \pm SE) of sediment (A) 40 days and (C) 155 days after transplanting from the tidal flat to hybrid *Spartina* habitat. Control tidal flat sediments were removed and replaced. Paired *t* tests (*P* values) compare transplanted and control sediments. Multidimensional scaling (MDS) plot of macrofaunal assemblages (B) 40 days and (D) 155 days after transplantation. Each point represents data from one core 18.1 cm² \times 6 cm deep.

After 155 days (November 2002), environmental conditions and sediment properties were similar to those observed after 40 days. Only temperature was higher in the tidal flat ($17.3^{\circ} \pm 0.3^{\circ}\text{C}$) relative to the transplanted treatment ($15.0^{\circ} \pm 0.1^{\circ}\text{C}$; paired *t* test, $t_9 = 6.8$, $P < 0.0001$). Transplanted sediments were less oxidized (Eh = $+25.2 \pm 38.5$ mV) than tidal flat sediments (Eh = $+214 \pm 18.6$ mV; paired *t* test, $t_9 = 3.5$, $P = 0.007$).

Mean macrofaunal densities were lower by 50% in the transplanted tidal flat sediments relative to the tidal flat control treatments after 40 days (paired *t* test, $t_9 = 4.1$, $P = 0.003$) and also after 155 days (paired *t* test, $t_9 = 3.6$, $P = 0.005$; Fig. 2A, C, Table 2). Also, after 40 days there was a reduction in species richness per core in the transplanted sediments relative to the tidal flat treatments, from 14.5 ± 0.5 to 9.7 ± 1.2 species (paired *t* test, $t_9 = 3.4$, $P = 0.008$; Table 2). Macrofaunal assemblage composition differed between transplanted and control treatments at 40 days (51.3% dissimilarity, ANOSIM, $P = 0.001$; Fig. 2B) and 155 days (58.7% dissimilarity, ANOSIM, $P = 0.001$; Fig. 2D).

We found poor survivorship of surface-feeding amphipods and bivalves in the transplanted sediment relative to the tidal flat. Densities of tube-building amphipods *Corophium* spp. and *Grandidierella japonica*, and the bivalve *Gemma gemma* declined by 90.4%

(paired *t* test, $t_9 = 4.9$, $P = 0.0007$), 88.7% (paired *t* test, $t_9 = 3.3$, $P = 0.009$), and 90.8% (paired *t* test, $t_9 = 5.1$, $P = 0.0007$), respectively (Table 2). These are the same taxa exhibiting reduced densities in hybrid *Spartina* habitat relative to tidal flat sediments (this study and Neira et al. 2005).

Subsurface-deposit feeders such as tubificid oligochaetes and capitellid polychaetes were not affected in transplanted treatments after 40 days. Tubificid densities increased 28.5% but not significantly (paired *t* test, $t_9 = 0.9$, $P = 0.377$), and capitellid densities (*Heteromastus filiformis* and *Capitella* spp.) did not change (paired *t* test, $t_9 = 0.2$, $P = 0.824$). After 155 days, the strong decline of *G. gemma* persisted (97.4%; paired *t* test, $t_9 = 5.4$, $P = 0.0005$) but was less or not evident for *Corophium* spp. (50% decline; paired *t* test, $t_9 = 1.9$, $P = 0.09$) and *G. japonica* (12.1%; paired *t* test, $t_9 = 0.2$, $P = 0.863$; Table 2).

Predator inclusion or exclusion experiment

Total macrofaunal densities differed among the five treatments (ANOVA, $F_{4,35} = 15.8$, $P < 0.0001$; Fig. 3A), and two distinct groups emerged: controls with tidal flat sediments (Treatment 5) and sediments transplanted into a full cage without crabs (Treatment 2) had similar densities that were higher than sediments transplanted

TABLE 2. Comparison of densities (mean \pm SE) of macrofaunal taxa 40 and 155 days after transplantation of intact tidal flat sediment to hybrid *Spartina* habitat.

Taxa	Tidal flat sediment, 40 days			Tidal flat sediment, 155 days		
	Control	Transplanted	<i>P</i>	Control	Transplanted	<i>P</i>
<i>Tubificoides</i> spp.	54.1 (8.7)	69.5 (18.0)	NS	67.3 (15.2)	19.2 (5.0)	0.007
<i>Tectidrilus diversus</i>	13.1 (3.9)	8.1 (5.2)	NS	14.4 (5.2)	1.1 (0.5)	0.034
Enchytraeidae	0.0 (0.0)	1.3 (1.3)	NS	0.0 (0.0)	1.6 (0.9)	NS
<i>Pseudopolydora kemp</i>	1.3 (0.8)	0.8 (0.7)	NS	2.1 (0.8)	0.0 (0.0)	0.029
<i>P. paucibranchiata</i>				0.1 (0.1)	0.0 (0.0)	NS
<i>Polydora cornuta</i>	0.8 (0.6)	0.2 (0.2)	NS	0.0 (0.0)	0.4 (0.3)	NS
<i>Polydora nuchalis</i>	1.2 (0.8)	0.3 (0.2)	NS	0.6 (0.2)	0.0 (0.0)	0.005
<i>Streblospio benedicti</i>	12.4 (3.5)	29.4 (11.9)	NS	11.2 (2.3)	9.0 (4.8)	NS
<i>Pygospio elegans</i>	0.5 (0.2)	0.6 (0.3)	NS	8.4 (2.7)	0.3 (0.2)	0.016
<i>Heteromastus filiformis</i>	8.6 (1.8)	8.1 (1.2)	NS	8.7 (1.4)	7.5 (1.3)	NS
<i>Capitella</i> sp.				1.3 (0.7)	2.9 (1.2)	NS
Arenicolidae sp.				2.9 (2.2)	0.0 (0.0)	NS
<i>Eteone californica</i>	1.4 (0.7)	0.2 (0.2)	NS	0.1 (0.1)	0.3 (0.3)	NS
<i>Eteone dilatata</i>	6.8 (2.0)	4.7 (1.4)	NS	1.2 (0.5)	0.9 (0.5)	NS
<i>Sphaerosyllis californiensis</i>	0.8 (0.4)	2.5 (1.6)	NS	1.8 (0.7)	21.2 (15.5)	NS
<i>Exogone lourei</i>	0.7 (0.7)	0.0 (0.0)	NS	12 (2.6)	33.7 (21.9)	NS
<i>Syllis gracilis</i>				0.4 (0.3)	1.2 (1.1)	NS
<i>Fabricia</i> spp.				0.0 (0.0)	0.2 (0.2)	NS
<i>Nereis succinea</i>	0.4 (0.2)	0.5 (0.3)	NS	0.1 (0.1)	0.6 (0.2)	0.015
<i>Tharyx</i> sp.	24.9 (4.5)	17.9 (4.9)	NS	13.8 (2.5)	3.8 (1.4)	0.011
Goniadidae sp.	0.3 (0.2)	0.0 (0.0)	NS	0.2 (0.1)	0.0 (0.0)	NS
<i>Dorvillea rudolphi</i>				0.1 (0.1)	0.0 (0.0)	NS
<i>Nephtys cornuta</i>				0.1 (0.1)	0.1 (0.1)	NS
<i>Mya arenaria</i>	0.4 (0.2)	0.3 (0.3)	NS	0.2 (0.2)	0.1 (0.1)	NS
<i>Macoma petalum</i>	0.4 (0.3)	0.3 (0.2)	NS	0.4 (0.2)	0.2 (0.1)	NS
<i>Gemma gemma</i>	62.1 (10.3)	5.7 (2.1)	0.0007	61.9 (11.6)	1.6 (0.8)	0.0005
<i>Venerupis philippinarum</i>	0.7 (0.3)	0.1 (0.1)	NS	0.8 (0.3)	0.0 (0.0)	0.037
<i>Musculista senhousia</i>				0.1 (0.1)	0.0 (0.0)	NS
<i>Corophium</i> spp.	73.6 (12.6)	7.1 (2.4)	0.0007	4.6 (1.0)	2.3 (1.0)	NS
<i>Elasmopus</i> sp.				0.4 (0.2)	0.0 (0.0)	NS
<i>Grandidierella japonica</i>	90.1 (20.6)	10.2 (6.0)	0.009	15.6 (5.4)	13.7 (7.6)	NS
<i>Traskorchestia traskiana</i>	0.1 (0.1)	0.7 (0.7)	NS			
<i>Hyale</i> sp.				0.0 (0.0)	3.9 (2.3)	NS
<i>Ampelisca</i> sp.	0.2 (0.1)	0.1 (0.1)	NS			
Caprellidae	0.1 (0.1)	0.0 (0.0)	NS	0.3 (0.2)	0.0 (0.0)	NS
<i>Exosphaeroma inornata</i>				0.0 (0.0)	0.1 (0.1)	NS
Tanaidacea	0.2 (0.1)	0.0 (0.0)	NS			
Cumacea	0.5 (0.4)	1.3 (0.7)	NS	2.3 (0.9)	0.2 (0.1)	0.025
Anthozoa	0.4 (0.2)	0.0 (0.0)	NS	1.6 (0.4)	0.1 (0.1)	0.003
Turbellaria	3.3 (1.2)	0.4 (0.4)	0.053	3.1 (1.4)	0.1 (0.1)	NS
Poduridae				0.0 (0.0)	0.1 (0.1)	NS
Total macrofauna (no. individuals per core)	359.4 (37.5)	170.3 (24.2)	0.003	238 (18.8)	126.9 (37.3)	0.005
Mean no. species per core	14.5 (0.5)	9.7 (1.2)	0.008	17.6 (0.7)	10.8 (1.4)	0.001

Notes: The core area was 18.1 cm² × 6 cm deep. Significance values (*P*) are from matched paired *t* tests with significance level set at $\alpha = 0.05$; NS, not significant.

into open cages (Treatment 1), into full cages with crabs (Treatment 3), and into full cages enclosing unmanipulated hybrid habitat (Tukey's hsd, $P < 0.05$; Fig. 3A). Comparison of transplanted sediments into open cages (Treatment 1) with those in full cages without crabs (Treatment 2) revealed a lower organic matter content ($t_{14} = 12.14$, $P = 0.003$) and chl *a* ($t_{14} = 8.06$, $P = 0.013$) in the open cage treatments. However, no differences in light (Wilcoxon $\chi^2 = 0.71$, $P = 0.401$), salinity, or temperature (both $t_{14} = 0.005$, $P = 0.945$) were found. To test for cage effects, we also compared Treatment 1 (open, two-sided cage) with ambient hybrid sediments and found lower chl *a* ($t_{14} = 3.71$, $P = 0.003$), but no differences in water content ($t_{14} = 1.62$, $P = 0.127$) or porosity ($t_{14} = 1.78$, $P = 0.095$) in the open cages relative to ambient hybrid sediment. To verify that our results

were not the result of transplant effects, we also compared the removed and replaced sediment (Treatment 5) with those of ambient tidal flat sediment. No differences were found in chl *a* ($t_{14} = 1.99$, $P = 0.066$), water content, or porosity (both Wilcoxon $\chi^2 = 1.21$, $P = 0.269$).

Crab presence (Treatments 1 and 3) led to lower macrofaunal densities (211.8 ± 29.8 individuals per 18.1 cm²; $t_{14} = 21.6$, $P = 0.0004$) and lower number of species (14 ± 0.6 per 18.1 cm²; $t_{14} = 17.2$, $P = 0.001$) than in controls without crabs (476 ± 52.4 individuals per 18.1 cm² and 18.5 ± 0.9 species per 18.1 cm², respectively). In crab enclosures, the densities of amphipods *Corophium* spp. and *G. japonica* declined by 87.2% ($t_{14} = 18.6$, $P = 0.0007$) and 57.5% ($t_{14} = 5.1$, $P = 0.037$), respectively, relative to the enclosure treatments without crabs, while

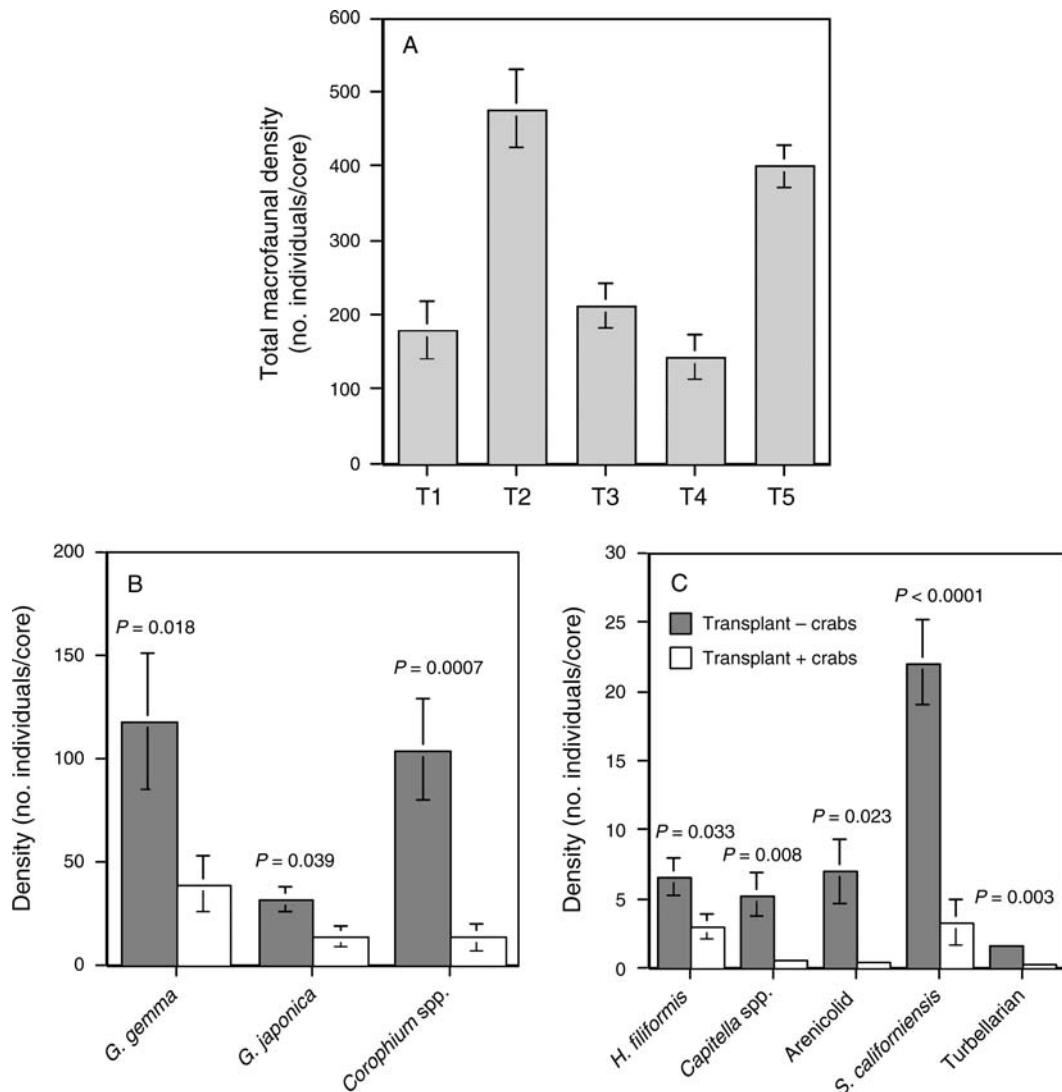


FIG. 3. Predation experiment. (A) Total macrofaunal densities (mean \pm SE) of five treatments: T1, tidal flat sediment transplanted into hybrid zone with open cage (two sided); T2, tidal flat sediment transplanted into hybrid zone with full cage and no crabs; T3, tidal flat sediment transplanted into hybrid zone with full cage and with one crab; T4, unmanipulated hybrid zone sediment with full cage and no crabs; T5, tidal flat sediment removed and replaced with no cage. (B) Densities per core area ($18.1 \text{ cm}^2 \times 6 \text{ cm}$ deep) of the bivalve *Gemma gemma* and the gammaridean amphipods *Grandidierella japonica* and *Corophium* spp. in enclosures containing transplanted sediment with crabs (T3) compared to "identical" enclosures without crabs (T2). (C) Densities per core of the capitellid polychaetes *Heteromastus filiformis* and *Capitella* spp., a species of arenicolid polychaete, the syllid polychaete *Sphaerosyllis californiensis*, and turbellarians in enclosures containing transplanted sediment with crabs (T3) compared with "identical" enclosures without crabs (T2). Paired *t* test *P* values compare treatment differences for each species.

the densities of the bivalve *G. gemma* declined by 67.1% ($t_{14} = 7.1$, $P = 0.018$; Fig. 3B). In addition, densities of other less abundant invertebrates, such as the subsurface deposit feeders *H. filiformis*, *Capitella* spp., and a juvenile arenicolid polychaete declined by 54.5% ($t_{14} = 5.6$, $P = 0.033$), 88.7% ($t_{14} = 9.4$, $P = 0.008$), and 92.9% ($t_{14} = 6.4$, $P = 0.023$), respectively (Fig. 3C). Also showing declines in density were the syllid polychaete *Sphaerosyllis californiensis* (85.1%; $t_{14} = 35.3$, $P <$

0.0001) and turbellarians (81.3%; Wilcoxon $\chi^2 = 8.72$, $P = 0.003$; Fig. 3C).

We found that the declines in the partial cages with ambient crab densities (Treatment 1) were similar to those of Treatment 3 (cages with crabs). At the end of the experimental period, a visual inspection of the experimental plots with crabs revealed strongly disturbed surface sediments, with depressions up to several centimeters deep. In contrast, sediments of control cages without crabs had a smooth surface. Sediment chl *a* was

about two times lower in the presence of crabs ($t_{14} = 5.3$, $P = 0.036$), as was total organic matter ($t_{14} = 10.2$, $P = 0.006$). Redox potential was lower in enclosures with crabs (-100.5 ± 26.7 mV) than in those without crabs ($+40.7 \pm 9.3$ mV; $t_{14} = 25.01$, $P = 0.0002$).

DISCUSSION

This study reveals multiple mechanisms by which invasive plants can modify coastal ecosystems. Many of the hybrid *Spartina* effects on benthic communities are indirect, involving changes in flow and depositional environments, chemical and textural characteristics, and the nature and intensity of recruitment and predation. Below we summarize the plant influences most likely to be responsible for broad-scale changes in the benthos that have accompanied the hybrid *Spartina* invasion, and discuss how they reflect the general impacts of invasive species on ecological processes.

Physicochemical changes

Our results demonstrated strong effects of *Spartina* on the physical and chemical environments in both the water column and on the sediment surface. Observed reductions in peak water velocities within the hybrid *Spartina* canopy (70–80% lower than in adjacent unvegetated tidal flat) were consistent with those documented for other *Spartina* marshes (e.g., Yang 1998, Christiansen et al. 2000, Leonard et al. 2002) and were most probably due to plant frictional effects (Knutson 1988, Yang 1998).

Mass loss of gypsum blocks was about two times greater on the unvegetated tidal flat, paralleling the reductions in flow velocities. The smaller difference measured by the gypsum blocks likely reflects the fact that they integrate flow conditions over the entire tidal cycle whereas the water velocity measurements reflect peak flow. While gypsum blocks do not distinguish between wave motion and currents, and dissolution can be influenced by temperature and salinity, this technique remains a viable proxy for relative water circulation (Howerton and Boyd 1992, Thompson and Glenn 1994, Porter et al. 2000). Attenuation of tidal and wave energy within *Spartina* habitat increased sediment deposition rates and reduced particles sizes relative to unvegetated tidal flats consistent with plant influences documented in *S. alterniflora* marshes (e.g., Christiansen et al. 2000), *Scirpus* spp. marshes (Yang 1998), *Phragmites australis* marshes (Leonard et al. 2002), and seagrass beds (e.g., Fonseca et al. 1982, Fonseca and Cahalan 1992).

We found that sediments in the hybrid *Spartina* habitat had significantly higher levels of organic matter, lower redox potential, higher porosity, higher levels of anoxia, and higher sulfide concentrations than those on the tidal flat. Most of the sediment changes observed in this study for *Spartina* habitat 10 m from the water's edge were even more severe than those described previously for *Spartina* habitat 1 m from the water edge (Neira et al. 2005), suggesting that harsher sediment

conditions develop as the invasion progresses. For sandy settings such as the Elsie Roemer tidal flat, a change in the sedimentary chemical environment can have a greater impact on benthos than does physical disturbance (Neira and Rackemann 1996). Lower redox potential, normally associated with enhanced sulfide concentrations, is one of several factors reducing species richness in salt marshes (Brewer et al. 1997).

Flow-mediated biological changes

A number of our observations reflect invader-induced flow mediation of biological patterns. There was a nine-fold reduction in barnacle recruitment in the hybrid *Spartina* relative to the tidal flat. If we normalize barnacle recruitment by flux based on our gypsum block results, which suggested that the hybrid *Spartina* experiences six-fold less flux, this indicates that the difference is not due to water movement alone. This very low recruitment in *Spartina* may have several nonexclusive causes: (1) lower concentrations of competent larvae within the *Spartina* canopy due to filtering or deposition, (2) the absence of strong boundary shear, known to increase barnacle exploratory locomotion and settlement rates (Crisp 1955, Mullineaux and Butman 1991), and (3) differences in postsettlement survival between the two habitats, which may also be mediated by flow and food availability.

Hydrodynamic events can deposit not only sediments but also associated zoobenthos in the water column as the presence of adult benthic animals in tube traps suggests. We interpret a doubling of trap animal recovery in *Spartina* vegetated habitat (relative to the tidal flat) as a deposition effect created by the plant canopy. Benthos on the tidal flats are likely to experience higher rates of resuspension, because of the higher flow velocities and greater bed stress in the absence of vegetation. However, the frictional effects of the plant canopy will result in diminished flow energy (Nepf et al. 1997) and will result in the deposition and concentration of animals inside the *Spartina* meadow. Species common in the tube traps were more abundant on the tidal flats (e.g., *Eteone californica*, barnacle larvae; 2.0 and 3.6 times, respectively) than in the hybrid *Spartina* areas, suggesting that they experienced transport from the tidal flat into the *Spartina* canopy and entrainment within the tube traps.

Consequences of sediment transplants

The results of transplant experiments clearly supported two predictions: (1) intact tidal flat sediment and associated fauna, when moved to invaded patches, would change to resemble those in vegetated habitat, and (2) the changes observed in community composition following invasion were due in part to poor survivorship of selected taxa. After 40 days and 155 days within the *Spartina* canopy, properties of sediment transplanted from the tidal flat plots were similar to those in hybrid *Spartina* habitat (Neira et al. 2005 and this study). Most

of the macrofaunal density decline in transplant communities was observed within the first 40 days and less took place in the following months (Table 2, Fig. 2A, C). The resulting loss of bivalves and amphipods was likely a response to increased organic matter deposition, which can result in hypoxic conditions and enhanced sulfide concentrations near or at the sediment surface (Rosenberg et al. 1991). Increased fine particle sediment deposition may bury individual species like *G. gemma*. This bivalve is a near-surface dwelling species and is able to survive several hours when buried by sandy sediments, but survival drops ~46% when *G. gemma* is buried by silty sediment (Shulenberg 1971). Loss of microtopographic relief by surface deposition may result in homogenization of the habitat, with negative effects for sensitive amphipod species (Nipper et al. 1989, Werner and Zedler 2002). In contrast, capitellid polychaetes and tubificid oligochaetes cope very well in sulfidic sediments (e.g., Pals and Paupit 1979).

Invader facilitates invader

Hybrid *Spartina* provides refuge for green crabs, themselves a recent invader, and thus enhances this predator's influence on the benthos. Our enclosure experiments demonstrated that green crabs may modify macrofaunal communities both through the alteration of habitat structure and the top-down effect of predation. While green crab feeding activity is usually concentrated in the top few centimeters of sediment (Sherer and Reise 1982, LeCalvez 1987), crabs have also been observed digging pits deeper to extract large clams (Cohen et al. 1995). In this study, green crabs caused significant decline in gammaridean amphipods (*Corophium* spp. and *G. japonica*) and bivalves (*G. gemma*), species whose densities decline during hybrid *Spartina* invasion (Neira et al. 2005). The intense digging activity of the green crab was further evidenced by the reduction in benthic microalgal biomass and the decline of subsurface deposit feeders (*H. filiformis*, *Capitella* spp., and juvenile arenicolid polychaetes), animals otherwise well-hidden from consumers. Diatoms associated with surface sediments are susceptible to resuspension following bioturbation (Blanchard et al. 1997) and crab disturbance can reduce diatom biomass (Boyer and Fong 2005, Armitage and Fong, *in press*).

In our experiment with *Carcinus maenas*, and in those of Armitage and Fong (*in press*) with *Pachygrapsus crassipes*, sediment enclosures with crabs showed reduced redox potential (i.e., anoxic sediment) relative to controls. A plausible explanation is that loss of bioturbating annelids combined with consumption of microalgae and physical disturbance could depress near-surface oxygen concentrations and raise the redox potential discontinuity layer (Fenchel 1969).

Trophic modifications

There is evidence to suggest that the faunal changes we observed were in part the result of changes in food

availability. A separate study compared in situ uptake of ^{15}N -labeled hybrid *Spartina* detritus and ^{13}C -labeled microalgae by infaunal species at the Elsie Roemer study site (Levin et al. 2006). The greatest uptake of ^{15}N from invasive *Spartina* detritus occurred mainly in annelid taxa traditionally assumed to be subsurface feeders: capitellid polychaetes and tubificid oligochaetes, taxa whose densities were generally unaffected by *Spartina* invasion and that showed the highest survival following transplantation into the *Spartina* zone (this study and Neira et al. 2005). Several of the taxa that failed to ingest significant amounts of ^{15}N -labeled *Spartina*, including amphipods (*Grandidierella japonica*, corophiid species), bivalves (*Gemma gemma*, *Macoma petalum*), and polychaetes (*Tharyx* sp.), exhibited elevated $\delta^{13}\text{C}$ signatures indicative of surface algae ingestion. Among these were species that experienced greatest reduction in density following plant invasion of the tidal flat (Neira et al. 2005) and exhibited the lowest survival following transplantation into the hybrid *Spartina* zone (this study).

The complementarity of results from stable isotope tracer studies (Levin et al. 2006) and the manipulative experiments in this study strongly supports a role for food limitation for surface feeders as one mechanism responsible for the changes witnessed in infaunal communities invaded by hybrid *Spartina*. The broad shifts we observed in the benthic communities of San Francisco Bay, from predominantly surface algal consumers to subsurface detritivores, are consistent with changes in the base of the food web (Levin et al. 2006); belowground plant detritus was 4.3 times more abundant in *Spartina*-invaded sediments than in the tidal flat during our study (Neira et al. 2005). To date the most fundamental changes documented in food web structure following species invasion have resulted from top-down effects of predatory fish (Hurlbert et al. 1972), zooplankton (Spencer et al. 1991, 1999), and suspension-feeding bivalves (Alpine and Cloern 1992). Our studies suggest that plant influences on trophic structure interact with modifications of flow and sediment conditions, recruitment, and predation to transform wetland ecosystems.

Conclusions

As a result of strong physical- and chemical-mediated changes, we find significant declines in both diversity and density of macrofauna in hybrid *Spartina* areas relative to unvegetated tidal flats. These results are consistent with observations in marshes dominated by *S. foliosa* (Levin et al. 1998), *S. anglica* (Jackson 1985), and *S. alterniflora* (Zipperer 1996, O'Connell 2002), but differ from existing paradigms about positive vegetation effects on macrofauna abundance and diversity (e.g., Netto and Lana 1999, Hedge and Kriwoken 2000, Pennings and Bertness 2001). Brusati and Grosholz (2006) recently found higher abundance of macroinfauna in areas vegetated by the Pacific native *S. foliosa* in San Francisco Bay than in open mudflats. This

is likely due to the positive effects of aboveground structure ameliorating sediment temperatures and wave stress. In addition, the lower belowground biomass of *S. foliosa* relative to the hybrid does not exclude infauna as does the hybrid (Brusati and Grosholz 2006). Clearly, not all habitat systems respond in the same way to hybrid *Spartina* invasion; age, flow regime, and native vegetation status all are important factors (Neira et al. 2005). At Elsie Roemer, hybrid *Spartina* acts as a refuge for predators, degrades sediment conditions, reduces food quality for surface-feeding animals, and preempts belowground habitat for infauna, thus counterbalancing the positive effects of aboveground vegetation structure on macrobenthos.

From the perspective of the entire ecosystem, the loss of open tidal flat may also impact species including migratory shorebirds, which continue to decline in western estuaries (Page et al. 1999). Most shorebirds will not forage in vegetated areas and are excluded from areas colonized by hybrid *Spartina*. At the same time, hybrid *Spartina* provides nesting habitat for several endangered bird species, the California Clapper Rail, and Salt Marsh Song Sparrows, although there is some question about its suitability given the reduced tidal elevations involved (Nordby et al. 2004).

Understanding what tips the balance between positive and negative effects of introduced vascular plants on benthic marine systems is an important goal for future studies. By focusing on mechanisms, we can help clarify why particular species decline while others do not, ultimately facilitating prediction and interpretation of ecological change under other invasion scenarios.

In closing, we note that *Spartina* invasion of tidal flats is a widespread phenomenon: *S. alterniflora* and its hybrids are invading tidal flats worldwide as are *S. anglica*, *S. patens*, and *S. densiflora* (summarized in Daehler and Strong 1996). Thus, the direct and indirect mechanisms and consequences identified here are likely to be of global significance. Beyond *Spartina*, the spread of other non-indigenous vascular plants into coastal wetlands (e.g., *Phragmites*, *Tamarix*, and *Zostera*) appears to be increasing (Ruiz et al. 1997, Adam 2002, Crooks 2002). Most of the general mechanisms we have studied for *Spartina* (e.g., flow, sediment, chemical, recruitment, predator, and detritus alterations) apply to those other invasions. Plants are recognized as ecosystem engineers; through structural influence on habitat complexity they have cascading ecosystem-level effects (Crooks 2002). Given that native plants typically have similar physical, chemical, and biological influences, we can ask, "When does a plant introduction create a state change likely to alter ecosystem processes and functions?" Based on our observations for *Spartina* in coastal ecosystems, we predict that state changes and system restructuring will occur when the invader (1) appears in a setting where comparable structural forms are absent, thereby modifying flow and associated physicochemical sedi-

ment conditions (e.g., plant invasion of tidal flats), (2) facilitates key consumers, whether native or invasive (e.g., *C. maenas*), and/or (3) introduces large quantities of a novel food source (e.g., detritus) that is used by a specific suite of organisms.

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