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Changes in Community Structure and Ecosystem Function Following *Spartina alterniflora* Invasion of Pacific Estuaries

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One of the most pervasive human impacts to salt marshes around the world is the introduction of nonnative species. Plant introductions to salt marsh systems have resulted in significant changes ranging from species replacement to broad-scale alteration of ecosystem properties. In this chapter, we examine the changes produced by the invasive Atlantic smooth cordgrass Spartina alterniflora *in two wetland ecosystems, one in San Francisco Bay, California, and one in Willapa Bay, Washington. We compare and contrast the impacts of* Spartina *invasion on a range of processes, focusing primarily on benthic invertebrate communities and the sediment environment. Our work shows that the structure of the plant itself and the changes it produces in the physical and chemical environment strongly influence benthic communities. The aboveground structure shades the substrate, reducing photosynthesis of benthic microalgae and restricts water flow, which contributes to decreased recruitment and slower growth of benthic suspension feeders. At the same time, the plant structure increases sedimentation of fine-grained particles and leads to the accumulation of detritus and low-quality organic matter. These changes, together with increased belowground plant biomass and peat production, influence sediment chemistry and metabolism. In addition, belowground plant biomass can preempt substantial amounts of belowground habitat, directly reducing benthic abundance and diversity. These physical and chemical changes can result in dramatic shifts in benthic communities including substantial reductions in larger, surface-feeding taxa concurrent with increases in smaller, subsurface detritivores. Such shifts in the functional identity of benthic species may negatively affect feeding of both invertebrate and vertebrate predators. The magnitude and direction of these various changes depend on the habitat invaded and are generally more substantial where* Spartina *has invaded open mudflats and less where* Spartina *invades areas of native vegetation. We discuss the consequences of these changes in the context of plant effects in other coastal systems in order to develop a set of predictions regarding future plant invasions. The ultimate consequences of plant invasion on benthic communities involve a dynamic balance of positive and negative effects.*

By understanding the mechanisms that determine the magnitude and direction of these effects, scientists and managers will be better able to understand the consequences of human-induced plant invasions in salt marsh systems and to predict the impacts of future introductions.

Salt marshes are among the many habitats worldwide experiencing rapid change as the result of human-mediated stressors (Vitousek et al. 1997; Chapin et al. 2000; Mooney and Hobbs 2000). Among the most important changes experienced by salt marshes is the introduction of nonnative plants. Wetlands generally are susceptible to invasion, and introduced plants can foster changes acting broadly across multiple spatial and temporal scales, producing long-lasting and system-wide effects (Zedler and Kercher 2004). These changes may include a host of physical and chemical alterations that can influence populations and communities of plants and animals as well as alter the storage and recycling of nutrients (Mack et al. 2000). Introduced plants can also directly affect the abundance, diversity, and functional identity of communities via the provision or preemption of physical habitat and as well as changes in the basis of trophic support.

The invasion of *Spartina alterniflora* in U.S. West Coast estuaries provides an excellent demonstration of the extent to which plant invasions can rapidly and extensively alter community and ecosystem dynamics in salt marsh systems. In this chapter, we will compare and contrast the invasions of the Atlantic smooth cordgrass *Spartina alterniflora* in two estuaries in western North America. The first is San Francisco Bay, California, where *S. alterniflora* hybridized with the native *Spartina foliosa*, and the resulting hybrid has spread rapidly throughout the central and southern portions of San Francisco Bay. The second is Willapa Bay, Washington, where in the absence of any native *Spartina, S. alterniflora* has colonized habitats throughout most of this bay.

We will address the impacts of *Spartina* on benthic systems in these two regions with a particular focus on infaunal and epifaunal communities and the changes in physical and chemical processes in the sediment environment. The changes brought about by *Spartina* are ultimately the result of the extensive above- and belowground growth of the plant. But the overall effects on community and ecosystem processes depend on the magnitude of change in a range of properties, including above- and belowground vascular plant biomass, production and decomposition of detritus, microalgal productivity, and sediment physicochemistry, all of which can have variable effects on the native plants and animals. The consequences of *Spartina* invasion strongly depend on the age of the invasion, the habitat being invaded, the presence or absence of native vegetation, and many site-specific characteristics including elevation, sediment grain size, and hydrodynamic regime.

The primary goal of this chapter is to synthesize recent studies of *Spartina* invasions in Washington and California to better understand and predict the impacts of *Spartina* and other marsh plants in the future. We do this by comparing our results with other studies of invasive *Spartina* in this western region and other regions, as well as with systems where *Spartina* is native.

An additional goal is to use this understanding to assist ongoing eradication programs in California and Washington that aim to eliminate invasive *Spartina* from this region. By quantifying the full extent of the changes being brought about by the *Spartina* invasion, as well as knowing the mechanisms underlying the changes, we hope to assist resource managers in determining when, where, and how eradication of *Spartina* will be most effective.

CONTRASTING INVASIONS

The invasion of *Spartina alterniflora* in San Francisco Bay, henceforth "SFB," began in 1975 with its intentional introduction from the Atlantic Coast of the United States by the Army Corp of Engineers for salt marsh restoration (Ayres, Strong, and Baye 2003; Ayres, Strong, et al. 2004). Following the initial introduction, a hybrid developed from *S. alterniflora* and the native *S. foliosa* (hereafter referred to as hybrid *Spartina*) (Daehler and Strong 1997). This hybrid grows more vigorously than either parent plant and has a higher and lower tidal range than native plants (Ayres et al. 2003; Ayres, Smith, et al. 2004; Ayres, Zaremba, and Strong 2004). The hybrid has successfully colonized nearly eight hundred hectares of the central and southern portions of SFB, where it has invaded open mudflat at the lower end of its tidal distribution. Although three other species of *Spartina* have been introduced into SFB (*S. densiflora*, *S. anglica*, and *S. patens*), and another hybrid (*S. densiflora* × *S. foliosa*) has been found (D. Ayers, personal communication), none have spread significantly (California Coastal Conservancy 2006). The hybrid has displaced the native *S. foliosa* as well as the original parent *S. alterniflora* in central SFB through hybridization and overgrowth (Ayres et al. 2003; Ayres, Smith, et al. 2004; Ayres, Zaremba, and Strong 2004) and competes with native plants such as *Sarcocornia pacifica, Distichlis spicata,* and *Jaumea carnosa*.

The invasion of Willapa Bay, henceforth "WB," began with the accidental introduction of *S. alterniflora* around 1890 (Feist and Simenstad 2000; Davis et al. 2004; Civille et al. 2005). Throughout most of the century since its initial introduction, the spread of *Spartina* has been fairly gradual. However, from 1995 to 2005, it rapidly spread to cover 1,600 hectares in WB for unknown reasons. Because there are no native *Spartina* species in the Pacific Northwest with which to hybridize, this invasion is entirely the result of the spread of *S. alterniflora*. As in SFB, *S. alterniflora* has rapidly colonized open mudflat and has been found among native plants in the upper intertidal zone, where it has the potential to compete with and even exclude species such as *Sarcocornia pacifica, Distichlis spicata,* and *Deschampsia caespitosa,* although this has not so far been demonstrated.

While both systems involve invasion of mudflats at the lower tidal range, noteworthy differences may further influence the impact of *Spartina*. In WB, the invasion is much older, the aerial cover is much greater, and other ecosystems, such as oyster reefs, are at risk of displacement. In addition, the invasive *Spartina* does not resemble any native marsh plant forms, and since there were no native *Spartina* species present prior to the invasion, none of the native plants or animals have coevolved with this genus. In contrast, the SFB invasion is relatively recent and involves a hybrid that became a superior competitor that threatens to eliminate the pure native *S. foliosa* (Ayres et al. 2003). The system that is adapting to the invasion in SFB is replete with birds, fish, and invertebrates that have evolved with native *Spartina* in upper intertidal elevations. SFB is also heavily invaded, and because many of these introductions came from the Atlantic Coast, these invaders have a long evolutionary history with the presence of *Spartina* across a broad tidal range (Cohen and Carlton 1998). These include bivalves such as *Geukensia demissa*, *Mya arenaria*, and *Gemma gemma* as well as gastropods such as *Urosalpinx cinerea* and *Ilyanassa obsoleta*; these are among the most common species in areas of SFB with invasive *Spartina*.

CONSEQUENCES OF INVASION

VASCULAR PLANT PRODUCTION

The productivity of *Spartina,* both above- and belowground, was greater than that of native vascular plants at both the WB and SFB sites. The magnitude of the differences between native and nonnative habitats varied depending on the initial conditions (vegetation type and substrate) and the age of the invasion. In SFB, the

TABLE 2.1 *Summary of studies to date examining changes in primary production, sediment respiration, and sediment organic C and N in invaded western salt marshes*

	SAN FRANCISCO BAY		WILLAPA BAY	
	Mudflat	*Spartina*	*Mudflat*	*Spartina*
	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)
AG biomass (g m^{-2})[1,2]	———	1823 ± 283	3 ± 1	1695 ± 245
BG biomass (g m^{-2})[1,2]	———	4197 ± 773	55 ± 8	878 ± 91
Benthic Chl *a* (mg m^{-2})[3]	184 ± 51	97 ± 15	117 ± 9	247 ± 23
GPP (mg Cm^{-2} d^{-1})[3]	459 ± 92	258 ± 52	———	———
Respiration (mg Cm^{-2} d^{-1})[3]	179 ± 34	752 ± 91	———	———
%N[4]	0.10 ± 0.03	0.17 ± 0.02	0.12 ± 0.00	0.23 ± 0.02
%C[4]	1.22 ± 0.30	2.70 ± 0.29	1.35 ± 0.04	3.36 ± 0.34
C:N[4]	14.8 ± 2.1	21.8 ± 2.2	12.9 ± 0.1	16.0 ± 0.6

NOTE: Aboveground (AG) and belowground (BG) biomass were measured at the end of the growing season (September–October).

SOURCES: [1]Tyler et al. 2007 (*Spartina* values); [2]mudflat biomass values are for the invasive intertidal seagrass *Zostera japonica* from A. C. Tyler, unpublished data, 2002; [3]Tyler and Grosholz (n.d.), except for Willapa Bay chlorophyll *a* values, which are from A. C. Tyler, unpublished data, 2003); [4]A. C. Tyler, unpublished data, fall 2002.

FIGURE 2.1 Introduced *Spartina alterniflora* seedlings competing for space with introduced eelgrass *Zostera japonica* in Willapa Bay, Washington.

aboveground biomass of invasive *Spartina* was significantly higher than the biomass of native *S. foliosa* and *Sarcocornia* sp. (see table 2.1; Brusati and Grosholz 2006; Tyler, Lambrinos, and Grosholz 2007). The belowground biomass of invasive *Spartina* was also generally higher than native plants including *S. pacifica,* although the difference was not as great as for aboveground biomass (table 2.1; Brusati and Grosholz 2006, Tyler et al. 2007). Also, the biomass of invasive *Spartina* was obviously much greater than the micro- and macroalgae on historically "unvegetated" mudflats. The belowground biomass of hybrid *Spartina* in SFB (top six to ten centimeters) changes with invasion stage. For example, at one site it increased from unvegetated tidal flats (less than one hundred grams per square meter) to 348 grams per square meter on the "growing edge" (about one meter inside vegetation—i.e., young invasion), to over 720 grams per square meter in the central area (thirty-year-old invasion) (Neira et al. 2007).

In WB, the introduced eelgrass *Zostera japonica* overlaps considerably in the tidal zone colonized by *S. alterniflora* (fig. 2.1). This eelgrass apparently produces only about a third of the biomass produced by *S. alterniflora* (Ruesink et al. 2005). The long history of invasion in WB has allowed us to determine the dynamics of *Spartina* production by using the different-aged meadows as a chronosequence to represent the trends in biomass through time. Based on a series of eighteen *S. alterniflora* meadows ranging from less than one year to more than thirty years old (age was determined based on the date when the areal extent of cordgrass in each region was greater than 50 percent), we found that aboveground biomass reached a peak within five to ten years and then declined as the meadow aged. In contrast, the buildup of a dense mat of roots and rhizomes required a longer time (ten to fifteen years) but then remained relatively constant (A. C, Tyler, unpublished data). This aboveground biomass of *S. alterniflora* in WB was similar to that of hybrid *Spartina* in SFB; however, the belowground biomass in WB was considerably less than in SFB (table 2.1).

PHYSICAL PROCESSES

The large amount of aboveground biomass produced by invasive *Spartina* necessarily results in changes in the physical regime of the invaded mudflats. The plant reduces both the light reaching the mudflat surface and tidal energy. In both SFB and WB, the aboveground canopy of invasive *Spartina* significantly reduced light penetration to the sediment surface by up to 83 percent (Neira, Levin, and Grosholz 2005; Neira et al. 2006; Tyler and Grosholz, forthcoming). Also, the plant canopy significantly restricted water flow and reduced velocity by up to 76 percent and bed stress relative to unvegetated areas (Neira et al. 2005, 2006). These reductions in light and flow produced by the invasive *Spartina* canopy were greater than those of native *S. foliosa* (Brusati and Grosholz 2006; Tyler and Grosholz, forthcoming), but they were comparable to those produced by *Sarcocornia pacifica*, which can result in more substantial reduction in light than *Spartina* (Neira et al. 2005; Tyler and Grosholz, forthcoming).

The aboveground structure of *Spartina* invasion also led to increased sediment accretion rates and reduced sediment grain size (Neira et al. 2006). Together with the buildup of belowground biomass and peat, this has resulted in increased tidal elevation of invaded areas. These changes are common to both SFB and WB. In areas of even moderate flow, unvegetated mudflats experience rapid changes in elevation of up to four centimeters over periods as short as a few weeks in comparison with changes usually much less than one centimeter in vegetated areas. By reducing flow, *Spartina* attenuated these short-term changes in elevation resulting in a pattern of gradual increase in elevation relative to the adjacent unvegetated areas (E. D. Grosholz, unpublished data).

MICROALGAL PRODUCTION

The *Spartina* invasion has a substantial impact on benthic microalgal photosynthesis. In many intertidal habitats, benthic microalgal production comprises a substantial proportion of overall system primary production and is an important contributor to local food webs (Zedler 1980, 1984; Page 1995; Deegan and Garritt 1997; Kwak and Zedler 1997; Page 1997). This is especially true on Pacific Coast mudflats and in *Sarcocornia*-dominated marshes, where microalgae are the primary carbon source for many secondary consumers (Kwak and Zedler 1997; Moseman et al. 2004). The impact of *Spartina* invasion on benthic microalgae was variable across sites and is dependent to some extent on the nature of the uninvaded habitat. Where *Spartina* had invaded mudflats in both SFB and WB, benthic chlorophyll *a* concentration (a proxy for microalgal biomass) was often, but not always, higher in *Spartina* meadows than in the adjacent uninvaded mudflats (table 2.1; Neira et al. 2005, 2006; Tyler and Grosholz, forthcoming; A. C. Tyler et al., unpublished data). However, microalgal production was consistently higher on the mudflats of SFB than in the adjacent *Spartina* marshes. Factors such as light availability and grazing (see “Food Web Structure”) may create a disparity between chlorophyll *a*–based standing stock and overall productivity. Overall, the *Spartina* invasion had a negative impact on microalgal productivity with important ramifications for overall food web support.

NUTRIENTS AND ORGANIC MATTER

The invasion of *Spartina* resulted in a shift in the overall cycling of organic matter and nutrients because of the refractory nature (higher carbon:nitrogen) of its tissues (A. C. Tyler et al., unpublished data). Following the invasion of WB, we observed an extensive accumulation of detritus associated with *S. alterniflora* litter that occurs primarily at the end of the growing season when the aboveground portion died back. This detritus accumulated in massive heaps in the high intertidal, where it slowly decomposed and had detrimental effects on native vegetation plant biomass, aboveground productivity, and species richness (A. C. Tyler et al., unpublished data; Lambrinos, forthcoming). In SFB, because hybrid *Spartina* decomposes more slowly than native *S. foliosa*, more wrack build-up can be attributed to the hybrid (A. C. Tyler et al., unpublished data).

In addition to the high aboveground litter production, belowground production generates large volumes of roots, rhizomes, and peat, leading to an increase in belowground organic matter and particulate organic carbon and nitrogen relative to the native systems in both SFB and WB (table 2.1; Neira et al. 2006; Levin, Neira, and Grosholz 2006; A. C. Tyler et al., unpublished data). We observed a subsequent increase in meadow sediment respiration rates relative to mudflats in SFB that fostered a shift from a net autotrophic system, dominated by microalgal production, to a new heterotrophic system, dominated by belowground microbial decomposition (table 2.1; Tyler and Grosholz, forthcoming). However, we found higher sediment respiration rates in native vegetation than in hybrid *Spartina*, most likely as a result of the more refractory nature of the *Spartina* detritus that is a less desirable substrate for microbial decomposers (Tyler and Grosholz, forthcoming). In all cases, the turnover of carbon and nutrients is slowed down, resulting in the accumulation of massive quantities of highly refractory organic matter.

In contrast to the dramatic increase in sediment particulate nitrogen upon invasion of unvegetated mudflats, we found a significant decrease in available porewater ammonium in invaded meadows compared to native mudflats in both SFB and WB (A. C. Tyler, unpublished data). Possible causes for this decrease are plant uptake, increased microbial immobilization, or increased coupling of nitrification-denitrification in the oxidized root zone of *Spartina*. On the Atlantic coast, the invasion of *Phragmites australis* also caused distinct changes in nitrogen cycling in sediments depending on the invaded community (Windham and Meyerson 2003). Even though hybrid *Spartina* is able to increase the redox potential in the vicinity of its roots, we observed an overall decrease in redox potential (Neira et al. 2005). Accordingly, our results from SFB also show that porewater sulfide concentrations are nearly one hundred times greater in *Spartina* meadows relative to uninvaded mudflats (meadow, 1,016 ± 121 μM; mudflat, 12 ± 1 μM; mean ± SE; A. C. Tyler, unpublished data; Neira et al. 2007), which is likely due to the increased organic matter pool and subsequent increase in both microbial oxygen demand and sulfate reduction.

BENTHIC COMMUNITIES

The altered physical and chemical environments can also strongly influence the recruitment, survival, growth, and reproduction of benthic invertebrates in the invaded areas. Both epifaunal and infaunal organisms respond to the changing light, flow, and sediment conditions in ways that affect not only the biomass and diversity of these organisms, but also the functional identity of many groups (Neira et al. 2006).

Our work has shown significant changes in the recruitment and growth of common taxa in the hybrid *Spartina* meadows relative to uninvaded areas. Measurements of barnacle (*Balanus glandula*) recruitment on standardized recruitment substrata (mussel shells) placed in the growing edge of hybrid *Spartina* meadow and on adjacent mudflat areas showed recruitment was ninefold higher on the mudflats (Neira et al. 2006). Experiments using marked *Macoma petalum* transplanted into hybrid *Spartina* meadows, and adjacent mudflat areas showed growth was significantly reduced by up to twofold in the hybrid *Spartina* treatments (Brusati and Grosholz 2007). Our results suggest reductions in flow; thus, reduced delivery of propagules (recruitment) and seston (for growth) likely contribute to these patterns.

Our work has also shown that both biomass and diversity of infauna can decline strongly in invaded areas relative to the previously unvegetated control areas (Neira et al. 2005, 2007; Levin et al. 2006; Neira et al., forthcoming). In SFB, invertebrate densities decline by as much 75 percent relative to unvegetated mudflat (Neira et al. 2005), although densities at some sites are not significantly different from those in native *Sarcocornia pacifica* areas. Species richness also showed a significant 25 percent decline in *Spartina* invaded areas compared with unvegetated controls, but it was elevated relative to *Sarcocornia*-vegetated habitat (Neira et al. 2005).

Similar patterns were measured in WB, where invertebrate species richness was significantly higher in mudflat/*Zostera* areas than in *S. alterniflora* areas (mudflat, 11.75 ± 2.62; *Spartina*, 6.0 ± 3.12; mean ± 1 SE; per 19.6 square centimeters). Species diversity was also higher in the mudflat/*Zostera* areas relative to the *Spartina* meadow (Shannon-Wiener H' [$\log_2$] = 3.92, mudflat; 2.79, *Spartina*), and the density of invertebrates was slightly greater in mudflat/*Zostera* areas, although not significantly so.

In SFB, we experimentally investigated the mechanisms underlying these changes in a series of transplant experiments, plant manipulations, predator inclusion and exclusion studies, and trophic investigations. This work demonstrated that the changes in the density and diversity of infauna were due to the combined effects of preemption of belowground habitat by *Spartina*, changes in the food supply and predation pressure, as well as the physical and chemical changes to sediments and porewater (Neira et al. 2006; Levin et al. 2006). For these reasons, the effects of *Spartina* on benthic abundance and diversity are less dramatic in areas previously occupied by native marsh plants (Neira et al. 2005).

FACILITATING OTHER INVASIVE SPECIES

The aboveground structure of *Spartina* can have other positive effects, including facilitating higher densities of other invasive species. In SFB, our data suggest that the invasive hybrid has facilitated several nonindigenous invertebrate species, creating invasive hot spots (areas of greater abundance) in the recently colonized *Spartina* edge areas not present on the open mudflat. At one site in SFB, we found that densities of several clams introduced from the Atlantic (*Macoma petalum*, *Mya arenaria*, *Geukensia demissa*) were two to ten times higher in the growing edge of the hybrid *Spartina* meadow than on the adjacent open mudflat (E. D. Grosholz et al., unpublished data). Although high *Geukensia* densities were largely due to the requirement of structure for attachment provided by *Spartina* (similar structure is virtually absent on open mudflats), densities of *Mya* and *Macoma* may be higher as the result of refuge from predation by bat rays (*Myliobatus californica*). At one site where greater than 40 percent of the substrate was disturbed by bat rays, densities of *Mya* and *Macoma* were two to three times greater in the growing edge of *Spartina* compared with adjacent mudflats. At a second site with less than 1 percent of the area disturbed by bat rays, there was no difference in clam densities between *Spartina* and mudflats (E. D. Grosholz et al., unpublished data).

In SFB, we also found high abundances of introduced Atlantic gastropods *Urosalpinx cinerea* and *Ilyanassa obsoleta* along the leading edge of the hybrid *Spartina*. In experiments where we simulated the aboveground structure of *Spartina* by adding wooden dowels to mudflat areas, we found twenty- to fiftyfold increases in the density of both *Urosalpinx* and *Ilyanassa* in dowel addition treatments compared with adjacent mudflat control areas (E. D. Grosholz et al., unpublished data). Data documenting sediment temperatures in dowel addition areas suggest that lower sediment temperatures may strongly influence these patterns.

We have also documented that the hybrid facilitates the European green crab *Carcinus maenas* in SFB. Our data show that this species is three to five times more abundant, particularly for smaller size classes, in hybrid in comparison with the adjacent mudflat (E. D. Grosholz et al., unpublished data; Neira et al. 2006). This predator, in turn, appears to have a significant

TABLE 2.2 *A comparison of the effects of both above- and belowground structure for invasive versus native* Spartina *on overall abundance and diversity of benthic invertebrates relative to unvegetated mudflats*

	INVASIVE *SPARTINA*		NATIVE *SPARTINA*	
	Growing Edge	*Developed Meadow*	*Growing Edge*	*Developed Meadow*
Aboveground	Increase	Increase	Increase	Increase
Belowground	Slightly decrease	Decrease	Minimal	Slightly decrease

NOTE: The growing edge areas for both are areas colonized within the last five years approximately and the developed meadows areas that have had vegetation for at least ten years (from Brusati and Grosholz 2006; Neira et al. 2007).

impact on the invertebrate taxa that are negatively affected by *Spartina* invasion and so may reinforce the changes brought about by this plant invasion (Neira et al. 2006). The extent to which *Spartina* facilitates other invasive species in WB is less certain. However, evidence suggests that *Spartina* fills a similar role facilitating younger size classes of green crabs (Yamada 2001).

We summarize the generalized effects of above- and belowground portions of *Spartina* on invertebrate diversity and abundance in table 2.2. The growing edge of the hybrid *Spartina* meadow that had been colonized within approximately five years functions similarly to the native *S. foliosa* and has a similar influence on invertebrate abundance and diversity. In this growing margin, the aboveground structure has the same generally positive effects on invertebrates, but the belowground portion of the hybrid has not developed sufficiently to reduce infaunal densities. In areas farther back from the growing edge, which are approximately five to ten years old, changes in sediment biogeochemistry and belowground biomass have progressed to the point of significantly depressing densities and diversity of infauna (Neira et al. 2005). Therefore, we suggest that the influence of hybrid *Spartina* on benthic communities varies with the successional stage of the invasion (table 2.2; Neira et al. 2007).

FOOD WEB STRUCTURE

The structure of benthic food webs was also affected by the changes in vascular plant and litter availability relative to other food sources. We used stable isotope enrichment experiments to follow consumption of *Spartina* detritus and microalgae by invertebrates and to determine the broader effects of *Spartina* invasion on benthic food web structure. Using ^{15}N-labeled *Spartina* detritus and ^{13}C-labeled microalgae simultaneously, we found that the *Spartina* invasion in SFB has dramatically shifted the tidal flat infaunal invertebrate community from one dominated by surface feeders that primarily consume microalgae (amphipods, bivalves) to one dominated by belowground feeders that primarily consume plant detritus (oligochaetes, capitellid polychaetes) (Levin et al. 2006). Using two- and three-end-member mixing models, we determined that a significant portion of the diet of these belowground detritivores was the detritus produced by hybrid *Spartina*. Therefore, this invasion has resulted in a qualitative shift of the entire food web from one based on fresh primary production to one based on detritus. We summarize the overall results of these changes on invertebrate functional groups in table 2.3.

When we compare these results with those from native *Spartina* areas that have not been invaded, we note some important differences. Natural abundance stable isotope studies conducted in native versus hybrid *Spartina* areas show little incorporation of the added detritus into the food web. Larger epifauna in hybrid areas did not show $\delta\,^{13}$C values consistent with the added detrital input of *Spartina* when compared with organisms collected from open mudflat habitats, though there was a slight

TABLE 2.3 *A summary of predicted effects of aboveground and belowground invasive* Spartina *on densities of different functional groups of benthic invertebrates*

	Aboveground	*Belowground*
Mobile epifauna	Positive	None
Surface-feeding infauna	Negative	Negative
Detrital-feeding infauna	Positive	Negative
Bivalves	Positive/negative	Negative

SOURCES: From Neira et al. (2005, 2006); Levin et al. (2006); Brusati and Grosholz (2006, 2007); E. D. Grosholz, unpublished data.

isotopic shift toward *Spartina* in invertebrates collected in native *S. foliosa* meadows compared with those on the open mudflat (Brusati and Grosholz 2007). This is also consistent with the idea that the detritus of *S. foliosa* is less refractory than that of the hybrid *Spartina* detritus, and benthic invertebrates may consume more detritus of the native than invasive *Spartina*. However, a comparison of ingestion of ^{15}N-labeled *S. foliosa* and ^{15}N-labeled hybrid *Spartina* in SFB indicated mostly similar infaunal uptake (oligochaetes and capitellid polychaetes) or avoidance patterns (Levin et al. 2006).

We investigated food web changes in WB using similar isotopic enrichment experiments. We found that the taxonomic range of benthic species that consumed detritus of *Spartina alterniflora* was similar to SFB (E. D. Grosholz et al., unpublished data). We found that tanaids, bivalves, spionid and cirratulid polychaetes, and chironomid larvae all showed enriched signals in treatments with *Spartina* detritus in the *Spartina* zone (E. D. Grosholz et al., unpublished data). Based on elevated $\delta\ ^{15}$N values (30 to 80 per mille), we found significantly more *Spartina* detritus was consumed in the *Spartina* zone than in mudflat/*Zostera* zone treatments. As in the SFB study, we found that $\delta\ ^{13}$C values (15 to 50 per mille) were higher for surface feeders including amphipods, tanaids, and cirratulid polychaetes, with values similar in both *Spartina* and mudflat/*Zostera* zone treatments. Although we see some differences between food web impacts in SFB and WB, these do not appear to be due to differences in palatability since the carbon:nitrogen ratios of *S. alterniflora* relative to the hybrid are similar (WB = 46.0 ± 1.9; SFB = 48.4 ± 1.8, and there was no difference in percent nitrogen; A. C. Tyler, unpublished data). Instead, the differences may reflect the much longer history of invasion in WB (nearly one hundred years) or the presence of extensive *Zostera* cover and detritus input in what was historically an unvegetated mudflat. We found that the detritus of the introduced *Z. japonica* was consumed to a much greater extent than *Spartina* in the WB experiments based on enriched $\delta\ ^{15}$N signatures. A wide range of surface-feeding consumers including several bivalves and terebellid polychaetes showed elevated $\delta\ ^{15}$N values with much greater values (100 to 500 per mille), supporting the higher edibility of *Zostera* relative to *Spartina* based on the lower carbon:nitrogen ratio (*Z. japonica* carbon:nitrogen 17.3 ± 0.7; A. C. Tyler, unpublished data).

VERTEBRATE CONSUMERS

The expansion of hybrid *Spartina* has also influenced grazing of cordgrasses by Western Canada geese (*Branta canadensis moffitti*) in SFB. Our studies have shown that the geese can distinguish differences in blade toughness between the native and hybrid forms of *Spartina* and completely avoid the hybrid while readily consuming the native *S. foliosa*. Data from both field studies and feeding trials using captive geese have shown that geese will graze more than 90 percent of the *S. foliosa* biomass at some sites while grazing less than 1 percent of the hybrid (E. D. Grosholz et al., unpublished data).

FIGURE 2.2 Hybrid *Spartina* colonizing open mudflat and preempting foraging habitat used by wintering populations of migratory shorebirds in San Francisco Bay.

The *Spartina* invasion may also have important implications for wintering populations of migratory shorebirds. Most shorebirds will not forage in vegetated areas (Page, Stenzel, and Kjelmyr 1999; Stenzel et al. 2002), so the colonization of naturally unvegetated mudflats by invasive *Spartina* is a de facto loss of foraging habitat (fig. 2.2). Also, our data show that the biomass of invertebrates is greater in tidal flat areas at higher tidal elevations (Christiansen et al., forthcoming). Therefore, as the *Spartina* invasion expands to occupy a greater portion of these higher-elevation areas, shorebirds will be increasingly forced to forage at lower tidal elevations, which are not only exposed for shorter periods of time, but also contain lower densities of invertebrate prey.

The consequences of *Spartina* invasion for shorebirds apply to WB as well. Although SFB is a more important area for wintering shorebirds, WB and adjacent Gray's Harbor represent important winter grounds in that region for shorebirds (Page et al. 1999). Nonetheless, the same overall consequences of habitat loss apply, although we do not have similar data on the abundances of benthic invertebrates at different tidal elevations. The *Spartina* influence in WB is also complicated by the extensive invasion of lower tidal elevations by the Japanese eelgrass *Z. japonica*, which during the summer months covers virtually the entire tidal range from the lower border of *Spartina* to the upper border of the native *Zostera marina*.

In contrast to shorebirds that forage on tidal flats at low tide, estuarine fish forage in these same areas at high tide. Fish such as Chinook salmon, California halibut, rainwater killifish, striped bass, and Tule perch could potentially experience the same habitat losses and density effects in SFB and WB as the shorebirds.

PREDICTING IMPACTS OF INVASION

We can identify three distinct invasion scenarios where *Spartina* effects appear to differ. The first is the invasion of unvegetated, higher-energy sand flats, which results in the largest changes in flow rates, sediment accumulation, elevation increase, and litter buildup, as well as the largest changes in plant and animal communities. This type of invasion has occurred in portions of both SFB and WB. A second type involves invasion of existing vegetation in high marsh habitats, which results in less alteration

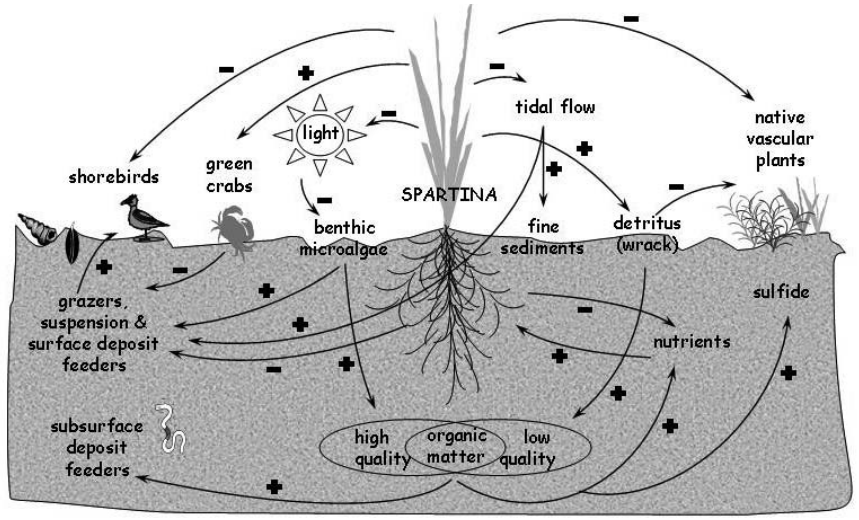

FIGURE 2.3 Conceptual model of changes following *Spartina* invasion. The many changes brought about by the *Spartina* invasion are illustrated in this diagram showing positive (+) and negative (−) effects on a range of physical, chemical, and biological processes. *Spartina* reduces light and tidal water flow and increases deposition of fine sediments and sediment organic matter. The increased belowground biomass together with changes in the sediments results in increased levels of sulfide and decreased ammonium levels, which can negatively affect other plants and animals. These changes result in increasing detrital loads and decreasing productivity of benthic microalgae, which favor subsurface deposit feeders and detritivores at the expense of grazers, suspension feeders, and surface deposit feeders. The shift toward smaller, subsurface species may reduce invertebrate food resources for larger consumers such as crabs, birds, and fishes.

of benthos and in some cases leads to enhanced diversity of associated fauna (which are often invasives as well) (Neira et al. 2005). Under these circumstances, displacement of native plants may occur through light/space or nutrient competition (Tyler et al. 2007). A third mode of invasion involves hybridization with native *Spartina*, threatening the integrity of native *Spartina* species (Ayers et al. 2003) and altering the above- and belowground habitat structure. Understanding that *Spartina* invasions can yield different consequences under different circumstances can help identify the most urgent conservation needs (Thompson 1991; Hacker et al. 2001; Hacker and Dethier 2006).

The changes caused by *Spartina* invasion can be viewed within the broader context of ubiquitous plant effects on wetland benthos. Plants have been recognized as ecosystem engineers (or foundation species) with major influence on the structure of marine communities, independent of invasion status (Levin and Talley 2002; Crooks 2002). The generalized influences of introduced plants on the benthos can be partitioned into two major pathways. We identify the details of these pathways and the targets in figure 2.3 and illustrate these points using the changes produced by *Spartina*.

The first pathway involves the indirect effects of plants on benthic organisms mediated through several changes in abiotic processes. First, *reduced flow* due to increased aboveground biomass generally reduces system energy; increases sediment stability, sedimentation rates, and organic matter accumulation; and reduces fluxes of reproductive propagules and food particles for consumers. Second, *reduced light*, also due to increased aboveground biomass, results in reduced evaporation and lower levels of sediment porewater salinity, sediment temperature, and higher water content. Third, *plant belowground structures* influence soil geochemical conditions (via root transport of oxygen, litter buildup and degradation), exploit space, and mechanically anchor sediments.

The second pathway involves direct effects on benthic invertebrates mediated by the structural habitat they provide. Introduced plants can provide substrate for sessile epibionts, both plant and animal, simply by their presence in benthic habitats such as mudflats with limited emergent structure. Plants can also provide refugia for mobile predator and prey species, both infaunal and epifaunal, as well as provide living plant tissue for herbivores or litter for detritivores (Levin et al. 2006; Neira et al. 2006).

COMPARISONS WITHIN THE PACIFIC REGION

To understand the overall effects of *Spartina* on benthic communities, we first compare our results with recent work on the benthic impacts of native *S. foliosa*. Studies comparing invertebrate communities in native versus invasive *Spartina* meadows in SFB showed that the native *Spartina* positively affects invertebrate abundance and, to a lesser extent, diversity in comparison to the largely negative effects of the hybrid (Brusati and Grosholz 2006). Invertebrate densities were up to five times greater in *S. foliosa* at some sites, although the magnitude of the effect was variable. This is largely the result of positive effects of aboveground structure but much lower belowground biomass. The density of roots and rhizomes apparently was not sufficient to reduce infaunal abundance as the hybrid does (see table 2.1). Recent removal and shading experiments conducted in southern California (Whitcraft and Levin 2007) suggest *S. foliosa* controls macrobenthic abundance and composition through light effects, which moderate soil temperature and salinity, enhance water retention, and promote microalgal growth.

This positive effect of *S. foliosa* on benthic fauna parallels what we see in the initial stages of the hybrid *Spartina* invasion along the growing edge. Within the first few meters of a hybrid clone, plant densities and belowground biomass are similar to *S. foliosa* areas resulting in the same facilitation of species abundance. This "edge effect" is similar to the increases in benthic abundance documented at the edges of seagrass meadows relative to the center (Bologna and Heck 2002). However, within five to ten years, the increasingly large above- and belowground biomass of the hybrid starts to reduce the benthic diversity and abundance through habitat changes at the surface and preemption of habitat space belowground.

Our results from SFB and WB showing strong effects of *Spartina* invasion on benthic animal communities are broadly consistent with other studies of *Spartina* in the western United States. Other studies in WB have shown reduced infaunal diversity and abundance in the middle of *Spartina* meadows (Zipperer 1996; Dumbauld et al. 1994; O'Connell 2002) and negative effects on bivalve growth (Ratchford 1995). Interestingly, other WB studies have also documented an "edge effect" with increased diversity and abundance of some taxa in the growing edge of the *Spartina* marsh. Dumbauld et al. (1994) found increased abundances of introduced clams (*Mya*) within *Spartina* meadows in WB. Zipperer (1996), also working in the same area, found increased abundances of infaunal invertebrates in the newly growing *Spartina* border. The facilitative effects of *S. alterniflora* in WB are again similar to what we find for both *S. foliosa* and for the growing edge of the hybrid *Spartina* invasion in SFB.

Our results showing dramatic shifts in the trophic mode of infaunal invertebrates following *Spartina* invasion are also in agreement with results from other studies in the U.S. West Coast region. In WB, Cordell et al. (1998) found a shift from surface-feeding bivalves and amphipods to deposit feeders and insect predators within the *Spartina* meadows. Also in WB, trophic shifts were documented by O'Connell (2002), who found increases in belowground detritivores in *S. alterniflora* marshes, consistent with our findings. Also, both Zipperer (1996) and Dumbauld et al. (1994) found reduced densities of bivalves and other surface feeders within *Spartina* clones and increasing numbers of larval insects in areas with higher tidal elevation as the community moved toward a more terrestrial assemblage.

Finally, many of the changes we have measured in the sediment ecosystem have also been documented following the invasion of *Spartina anglica* in Australia, England, and the Puget Sound region of Washington State. In Australia, Hedge and Kriwoken (2000) found that both the diversity and abundance of invertebrates were not significantly different between *S. anglica*–invaded areas and naturally vegetated marsh, but there was reduced diversity and abundance of invertebrates on nearby mudflats. In England, *S. anglica* has lowered densities of bivalves and *Corophium* and enhanced densities of tubificid oligochaetes relative to mudflat settings (Jackson 1985), with an overall effect of reduced species richness (Frid and James 1989). Studies of *S. anglica* invasion in Washington by Reeder and Hacker (2004) and Hacker and Dethier (2006) at sites with varying substrate and salinity found above- and belowground biomass varied substantially with habitat type, as did sediment accretion rates, sediment water content, salinity, and redox potential. In their mudflat and high-salinity marshes (most similar to our studies), sediment salinity was lower and water content was higher in the presence of invasive *S. anglica*. However, they found a predictable increased in redox potential in areas invaded by *S. anglica*, in contrast to our data showing lower redox in areas with hybrid *Spartina*. This difference is expected based on studies by Maricle and Lee (2001), who showed that *S. anglica* transports oxygen to their roots much more effectively than *S. alterniflora*.

COMPARISONS WITH OTHER REGIONS

Studies from the native range of *S. alterniflora* have also shown that *Spartina* strongly influences the diversity and abundance of benthic species. Several studies from the Atlantic and Gulf coasts of the United States have generally shown a positive effect of *S. alterniflora* on the abundance of invertebrates relative to unvegetated sediments (Rader 1984; LaSalle, Landin, and Simms 1991; West and Williams 1986). Similar results have been shown in studies of native *Spartina alterniflora* effects on infauna marshes in Brazil (Lana and Guiss 1991; Netto and Lana 1991).

Shifts in trophic modes have also been measured in studies from the native range of *S. alterniflora*. Declines in the abundance of surface-feeding bivalves has been demonstrated in the native range of *Spartina alterniflora* in the eastern United States (Capehart and Hackney 1989), as have changes in trophic modes of infauna with successional stage of *Spartina* areas (Kneib 1984). Declines in suspension feeders in *Spartina* areas in comparison with open mudflats have also been documented in the native South American range of *S. alterniflora* (Lana and Guiss 1991).

Finally, other studies have also shown impacts at higher trophic levels involving vertebrate consumers. In perhaps the best-documented study of impacts of invasive *Spartina* on shorebirds, Goss-Custard and Moser (1988) showed significant declines in the numbers of Dunlin (*Calidris alpina*) in estuaries in the United Kingdom that had been invaded by *S. anglica*.

Overall, the conclusions from studies of *Spartina* in its native range suggest that it generally has a positive effect on the diversity and abundance of native benthos. This provides an interesting contrast with the largely negative effects of *Spartina* in the introduced range. One theory for opposing effects of *Spartina* on the two coasts is that predation pressure is considered much greater in Atlantic coastal systems (e.g., due to the presence of blue crabs, horseshoe crabs); thus, *Spartina* stands are more likely to function as refugia on the Atlantic coast. The much higher animals densities on Pacific than Atlantic mudflats supports this hypothesis (Levin, Talley, and Hewitt 1998). These findings are broadly consistent with our finding that *Spartina* tends to facilitate many species that have evolved within its native range and thrive in the microenvironment produced by this plant, but it negatively affects many species that have evolved in systems devoid of large vascular plants like *Spartina* and that generally do not tolerate the changed conditions.

PROSPECTS FOR ERADICATION AND RECOVERY

Extensive *Spartina* eradication programs are currently being carried out in SFB and WB (fig. 2.4). In both bays, the primary means of eradication is aerial and boat-based spraying of the commonly used herbicide Imazypyr (known as "Arsenal"). The expectation is that complete eradication is a reality with sufficient effort invested over a long enough period of time. The goal in each case is restoration to the preinvasion condition. It is clear that some of the changes can be rapidly reversed. By removing the aboveground portion of the plant with herbicide, eradication efforts will be able to locally reverse the immediate physical modification of flow, light, and sedimentation. Our data suggest the aboveground contribution to added detrital buildup following eradication will be relatively short-lived. In areas that were previously vegetated by native plants, there is the expectation that native species will recolonize successfully, although additional efforts may be needed to jump-start this process in some areas. The short-lived seed bank of the invasive *Spartina* provides hope that once eradication from large areas has occurred, it will be maintained notwithstanding dispersal from other areas. However, this will take vigilance in removing *Spartina* seedlings.

Our work in areas that have undergone trial eradication or natural dieback suggests that there are more lasting effects of the roots and rhizomes that may require several years to decompose (Neira et al. 2007; A. C. Tyler and E. D. Grosholz, unpublished data). The rate of breakdown appears to be dependent on rates of flushing, sediment grain size, and other local habitat variables. The decay of belowground biomass and the sulfide and anoxia that result can slow the return of sediment conditions that would permit reestablishment of native plants and animals. Also, the increased tidal elevation created by enhanced accretion in invasive *Spartina* stands may not be quickly reversed. Because the increased elevation reduces tidal inundation, the mat of roots and rhizomes may continue to maintain the increased tidal elevation and substantially delay recovery. In some areas, if native plants colonize prior to the return of sediment to its preinvasion elevation, there may be a permanent shift from intertidal mudflat to vegetated tidal marsh, as has been documented following eradication of *S. anglica* in Puget Sound, Washington (Reeder and Hacker 2004; Hacker and Dethier 2006).

FIGURE 2.4 Ongoing eradication of *Spartina alterniflora* at a higher tidal elevation site in Willapa Bay, Washington.

However, there is room for optimism based on our monitoring of sites in WB that had been treated with herbicide seven years earlier. Our data indicate that recovery of sediment characteristics and porewater chemistry as well as invertebrate community indices can be achieved within six years and possibly faster (E. D. Grosholz and A. C. Tyler, unpublished data). However, these treated areas were small, isolated clones in relatively sandy sediments. In large continuous meadows or in muddier sediments, we predict that the recovery rate for native plants will be similar to that following *S. anglica* eradication (Reeder and Hacker 2004).

OVERALL CONCLUSIONS

Introductions of nonnative species are clearly among the most pervasive anthropogenic changes in salt marsh systems and threaten to alter their structure and function on a broad scale. Our work has documented that *Spartina* invasions in two major estuaries in western North America are rapidly changing a wide range of physical, chemical, and biological processes. First, there are immediate changes to rates of light penetration, water flow, and sedimentation that then more gradually influence sediment physicochemistry as well as recruitment, growth, and survival of benthic organisms. The *Spartina* invasion has shifted the dominant primary producers from short-stature native plants and benthic microalgae to tall, dense plants that create approximately two kilograms per square meter of refractory aboveground detritus annually. This change results in a less "available" food source and slows down carbon and nutrient recycling. These changes in turn result in dramatic shifts in benthic communities and food web structure.

In San Francisco Bay, our studies support the idea that this changing resource base appears to have contributed to a shift in benthic communities from surface feeders to subsurface feeders. The shifts in benthic communities may also have consequences for higher trophic levels (fig. 2.5). Within the *Spartina* meadow, the reduced densities of larger, surface-feeding invertebrates and increase in smaller infaunal detritivores may reduce the food base available to birds, fishes, and crabs. The presence of the invasive grass itself may also negatively affect wintering shorebirds by reducing the quality and availability of foraging areas on open tidal flats.

FIGURE 2.5 Federally endangered California clapper rails (*Rallus longirostris obsoletus*) are impacted by the hybrid *Spartina* invasion in San Francisco Bay.

Reversing the changes brought about by the *Spartina* invasion will require extensive management resources over a significant period of time. But our results provide reason for optimism regarding the success of recovery following eradication efforts. While complete eradication of *Spartina* in these systems may require several years of follow-up efforts, the elimination of most of the aboveground biomass and the decay of belowground biomass appear to begin within just a few years of the initial treatment. Our limited evidence suggests that these systems can return to something similar to the preinvasion state within approximately five years and possibly sooner. However, we have now documented that these changes are habitat-specific and that many factors such as tidal exchange, sediment grain size, elevation, and other variables will strongly affect the rate at which the system can recover (Reeder and Hacker 2004).

Finally, our work provides examples of the many different kinds of effects that plants can have in estuarine systems. By altering hydrodynamics, sediment geochemistry, productivity, and sedimentation regimes—through food web modification and via substrate provision, stabilization, and refuge—invasive cordgrasses are certainly among the foremost agents of landscape-scale change in the coastal zone.

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REFERENCES

Ayres, D. R., D. L. Smith, K. Zaremba, S. Klohr, and D. R. Strong. 2004. Spread of exotic cordgrasses and hybrids (*Spartina* sp.) in the tidal marshes of San Francisco Bay. *Biological Invasions* 6: 221–231.

Ayres, D. R., D. R. Strong, and P. Baye. 2003. *Spartina foliosa* (Poaceae): A common species on the road to rarity. *Madroño* 50: 209–213.

Ayres, D. R., K. Zaremba, and D. R. Strong. 2004. Extinction of a common native species by hybridization with an invasive congener. *Weed Technology* 18: 1288–1291.

Bologna, P. A. X., and K. L. Heck. 2002. Impact of habitat edges on density and secondary production of seagrass-associated fauna. *Estuaries* 25: 1033–1044.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18: 119–125.

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

———. 2007. Effect of native and invasive cordgrass on *Macoma petalum* density, growth, and isotopic signatures. *Estuarine, Coastal and Shelf Science* 71: 517–522.

California Coastal Conservancy. 2006. San Francisco estuary invasive *Spartina* project. Project Web site: http://www.spartina.org/about.htm.

Capehart, A. A., and C. T. Hackney. 1989. The potential role of roots and rhizomes in structuring saltmarsh benthic communities. *Estuaries* 12: 119–122.

Chapin, F. S., III, E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. *Nature* 405: 234–242.

Christiansen, N. C., E. D. Grosholz, and P. Rosso. Forthcoming. Quantifying the potential impact of the *Spartina* invasion on invertebrate food resources for foraging shorebirds in San Francisco Bay. *In Proceedings of the Third Annual Invasive* Spartina *Conference*. Cambridge: Cambridge University Press.

Civille J. C., K. Sayce, S. D. Smith, and D. R. Strong. 2005. Reconstructing a century of *Spartina alterniflora* invasion with historical records and contemporary remote sensing. *Ecoscience* 12: 330–338.

Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279: 555–558.

Cordell, J. R., C. A. Simenstad, B. Feist, K. L. Fresh, R. M. Thom, D. J. Stouder, and V. Luiting. 1998. Ecological effects of *Spartina alterniflora* invasion of the littoral flat community in Willapa Bay, Washington. *Abstracts from the Eighth International Zebra Mussel and Other Nuisance Species Conference, Sacramento, California, March 16–19*, http://www.sgnis.org/publicat/7307.htm.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. *Oikos* 97: 153–166.

Daehler, C. C., and D. R. Strong. 1997. Hybridization between introduced smooth cordgrass (*Spartina alterniflora*; Poaceae) and native California cordgrass (*S. foliosa*) in San Francisco Bay, California, USA. *American Journal of Botany* 84: 607–611.

Davis, H. G., C. M. Taylor, J. C. Civille, and D. R. Strong. 2004. An Allee effect at the front of a plant invasion: *Spartina* in a Pacific estuary. *Journal of Ecology* 92: 321–327.

Deegan, L. A., and R. H. Garritt. 1997. Evidence for spatial variability in estuarine food webs. *Marine Ecology Progress Series* 147: 31–47.

Dethier, M. N., and S. D. Hacker. 2005. Physical factors vs. biotic resistance in controlling the invasion of an estuarine marsh grass. *Ecological Applications* 15: 1273–1283.

Dumbauld, B. R., M. Peoples, L. Holcomb, J. Tagart, and S. Ratchford. 1994. The potential influence of cordgrass *Spartina alterniflora* on clam resources in Willapa Bay, Washington. *Journal of Shellfish Research* 14: 228.

Feist, B. E., and C. A. Simenstad. 2000. Expansion rates and recruitment frequency of exotic smooth cordgrass, *Spartina alterniflora* (Loisel), colonizing unvegetated littoral flats in Willapa Bay, Washington. *Estuaries* 23: 267–274.

Frid, C., and R. James. 1989. The marine invertebrate fauna of a British coastal salt marsh. *Holarctic Ecology* 12: 9–15.

Goss-Custard, J. D., and M. E. Moser. 1988. Rates of change in the numbers of dunlin, *Calidris alpina*, wintering in British estuaries in relation to the spread of *Spartina anglica*. *Journal of Applied Ecology* 25: 95–109.

Hacker, S. D., and Dethier, M. N. 2006. Community modification by a grass invader has differing impacts for marine habitats. *Oikos* 113: 279–286.

Hacker, S. D., D. Heimer, C. E. Hellquist, T. G. Reeder, B. Reeves, T. J. Riordan, and M. N. Dethier. 2001. A marine plant (*Spartina anglica*) invades widely varying habitats: Potential mechanisms of invasion and control. *Biological Invasions* 3: 211–217.

Hedge, P., and L. K. Kriwoken. 2000. Evidence for effects of *Spartina anglica* invasion on benthic macrofauna in Little Swanport estuary, Tasmania. *Austral Ecology* 25: 150–159.

Jackson, D. 1985. Invertebrate populations associated with *Spartina anglica* salt-marsh and adjacent intertidal mud flats. *Estuary and Brackishwater Science Association Bulletin* 40: 8–14.

Kneib, R. T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: Causes and questions. *Estuaries* 7: 392–412.

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

Lambrinos, J. L., D. R. Strong, J. C. Civille and J. Bando (in press). Implications of variable recruitment for the management of *Spartina alterniflora* in Willapa Bay, WA. In: Ayres, D. R., D. W. Kerr, S. D. Ericson and P. R. Olofson, eds. Proceedings of the Third International Conference on Invasive *Spartina* (San Francisco, CA), San Francisco Estuary Invasive *Spartina* Project of the State Coastal Conservancy (California), Cambridge Publications Limited, Cambridge, UK.

Lana, P. D., and C. Guiss. 1991. Influence of *Spartina alterniflora* on structure and temporal variability of macrobenthic associations in a tidal flat of Paranagua Bay (southeastern Brazil). *Marine Ecology Progress Series* 73: 231–244.

LaSalle, M. W., M. C. Landin, and J. G. Simms. 1991. Evaluation of the flora and fauna of a *Spartina alterniflora* marsh established on dredged material in Winyah Bay, South Carolina. *Wetlands* 11: 191–208.

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

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

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

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710.

Maricle, B. R., and R. W. Lee. 2002. Aerenchyma development and oxygen transport in the estuarine cordgrasses *Spartina alterniflora* and *S. anglica*. *Aquatic Botany* 74: 109–120.

Mooney, H. A., and R. J. Hobbs. 2000. *Invasive species in a changing world*. Washington, DC: Island.

Moseman, S., L. Levin, C. Currin, and C. Forder. 2004. Infaunal colonization, succession and nutrition in a newly restored wetland at Tijuana Estuary, California. *Estuarine, Coastal and Shelf Science* 60: 755–770.

Neira, C., E. D. Grosholz and L. A. Levin (in press). Mechanistic processes driving shifts in benthic infaunal communities following *Spartina* hybrid tidal flat invasion. In: Ayres, D. R., D. W. Kerr, S. D. Ericson and P. R. Olofson, eds. Proceedings of the Third International Conference on Invasive *Spartina* (San Francisco, CA), San Francisco Estuary Invasive *Spartina* Project of the State Coastal Conservancy (California), Cambridge Publications Limited, Cambridge, UK.

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

Neira, C., L. Levin, and E. D. Grosholz. 2005. Benthic macrofaunal communities of three sites in San

Francisco Bay invaded by hybrid *Spartina*, with comparison to uninvaded habitats. *Marine Ecology Progress Series* 292: 111–126.

Neira, C., L. A. Levin, E. D. Grosholz, and G. Mendoza. 2007. The influence of invasive *Spartina* growth phases on associated macrofaunal communities. *Biological Invasions* 9: 975–993.

Netto, S. A., and P. C. Lana. 1999. The role of above- and below-ground components of *Spartina alterniflora* (Loisel) and detritus biomass in structuring macrobenthic associations of Paranaguá Bay (SE Brazil). *Hydrobiologia* 400: 167–177.

O'Connell, K. A. 2002. Effects of invasive Atlantic smooth-cordgrass (*Spartina alterniflora*) on infaunal macroinvertebrate communities in southern Willapa Bay, WA. Unpublished MS thesis, Western Washington University, Bellingham.

Page, H. M. 1995. Variation in the natural abundance of 15N in the halophyte, *Salicornia virginica*, associated with groundwater subsidies of nitrogen in a southern California salt-marsh. *Oecologia* 104: 181–188.

———. 1997. Importance of vascular plant and algal production to macro-invertebrate consumers in a southern California salt marsh. *Estuarine, Coastal and Shelf Science* 45: 823–834.

Page, G. W., L. E. Stenzel, and J. E. Kjelmyr. 1999. Overview of shorebird abundance and distribution in wetlands of the Pacific Coast of the contiguous United States. *Condor* 101:461–471.

Rader, D. N. 1984. Salt-marsh benthic invertebrates: Small-scale patterns of distribution and abundance. *Estuaries* 7: 413–420.

Ratchford, S. G. 1995. Changes in the density and size of newly-settled clams in Willapa Bay, WA, due to the invasion of smooth cordgrass, *Spartina alterniflora* Loisel. Unpublished MS thesis, University of Washington, Seattle.

Reeder, T. G., and S. D. Hacker. 2004. Factors contributing to the removal of a marine grass invader (*Spartina anglica*) and subsequent potential for habitat restoration *Estuaries* 27: 244–252.

Ruesink, J. L., B. E. Feist, C. J. Harvey, J. S. Hong, A. C. Trimble, and L. M. Wisehart. 2006. Changes in productivity associated with four introduced species: ecosystem transformation of a "pristine" estuary. *Marine Ecology Progress Series* 311: 203–215.

Stenzel, L. E., C. M. Hickey, J. E. Kjelmyr, and G. W. Page. 2002. Abundance and distribution of shorebirds in the San Francisco Bay area. *Western Birds* 33: 69–98.

Thompson, J. D. 1991. The biology of an invasive plant: What makes *Spartina anglica* so successful? *BioScience* 41: 393–401.

Tyler, A. C., and E. D. Grosholz. Forthcoming. *Spartina* invasion changes intertidal ecosystem metabolism in San Francisco Bay. *In Proceedings of the Third Annual Invasive* Spartina *Conference*. Cambridge: Cambridge University Press.

Tyler, A. C., J. G. Lambrinos, and E. D. Grosholz. 2007. Nitrogen inputs promote the spread of an invasive marsh grass. *Ecological Applications* 17: 1886–1898.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277: 494–499.

West, D. L., and A. H. Williams. 1986. Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. *Journal of Experimental Marine Biology and Ecology* 100: 75–95.

Whitcraft, C. R., and L. A. Levin. 2007. Regulation of benthic algal and animal communities by salt marsh plants: Impact of shading. *Ecology* 88: 904–917.

Windham L., and L. A. Meyerson. 2003. Effects of common reed (*Phragmites australis*) expansions on nitrogen dynamics of tidal marshes of the northeastern US. *Estuaries* 26: 452–464.

Yamada, S. Y. 2001. Global invader: The European green crab. Unpublished manuscript, Oregon Sea Grant, Oregon State University.

Zedler, J. B. 1980. Algal mat productivity: Comparisons in a salt marsh. *Estuaries* 3: 122–131.

———. 1984. *The Ecology of Southern California Coastal Salt Marshes: A Community Profile*. Washington, DC: U.S. Fish and Wildlife Service.

Zedler J. B., and S. Kercher. 2004. Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences* 23: 431–452.

Zipperer, V. T. 1996. Ecological effects of the introduced cordgrass *Spartina alterniflora* on benthic community structure in Willapa Bay, Washington. Unpublished MS thesis, University of Washington, Seattle.