# Impacts of the invasive grass *Spartina anglica* on benthic macrofaunal assemblages in a temperate Australian saltmarsh

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ABSTRACT: Reported impacts of the invasive saltmarsh grass *Spartina anglica* on benthic macrofaunal assemblages around the world vary considerably, and there is little understanding of the reasons for this variation. We compared macrofaunal assemblages and sediment characteristics among patches of *S. anglica* and adjacent uninvaded habitats (bare mudflat and native saltmarsh) in southeastern Australia. Invaded patches showed reduced species richness (by 50%) and diversity compared to both uninvaded habitats. Macrofaunal abundance in *S. anglica* patches was also lower than in native marsh (by 60%), but not different from mudflat. There were no differences in biomass among habitats. Ordination clearly separated the species assemblage of invaded patches from uninvaded habitats, suggesting a unique community in the *Spartina* habitat. Molluscs and crustaceans were the most depleted in *S. anglica* patches, while the polychaete *Nephtys australiensis* was enhanced. Infauna and epifauna were both depleted in *S. anglica*, although the mechanisms for these impacts should differ. Burrowing by infauna in *S. anglica* patches was likely impeded by dense roots and rhizomes, because the below-ground plant biomass was 72% greater than in native saltmarsh. Epifauna were likely depleted in *S. anglica* patches due to shading-induced inhibition of microphytobenthos growth, consistent with measured reductions of porewater salinity and increased mud content. Salinity and mud content were the sediment parameters that correlated most strongly with macrofaunal assemblage composition. These results, combined with a synthesis of published *S. anglica* impacts, suggest predictions of when *S. anglica* facilitates or inhibits macrofauna, considering infauna and epifauna separately.

KEY WORDS: *Spartina anglica* · Invasive species · Cordgrass · Macrofauna · Saltmarsh · Estuary · Australia

## INTRODUCTION

Saltmarshes are recognized globally as ecosystems of significant ecological value that are under increasing threat (Adam 2002). Their importance extends beyond their boundaries, as plant material can be flushed into neighbouring waters, providing input for marine food webs, including those that contribute to aquaculture. Human impact has destroyed >65% of these habitats over the last 300 yr, thereby reducing nursery habitats and sinks for nutrients and sediment (Lotze et al. 2006). Invasive species are recognized as the single greatest threat to the biodiversity of saltmarshes and other coastal habitats around the world (Rönnbäck et al. 2007). The introduction of exotic species (deliberately or unintentionally), along with the increase of human disturbance to ecosystems, has facilitated a significant increase in biological invasions (Hobbs 2000).

*Spartina* species are temperate, intertidal saltmarsh grasses that are present as natives and non-natives in Europe, North America, Asia, and Aus-

tralasia (Ranwell 1964, Chung 1983, Groenendijk 1986, Kriwoken & Hedge 2000). They can invade unvegetated sediment flats as well as saltmarshes, seagrass beds, mangroves, and cobble beds (Bridgewater 1975, Dethier & Hacker 2005). By forming expansive monospecific swards with dense roots and rhizomes, invasive *Spartina* spp. are potent ecosystem engineers that severely impact native systems, e.g. by enhancing sediment accretion and stabilizing sediment against erosion (Blood 1995, Mudd et al. 2010), altering water flow (Bouma et al. 2005), and changing sediment characteristics such as grain size distribution (Whitlatch 1981, Edgar & Shaw 1993), pH and salinity (Chung 1990), water content (Cottet et al. 2007), oxygen levels (da Cunha Lana & Guiss 1991), organic matter (Peralta et al. 2008), and the biomass of subsurface root and rhizome material (Brusati & Grosholz 2006, Neves et al. 2010).

These habitat-engineering effects can lead to changes in faunal communities such as displacement of species, colonization by new species, and associated changes in species richness and diversity (Neira et al. 2005, 2007, Zhou et al. 2009, Wang et al. 2010). Alteration of intertidal habitat and negative impacts on sediment invertebrate assemblages are of particular concern because these features of estuarine and saltmarsh ecosystems provide shelter and food for foraging birds, fishes, and economically important invertebrates (Bertness 1984, Simpson 1996, Hobbs 2000). There is some indication that *Spartina* invasion can alter trophic interactions; e.g. Levin et al. (2006) identified a trophic shift favoring polychaetes and oligochaetes (which consume *Spartina* detritus) over bivalves and amphipods that rely on microphytobenthos. Such a shift could cause loss of support for higher trophic levels such as fishes and migratory birds that feed on bivalves and amphipods (Levin et al. 2006).

Understanding and predicting the ecological impacts of *Spartina* spp. has been problematical because of contrasting findings within and between species that have been studied at various locations, especially regarding impacts on sediment macrofauna. Impacts of *Spartina* colonization have ranged from reduced macrofaunal density and species richness to enhanced density, richness, and biomass, or no impact compared to unvegetated sediment or areas of native vegetation (e.g. da Cunha Lana & Guiss 1991, Neira et al. 2005, Chen et al. 2009, Wang et al. 2010). Neira et al. (2005) reviewed published impacts, emphasizing studies on *S. alterniflora*, *S. foliosa*, and the hybrid *S. foliosa* × *S. alterniflora*. They came to the generalization that where it is

native and has grown to a mature state, colonized areas of *Spartina* spp. (especially *S. alterniflora*) enhance macrofaunal populations compared to unvegetated sediment, whereas in areas where it is non-native it depletes the macrofauna — although there are exceptions (Neira et al. 2005, Wang et al. 2010).

Mechanisms underlying variable impacts are not well understood, but they appear related to factors such as the species of *Spartina*, age and extent of invasion, susceptibility of the habitat being overrun, extent and structure of above-ground and below-ground plant biomass, and hydrodynamic regime (Neira et al. 2005, 2006, 2007, Brusati & Grosholz 2006, Hacker & Dethier 2006). A number of mechanisms by which saltmarsh vegetation and habitat factors influence invertebrates have been studied (e.g. plant structure, food resources from plants, elevation, grain size, salinity, oxygen, and organic matter; reviewed by Levin & Talley 2000), yet a clear predictive understanding of the conditions under which *Spartina* spp. produce the various documented impacts on macrofauna has not emerged.

*Spartina anglica* is the most widespread invasive *Spartina* species, occurring in mainland Europe, the UK, North America, China, New Zealand, and Australia (Lee & Partridge 1983, Jackson et al. 1985, Chung 1990, Kriwoken & Hedge 2000, Lowe et al. 2000, Nehring & Hesse 2008). It is of recent origin, arising in England by chromosome doubling from the sterile hybrid *S. maritima* × *alterniflora* (Thompson 1991). It is a strong competitor, with exceptional growth rates and tolerance to a wide range of temperature, salinity, and inundation conditions (Thompson 1991, Nehring & Hesse 2008). For these reasons it should not be assumed to have the same impacts as other *Spartina* species.

Despite great concern over *Spartina anglica* as an invasive species, its impacts on macrofauna have been studied less than those of other *Spartina* species, and the limited studies have shown variable effects. Compared to unvegetated sediment, areas colonized by *S. anglica* showed reduced macrofaunal abundance and/or diversity in the UK (Jackson 1985, Frid & James 1989) and the Danish Wadden Sea (Tang & Kristensen 2010), but increased abundance and species richness in Australia (Hedge & Kriwoken 2000). Other studies found variable or little impact in the UK (Millard & Evans 1984, Jackson et al. 1985), on the Atlantic coast of France (Cottet et al. 2007), and in the Netherlands (Bouma et al. 2009). Not all of these studies, however, compared habitats sampled simultaneously; some compared the macrofauna in *S. anglica* infestations to historical data from unin-

vaded sites (Jackson et al. 1985, Frid & James 1989), therefore not controlling for any shifts of the communities over time. Even fewer studies have made comparisons to areas of native vegetation (saltmarsh plants or seagrasses), and again the differences in macrofaunal populations were variable (Cottet et al. 2007, Bouma et al. 2009) or insignificant (Hedge & Kriwoken 2000). Because of its origin, *S. anglica* is exotic everywhere it colonizes and therefore it does not fit Neira et al.'s (2005) generalization that non-native *Spartina* spp. typically have negative impacts on macrofauna. Factors determining whether *S. anglica*'s impacts on macrofauna are positive, negative, or neutral are unknown.

*Spartina anglica* was introduced deliberately to Australia in the late 1920s (Boston 1981). It covers an estimated 600 and 300 ha in the states of Victoria and Tasmania, respectively (Wells 1995, Weiss & Iaconis 2002). There is concern that rising sea levels associated with climate change may accelerate the spread of *S. anglica* inland, possibly faster than native marsh will shift (Saintilan 2009). Extensive control programs are in place in both states where *S. anglica* occurs, spraying infested habitats with herbicides. Despite these concerns, there are few data on the impacts of invasion on macrofaunal assemblages in Australia. The only previously published study was in Tasmania and found that macrofaunal populations in *S. anglica* patches were enhanced compared to mudflats, suggesting that invasion converts mudflat into the equivalent of native saltmarsh in terms of macrofaunal abundance and species richness (Hedge & Kriwoken 2000).

To better understand the impacts of *Spartina anglica* on macrofaunal invertebrates, we conducted simultaneous sampling of invaded patches and adjacent mudflat and native saltmarsh in Victoria, Australia. We measured a variety of habitat parameters in an attempt to identify mechanisms accounting for any effects on the macrofauna. Our results, together with a detailed review of previous papers on *S. anglica*, lead to hypotheses concerning factors that determine whether impacts of *S. anglica* on macrofauna are beneficial or detrimental.

## MATERIALS AND METHODS

### Sampling

Anderson Inlet, Victoria, is a creek-fed estuary in the southeast of Australia, 12.5 km long × 2.7 km wide, with an opening to the coast of 2.1 km width

(Fig. 1). It has an assortment of intertidal mudflat, sandflat, higher-intertidal native saltmarsh, lower-intertidal mangroves *Avicennia marina*, and areas invaded by *Spartina anglica*, the latter of which total 196 ha (Boon et al. 2011). We collected samples in the transition zone between unvegetated mudflat and native saltmarsh dominated by *Sarcocornia quinqueflora*. This area has been infested with *S. anglica* for the past 8 yr (Parks Victoria pers. comm.), occurring in patches from 1 to 2 m$^2$. The site is bordered by farms, a canal, and a levee and is therefore relatively inaccessible. The inlet is predominantly used for recreational fishing.

We sampled in 5 replicate blocks of approx. 400 m$^2$ that each contained areas of unvegetated mudflat, native saltmarsh (predominantly *Sarcocornia quinqueflora*), and discrete *Spartina anglica* patches in the upper-mid-intertidal. Each block was separated from the others by ≥100 m. In each block, we sampled from 3 uniform patches (1 each of mudflat, native marsh, and *S. anglica*) at the same elevation. Over a 1 wk period in late May to early June 2009 (austral autumn), we collected triplicate sediment cores (15 cm diameter × 10 cm deep) for macrofauna from haphazard locations (≥50 cm inside the patch boundary) in each patch of each block. Adjacent to each of these macrofaunal cores we collected 2 cores (3 cm diameter × 10 cm deep) for measuring sediment parameters.

Macrofauna were separated from cored sediment on a 500 µm mesh sieve, preserved in 10% buffered formalin, and transferred after 7 d to 70% ethanol. Specimens were identified to the lowest possible taxonomic level under a dissecting microscope. They were dried at 75°C for measuring dry weight, after which biomass was measured as the dried mass lost on combustion at 500°C for 4 h. From each set of
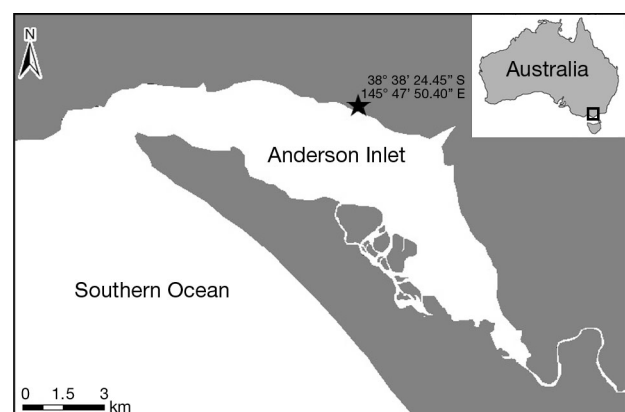


Fig. 1. Sampling site, Anderson Inlet, Australia

6 replicate cores per patch collected for sediment parameters, 4 were chosen randomly to measure moisture content by oven-drying at 90°C for 2 d. Three of these samples were then chosen randomly to measure organic matter content as dry mass lost on combustion at 500°C for 4 h. The fourth sample was rehydrated and wet-sieved to determine the particle-size distribution, measured as the percent mass in each size class after final drying. The remaining 2 cores from each set of 6 replicates were used to measure salinity and pH in porewater separated by centrifugation. For each type of measure (biotic and abiotic), data from replicate cores within each patch were pooled.

Additional data on below-ground plant biomass were collected at the same locations in the summer of 2011. Cores of 15 cm diameter × 10 cm deep were taken in patches of *Spartina anglica* and patches of native marsh. Below-ground plant material retained on a 500 μm mesh sieve was separated from animals and washed to remove sediment, then dried and weighed.

### Statistical analyses

Several assemblage indices were calculated to compare macrobenthic communities among the 3 habitats. These included species richness (number of species), abundance (number of individuals), and Shannon-Wiener species diversity ($H'$; Pielou 1966). The indices were calculated for total macrofauna as well as for major taxonomic groups (molluscs, annelids, and crustaceans).

Differences in assemblage indices and environmental variables among habitats were tested with a linear mixed-model ANOVA on Systat 13, with habitat as a fixed factor and sampling blocks as a random factor. Significant results ($\alpha = 0.05$) were followed by Tukey pairwise comparisons. Below-ground plant biomass, however, was tested with a paired *t*-test because these data were only collected for the 2 types of vegetated habitat. Before testing, all data were $\log(x + 1)$ transformed to improve normality and reduce heteroscedasticity.

Differences in $\log(x + 1)$-transformed species abundances and presence/absence were tested using non-parametric multidimensional scaling (MDS), based on Bray-Curtis dissimilarity matrices. Pairwise comparisons for differences in macrofaunal assemblages between habitats were made using the analysis of similarity (ANOSIM) test. Similarity percentage (SIMPER) analyses were used to determine the percent of dissimilarity between habitats.

BIOENV analyses were run on macrofaunal abundances and sediment data (both $\log(x + 1)$ transformed) to determine which sediment parameters best explained the distribution of the macrofaunal assemblages. Below-ground plant biomass was excluded from the analysis because it was not collected simultaneously with the other data. BIOENV analyses provided Spearman's ranked correlation coefficients for the sediment parameters, suggesting their level of influence on the macrofaunal assemblages. However, this analysis is strictly observational, and does not necessarily indicate a causal relationship. The MDS, ANOSIM, SIMPER, and BIOENV analyses were run in Primer 6.

### RESULTS

A total of 20 benthic macrofaunal species were identified from the 3 habitats (Table 1). Patches of native saltmarsh yielded the most species (17) and most individuals (414), consisting predominantly of the detritivorous snails *Tatea huonensis* and *Ophi-*

Table 1. Total numbers of macrofauna (individuals) according to habitat in all samples combined, and species richness (number of species, bottom row). E: epifaunal; I: infaunal

| | Native saltmarsh | *Spartina anglica* | Mud-flat |
|---|---|---|---|
| **Mollusca** | | | |
| *Salinator fragilis* (E) | 5 | 0 | 0 |
| *Salinator solida* (E) | 50 | 50 | 69 |
| *Eulima* sp. (E) | 7 | 0 | 0 |
| *Tatea huonensis* (E) | 120 | 28 | 28 |
| *Ophicardelus ornatus* (E) | 89 | 8 | 19 |
| *Ophicardelus quoyi* (E) | 63 | 24 | 4 |
| *Tellina deltoidalis* (I) | 6 | 0 | 5 |
| *Mysella donaciformis* (I) | 4 | 4 | 5 |
| *Assiminea buccinoides* (E) | 6 | 0 | 8 |
| **Crustacea** | | | |
| *Heloecius cordiformis* (I) | 13 | 0 | 56 |
| *Helograpsus haswellianus* (I) | 19 | 18 | 14 |
| *Parasesarma erythrodactyla* (I) | 6 | 0 | 6 |
| *Paragrapsus gaimardii* (E) | 5 | 0 | 3 |
| *Paragrapsus laevis* (E/I) | 0 | 12 | 0 |
| *Macrophthalmus latifrons* (I) | 5 | 0 | 22 |
| *Mictyris platycheles* (I) | 0 | 0 | 4 |
| *Allorchestes compressa* (E) | 8 | 2 | 21 |
| **Annelida** | | | |
| *Capitella capitata* (I) | 3 | 0 | 0 |
| *Nephtys australiensis* (I) | 5 | 22 | 3 |
| *Scoloplos cylindrifer* (I) | 0 | 0 | 4 |
| **Species richness** | 17 | 9 | 16 |

*cardelus ornatus*. Mudflat patches yielded slightly fewer species (16) and individuals (271), dominated by the detritivorous snail *Salinator solida* and the deposit-feeding semaphore crab *Heloecius cordiformis*. Patches of *Spartina anglica* yielded the fewest species (9) and the fewest individuals (168), dominated by *Salinator solida*.

Populations that were most depleted in the *Spartina anglica* patches were molluscs and crustaceans (the snails *Ophicardelus ornatus* and *Assiminea buccinoides*; the bivalve *Tellina deltoidalis*; the crabs *Heloecius cordiformis*, *Parasesarma erythrodactyla*, *Paragrapsus gaimardii*, and *Macrophthalmus latifrons*; and the amphipod *Allorchestes compressa*; Table 1). Eleven species that were found in at least one of the uninvaded habitats were absent in our samples from *S. anglica* patches. There was no evident difference between the effects on infaunal and epifaunal taxa. Reduced (or absent) populations in *S. anglica* compared to one or both uninvaded habitats occurred for 7 of the 10 infaunal species and 9 of the 10 epifaunal species (Table 1). The only species that were enhanced in invaded patches were the shore crab *Paragrapsus laevis* and the polychaete *Nephtys australiensis*.

Mean species richness of total macrofauna differed significantly among habitats (Fig. 2). Richness was ca. 50% lower in the *Spartina anglica* patches compared to the native saltmarsh and mudflat habitats, while there was no difference between native marsh and mudflat. In particular, *S. anglica* patches had significantly reduced richness of molluscs and crustaceans compared to native saltmarsh, and the crustaceans were also less rich than in the mudflat (Table 2).

Mean species diversity of total macrofauna showed the same pattern as species richness, being lowest in the *Spartina anglica* patches, while the native saltmarsh and mudflat did not differ from each other (Fig. 2). *S. anglica* patches had lower diversity of molluscs and crustaceans com-

pared to native saltmarsh, and the crustaceans were also less diverse than in the mudflat (Table 2).

Mean abundance of total macrofauna differed significantly among habitats (Fig. 2). Abundance in *Spartina anglica* patches was 40% of that in native saltmarsh, but it did not differ from mudflat. Molluscs were less abundant in *S. anglica* than in native
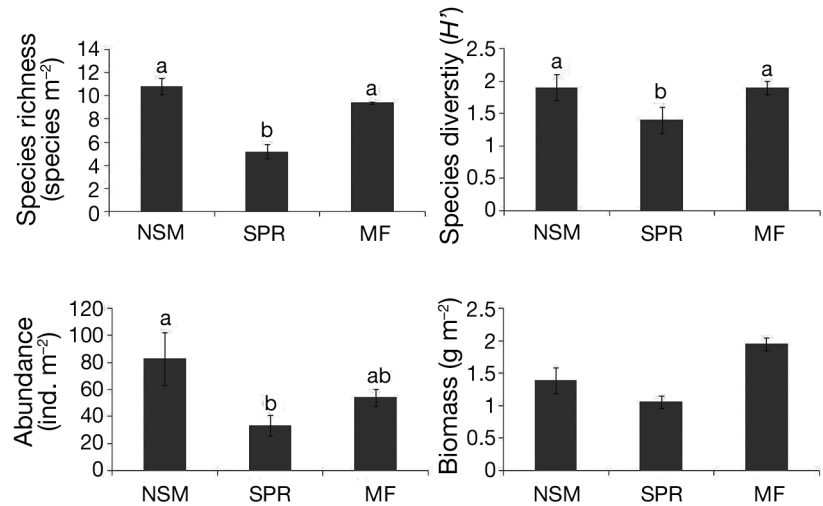


Fig. 2. Mean (±SE) species richness, diversity, abundance and biomass of total macrofauna averaged among sampling blocks for each habitat type; p = 0.001, 0.020, 0.026 and 0.206, respectively (linear mixed-model ANOVA). In each panel, means with different letters are significantly different (p < 0.05 in pairwise tests). NSM: native saltmarsh; SPR: *Spartina anglica*; MF: mudflat

Table 2. Mean (±SE) species richness, diversity, abundance, and biomass for taxonomic groups of macrofauna averaged among sampling blocks for each habitat type (p-values from linear mixed-model ANOVA). Means with different superscript letters in the same row are significantly different (p < 0.05 in pairwise tests)

| | Native saltmarsh | *Spartina anglica* | Mudflat | p |
|---|---|---|---|---|
| **Species richness (species m$^{-2}$)** | | | | |
| Mollusca | 5.8 ± 0.55[a] | 3.0 ± 0.55[b] | 4.9 ± 0.32[a,b] | 0.045 |
| Annelida | 0.8 ± 0.59 | 0.6 ± 0.55 | 0.8 ± 0.32 | 0.860 |
| Crustacea | 3.8 ± 0.34[a] | 1.6 ± 0.57[b] | 4.8 ± 0.49[a] | 0.010 |
| **Species diversity ($H'$)** | | | | |
| Mollusca | 1.4 ± 0.13[a] | 0.7 ± 0.20[b] | 1.0 ± 0.09[a,b] | 0.034 |
| Annelida | 0.6 ± 0.13 | 0.0 ± 0.00 | 0.0 ± 0.00 | 0.410 |
| Crustacea | 1.3 ± 0.09[a] | 0.5 ± 0.25[b] | 1.2 ± 0.10[a] | 0.009 |
| **Abundance (ind. m$^{-2}$)** | | | | |
| Mollusca | 70.0 ± 19.61[a] | 22.8 ± 7.41[b] | 27.4 ± 4.76[a,b] | 0.033 |
| Annelida | 1.6 ± 0.81 | 4.4 ± 2.01 | 1.4 ± 0.04 | 0.609 |
| Crustacea | 11.2 ± 1.98[a,b] | 6.4 ± 1.69[a] | 24.8 ± 1.97[b] | 0.019 |
| **Biomass (g m$^{-2}$)** | | | | |
| Mollusca | 0.7 ± 0.10 | 0.4 ± 0.07 | 0.8 ± 0.12 | 0.105 |
| Annelida | 0.013 ± 0.008 | 0.047 ± 0.021 | 0.011 ± 0.005 | 0.075 |
| Crustacea | 0.7 ± 0.10 | 0.6 ± 0.15 | 1.13 ± 0.19 | 0.079 |

marsh, and crustaceans were less abundant in *S. anglica* than in mudflat (Table 2). There were no significant differences in macrofaunal biomass among the habitats, either for total macrofauna or for taxonomic groups (Fig. 2, Table 2).

MDS of the macrofaunal assemblages based on species presence/absence clearly separated *Spartina anglica* assemblages from the native saltmarsh and mudflat communities (Fig. 3). The native saltmarsh and mudflat sites had some overlap in the ordination space. ANOSIM and SIMPER tests found the greatest dissimilarities between the invaded patches and either the native saltmarsh or mudflat assemblages (dissimilarity of 51%, ANOSIM R = 0.52, p = 0.008; and dissimilarity of 57%, R = 0.58, p = 0.008, respectively; Table 3). Native saltmarsh and mudflat assemblages were not significantly different (dissimilarity of only 33%, ANOSIM R = −0.02, p = 0.5; Table 3). When the fauna were grouped into categories of molluscs, annelids, and crustaceans, the separations among habitats in ordination space were not as evident. Nonetheless, both molluscs and crustaceans in the invaded patches were most dissimilar from the native saltmarsh and mudflat habitats, being significantly different in most cases (p < 0.05; Table 3). Annelid assemblages did not differ significantly among habitats (p > 0.05; Table 3).

Ordination based on species abundance clearly separated all habitat assemblages from one another (combined taxa; Fig. 4), with all pairwise ANOSIM tests significant (p < 0.05; Table 4). The mollusc assemblage was significantly different between *Spartina anglica* and native saltmarsh, while the

Table 3. Pairwise ANOSIM (R, p) and SIMPER (dissimilarity %) comparisons of Bray-Curtis dissimilarities, based on presence/absence of species in the assemblages. SPR: *Spartina anglica*; NSM: native saltmarsh; MF: mudflat

| Group | R | Adjusted p-value | Dissimilarity % |
|---|---|---|---|
| **Mollusca** | | | |
| SPR vs. NSM | 0.19 | 0.040 | 40.0 |
| SPR vs. MF | −0.01 | 0.484 | 40.5 |
| NSM vs. MF | 0.11 | 0.175 | 31.3 |
| **Crustacea** | | | |
| SPR vs. NSM | 0.60 | 0.008 | 69.1 |
| SPR vs. MF | 0.65 | 0.008 | 75.9 |
| NSM vs. MF | −0.05 | 0.595 | 26.4 |
| **Annelida** | | | |
| SPR vs. NSM | 0.00 | 0.587 | 76.9 |
| SPR vs. MF | 0.00 | 0.524 | 73.9 |
| NSM vs. MF | 0.04 | 0.460 | 85.5 |
| **Combined taxa** | | | |
| SPR vs. NSM | 0.52 | 0.008 | 51.1 |
| SPR vs. MF | 0.58 | 0.008 | 57.0 |
| NSM vs. MF | −0.02 | 0.500 | 33.3 |



Fig. 4. MDS ordination of species abundance in replicate sampling blocks, based on the 20 macrofaunal species in Table 1. SPR: *Spartina anglica*; NSM: native saltmarsh; MF: mudflat
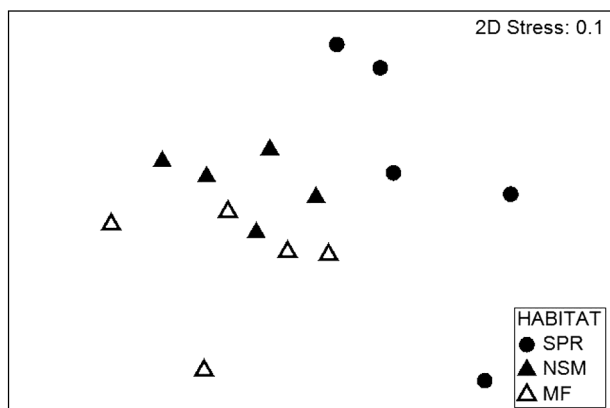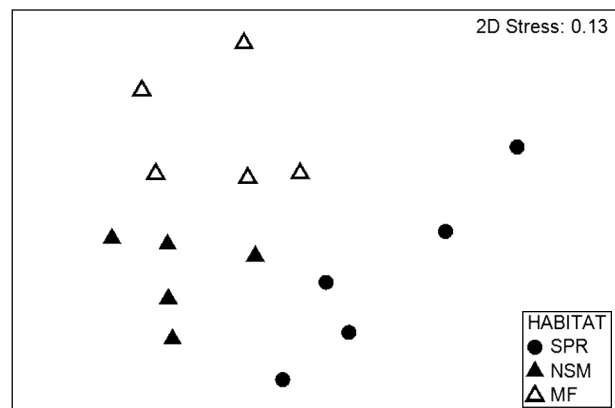


Fig. 3. MDS ordination of species presence/absence in replicate sampling blocks, based on the 20 macrofaunal species in Table 1. SPR: *Spartina anglica*; NSM: native saltmarsh; MF: mudflat

crustacean assemblage in *S. anglica* differed from both uninvaded habitats (p < 0.05; Table 4). For molluscs, crustaceans, and annelids the assemblages in the 2 uninvaded habitats also differed (p < 0.05 for native saltmarsh vs. mudflat; Table 4).

The sediment in patches invaded by *Spartina anglica* had significantly greater mud content (ca. 2-fold) and lower porewater salinity compared to native saltmarsh and mudflat patches (Table 5). The pH in *S. anglica* patches was lower than in mudflat,

Table 4. Pairwise ANOSIM (R, p) and SIMPER (dissimilarity %) comparisons of Bray-Curtis dissimilarities, based on abundances of species in the assemblages. SPR: *Spartina anglica*; NSM: native saltmarsh; MF: mudflat

| Group | R | Adjusted p-value | Dissimilarity % |
|---|---|---|---|
| **Mollusca** | | | |
| SPR vs. NSM | 0.38 | 0.032 | 65.2 |
| SPR vs. MF | −0.13 | 0.825 | 55.0 |
| NSM vs. MF | 0.37 | 0.040 | 65.6 |
| **Crustacea** | | | |
| SPR vs. NSM | 0.43 | 0.008 | 70.8 |
| SPR vs. MF | 0.65 | 0.008 | 87.6 |
| NSM vs. MF | 0.62 | 0.016 | 62.1 |
| **Annelida** | | | |
| SPR vs. NSM | 0.01 | 0.365 | 86.4 |
| SPR vs. MF | 0.06 | 0.286 | 90.5 |
| NSM vs. MF | 0.05 | 0.016 | 91.4 |
| **Combined taxa** | | | |
| SPR vs. NSM | 0.44 | 0.024 | 67.1 |
| SPR vs. MF | 0.61 | 0.008 | 70.0 |
| NSM vs. MF | 0.62 | 0.008 | 65.4 |

but similar to native saltmarsh. Below-ground plant biomass in the *S. anglica* patches was 72% greater than that in the native marsh patches. There were no significant differences in organic matter, moisture content, or median grain size.

The multivariate analysis BIOENV found that salinity and mud content were the sediment parameters that correlated most strongly with macrofaunal assemblage composition (Table 6). Below-ground plant biomass was not included in the analysis because those data were not collected simultaneously with the rest.

Table 5. Environmental parameters (mean ± SE) averaged among sampling blocks for each habitat type; p-values are from linear mixed model ANOVA, except below-ground plant biomass from a paired *t*-test. Means with different superscript letters in the same row are significantly different (p < 0.05 in pairwise tests). NA: not applicable

| | Native saltmarsh | *Spartina anglica* | Mudflat | p |
|---|---|---|---|---|
| Organic matter (%) | 17.6 ± 2.2 | 12.2 ± 1.9 | 13.3 ± 2.3 | 0.260 |
| Moisture content (%) | 54.9 ± 2.6 | 48.1 ± 2.4 | 47.5 ± 2.1 | 0.368 |
| Salinity (g kg$^{-1}$) | 24.5 ± 0.4[a] | 20.8 ± 0.3[b] | 25.0 ± 0.4[a] | <0.001 |
| pH | 7.2 ± 0.4[a] | 7.2 ± 0.3[a] | 7.7 ± 0.1[b] | <0.001 |
| Median grain size (μm) | 193.0 ± 27.0 | 228.5 ± 11.7 | 250.0 ± 12.7 | 0.096 |
| Mud content (%, <63 μm) | 4.6 ± 0.4[a] | 7.6 ± 0.6[b] | 3.5 ± 0.4[a] | <0.001 |
| Below-ground plant biomass (kg m$^{-2}$) | 3.2 ± 0.3[a] | 5.5 ± 0.8[b] | NA | 0.008 |

Table 6. BIOENV ranking of correlations (ρ-values) between sediment parameters and macrofaunal assemblage composition

| Rank | Environmental variable | Correlation coefficient |
|---|---|---|
| 1 | Salinity | 0.266 |
| 2 | Mud content | 0.195 |
| 3 | pH | 0.024 |
| 4 | Median grain size | −0.041 |
| 5 | Organic content | −0.056 |
| 6 | Moisture content | −0.097 |

## DISCUSSION

### Mechanisms of *Spartina anglica* impact

Patches of *S. anglica* had significant reductions of macrofaunal abundance (by as much as 60%), species richness (by 50%), and diversity compared to uninvaded habitat. Populations of infaunal and epifaunal species were both depleted in *S. anglica*, but they were likely affected by different mechanisms.

Infaunal species could have been depleted from *Spartina anglica* patches by inhibition of burrowing, as suggested by the greater below-ground biomass of roots and rhizomes compared to both the native marsh and mudflat. Although we measured plant biomass in the summer of a subsequent year after the macrofauna were collected in autumn, *S. anglica* and the dominant native marsh plant, *Sarcocornia quinqueflora*, are perennials, and their below-ground components should be relatively stable.

Among those species depleted from *Spartina anglica* patches, *Heloecius cordiformis*, *Macrophthalmus latifrons*, and *Mictyris platycheles* are side-burrowing crustaceans that descend at a shallow angle into the sediment (Ringold 1979, Brenchley 1982, Poore 2007), such that they would be blocked by the denser root systems of *S. anglica* compared to native marsh vegetation. van Wesenbeeck et al. (2007) and Bouma et al. (2009) also concluded that enhanced sediment compaction and fine-grained sediment abundance in *S. anglica* habitat hampered the burrowing ability of crustaceans and polychaetes. Likewise, Brusati & Grosholz (2006) concluded that the dense below-ground structure of the invasive hybrid *S. foliosa × alterniflora* excludes infauna, and they further-

more showed a threshold effect by finding that the less dense roots and rhizomes of native *S. foliosa* have no inhibitory effect. Our results are consistent with a similar threshold effect in that, compared to the mudflat, infauna were excluded from the below-ground structure of the *S. anglica* habitat, but not from the less dense native marsh habitat. In another *Spartina* species, Capehart & Hackney (1989) found that burrowing by the clam *Polymesoda caroliniana* was inhibited by *S. alterniflora* roots and rhizomes more than by other marsh vegetation. As a different explanation for inhibition of infauna, Neira et al. (2006) showed that the canopy structure of the hybrid *S. foliosa × alterniflora* reduces flow and enhances deposition of fine sediment, leading to reduced oxygen levels in sediment. Our similar findings of enriched mud content in *S. anglica* patches compared to both native marsh and mudflat could likewise indicate exclusion of infauna by low oxygen levels.

Other authors have suggested or demonstrated an opposite effect, i.e. that the subsurface biomass of *Spartina* spp. can be favourable to infauna by increasing habitat heterogeneity and sediment oxygenation (da Cunha Lana & Guiss 1991, 1992, Gribsholt & Kristensen 2002, Brusati & Grosholz 2006). Levin & Talley (2000) reviewed various other positive and negative relationships between invertebrates and the biomass and density of *Spartina* spp. The only species we found to be notably enhanced in *S. anglica* patches were the burrowing predatory polychaete *Nephtys australiensis* and the shore crab *Paragrapsus laevis* (primarily epifaunal but can dig burrows). These species presumably benefit from the subsurface structuring effects more than they are inhibited by the roots and rhizomes—although the population of *P. laevis* might be more influenced by the above-ground habitat provided by *S. anglica* (see below). Hedge & Kriwoken (2000) also found abundances of *N. australiensis* to be greater in patches of *S. anglica* compared to uninvaded habitats.

Epifaunal species at our site could have been depleted in *Spartina anglica* patches due to reduced microalgal food resources for grazers. Evidence for this effect is the reduced porewater salinity compared to both mudflat and native marsh, indicating a shading effect from *S. anglica* that reduces evaporation on the sediment and which could lower the productivity of microalgae. Salinity was also the physical factor most strongly correlated with our macrofaunal assemblage structure. Similarly, Hacker & Dethier (2006) found reduced porewater salinity in *S. anglica* infestations compared to mudflat and native marsh in the United States. Also, Neira et al. (2005) found

reduced salinity in areas of invasive *S. foliosa × alterniflora* compared to both unvegetated sediment and marsh dominated by *Salicornia quinqueflora*, a glasswort similar in structure to the *Sarcocornia virginica* at our site.

Consistent with our hypothesis, canopy size of *Spartina* spp. has been shown to be related to the amount of shading (Brusati & Grosholz 2006) and microalgal production (Sullivan & Currin 2000) at the sediment surface. da Cunha Lana & Guiss (1992) even documented an inverse relationship between aerial biomass of *S. alterniflora* and epifaunal abundance, offering a similar explanation of reduced microalgal production caused by shading. Also, Levin et al. (2006) found that reduced biomass of surface-feeding infauna in *S. foliosa × alterniflora* habitat compared to unvegetated sediment corresponded to reduced sediment microalgal productivity. At our site, *S. anglica* has a much taller and denser canopy than the creeping glasswort *Sarcocornia quinqueflora* that dominates the native marsh (ca. 50 vs. 15 cm, respectively), which suggests greater shading by *S. anglica* than by *S. quinqueflora*. The effects of a larger canopy are also seen in the increased mud content of the *S. anglica* sediment compared to the native marsh and mudflat (Table 5), caused by a baffling effect on the flow that enhances deposition of fine particles (Neira et al. 2006).

Other authors, though, have found enhanced populations of epifauna in areas of *Spartina* spp. compared to uninvaded sites and suggested that the above-ground structure of the plant favours epifauna by providing habitat and larger surface for grazing (reviewed by Levin & Talley 2000; also Bouma et al. 2009, Tang & Kristensen 2010). The only epifaunal species we found enhanced in *S. anglica* habitat was the shore crab *Paragrapsus laevis*, perhaps because it finds protection or foraging space among the *S. anglica* culms.

## Comparison to other studies on *Spartina anglica*

In light of conflicting studies reviewed in the 'Introduction' on the effects of *Spartina* spp. on macrofauna, particularly for *S. anglica*, we looked for trends in the results of our study and those of others on *S. anglica* (Table 7). We considered only published studies that sampled simultaneously in invaded and uninvaded habitats for comparison. Most of the papers only compared *S. anglica* infestations to unvegetated sediment. In these comparisons, indices for total macrofauna (species richness, diversity,

Table 7. Impacts of *Spartina anglica* in studies that made simultaneous comparisons to local non-invaded habitats. Aus: Australia; F: France; NL: Netherlands; DK: Denmark; chl *a*: chlorophyll *a* content; OC: organic carbon content; OM: organic matter content; *S.a.*: *Spartina anglica*; var.: variable, no overall pattern evident; ND: no difference; NA: not applicable

| Location | Scale of sampled infestation | Macrofauna in *S.a.* compared to bare sediment | Macrofauna in *S.a.* compared to native vegetation (type) | Macrofaunal assemblage | Functional groups | Effects on habitat | Hypothesized mechanisms | Age of infestation | Source |
|---|---|---|---|---|---|---|---|---|---|
| UK | Patches, meadows | Sheltered site: Richness ↓ Abundance ↓ Exposed site: Richness ↑ Abundance ↑ | NA | Not tested | Infauna abundance ↓ in *S.a.*; Epifauna abundance ↑ in *S.a.* | Salinity ND. Mud %, moisture, OC ↑ in *S.a.* (impact on mud % greater at sheltered site) | Infauna inhibited at sheltered site by large increase in mud %, moisture, and low O$_2$ | Not stated | Millard & Evans (1984) |
| UK | Meadow | Richness ND Abundance ↓ | NA | Not tested | Infauna abundance ↓ in *S.a.*; Epifauna abundance ↑ in *S.a.* | Not measured | None given | Not stated | Jackson (1985) |
| Aus | Patches | Richness ↑ Abundance ↑ | Richness ND Abundance ND (marsh plant *Sarcocornia quinqueflora*) | *S.a.* same as native marsh, different from mudflat | Infauna var.; Predator *Nephtys* ↑ in *S.a.*; Epifauna abundance ↑ compared to mudflat | Salinity, OM, grain size ND. Root biomass of *S.a.* = native marsh. Redox in native marsh > *S.a.* > mudflat | *S.a.* roots and culms promote macrofauna by oxygenation and habitat complexity | Not stated | Hedge & Kriwoken (2000) |
| F | Patches | Richness, Abundance, Biomass var. | Richness, Abundance, Biomass var. (seagrass *Zostera noltii*) | Var. | Infauna ND. Some epifauna abundance ↑ in *S.a.* and *Zostera* compared to sandflat | Median grain size ND. OM, mud % var. | Duration of emersion is more important than habitat structure for determining macrofaunal community | 'Pioneering stage' | Cottet et al. (2007) |
| NL | Patches, Meadow | Richness → Diversity → Abundance ↑ Biomass ↑ | Richness → Diversity var. Abundance ↑ Biomass ↑ (seagrass *Zostera noltii*) | *S.a.* different from *Zostera* and mudflat | Infauna richness, diversity, biomass ↓ in *S.a.* compared to *Zostera* and mudflat, whereas epifauna richness, diversity, abundance, biomass ↑. Trophic groups var. | Root biomass of *S.a.* > *Zostera*. Mud % in *S.a.* = *Zostera* > mudflat. Median grain size in *S.a.* = *Zostera* < mudflat. OC, Chl a in *S.a.* meadow > *Zostera* = mudflat | Above-ground habitat complexity of *S.a.* promotes epifauna. *S.a.* meadow generally had larger impacts than *S.a.* patches | Variable, unspecified | Bouma et al. (2009) |
| DK | Meadow | Diversity ↓ Abundance var. Biomass var. | NA | Different between *S.a.* and mudflat | Infauna abundance, biomass ↓ in *S.a.*; Epifauna abundance, biomass ↑ in *S.a.* | OM, Chl a ↑ in *S.a.*; Median grain size ND | Roots inhibit infauna. Above-ground structure of *S.a.* promotes epifauna | Not stated | Tang & Kristensen (2010) |
| Aus | Patches | Richness → Diversity → Abundance ND Biomass ND | Richness → Diversity → Abundance ND Biomass ND (marsh plant *Sarcocornia quinqueflora*) | *S.a.* different from native marsh and mudflat | Infauna and epifauna abundance ↓ in *S.a.*; Predator *Nephtys* ↑ in *S.a.* | Salinity ↓, mud % and root biomass ↑ in *S.a.*; OM, moisture, median grain size ND | Roots inhibit infauna. Shading by *S.a.* inhibits epifauna by reducing microalgae | ca. 8 yr | Present study |

abundance, biomass) yielded highly variable results, from which it is difficult to generalize. For example, reduced values for some of these indices in *S. anglica* infestations were found by Jackson (1985), Bouma et al. (2009), Tang & Kristensen (2010), and in the present study, whereas enhanced values were found by Hedge & Kriwoken (2000) and Bouma et al. (2009). Some authors found highly variable results or a clear lack of difference for some indices (Jackson 1985, Cottet et al. 2007, Tang & Kristensen 2010, present study), and Millard & Evans (1984) found opposite results for sheltered and exposed sites.

Fewer studies compared macrofauna between *Spartina anglica* and native vegetation, and the findings are no clearer. Two studies made the comparison to seagrass habitat, finding some increases in abundance and biomass in *S. anglica*, some reduction of richness, and several highly variable results that revealed no clear pattern (Cottet et al. 2007, Bouma et al. 2009). Only Hedge & Kriwoken (2000) and our study compared *S. anglica* to native saltmarsh (similar native marshes in Australia), yielding quite different results (discussed in more detail below).

These highly variable findings for total macrofauna indices reflect the impression in the literature for *Spartina* spp. as a whole, reviewed in the 'Introduction'. However, in papers that compared macrofaunal species assemblages using multivariate statistics, there were differences between *S. anglica* infestations and uninvaded habitats in all but one (Table 7), suggesting that a closer examination of results at the level of taxa or functional groups might reveal patterns. Indeed, a clearer picture of trends emerges when examining impacts of *S. anglica* on infauna and epifauna separately. Some of these papers did not distinguish between impacts on infauna and epifauna in their analyses, but we examined their species lists and drew the comparisons shown in Table 7.

In all studies including our own, infauna in *Spartina anglica* were either depleted or showed no clear difference compared to bare sediment or native vegetation (Table 7). In no case was the infauna promoted by the presence of *S. anglica*. Where authors have offered hypotheses to explain these findings, they include inhibition of infauna by below-ground plant structure, increased content of mud and moisture, and reduced oxygen. Some of the studies reported measurements of physical habitat parameters that corroborated these hypotheses (Table 7).

In contrast, epifauna in *Spartina anglica* showed enriched assemblages compared to bare sediment, and in one case compared to native vegetation (seagrass) (Table 7). The hypothesis to explain facilitation

of epifauna was the aerial habitat complexity provided by *S. anglica*. The sole exception is our study, finding depleted epifauna in *S. anglica*. As discussed above, the reduced porewater salinity we measured in *S. anglica* patches can explain the depletion of epifauna by a shading effect on microalgal production. Consistent with this explanation is that in other studies in which epifauna were enhanced in *S. anglica* and porewater salinity was reported (Millard & Evans 1984, Hedge & Kriwoken 2000; Table 7), there were no differences in salinity among habitats (thus, no evidence for a shading effect). Also, in papers that reported chlorophyll *a* content in the surficial sediment, it was enhanced in *S. anglica* habitat along with the epifauna (Bouma et al. 2009, Tang & Kristensen 2010; Table 7), again showing no evidence of a shading effect. From these comparisons we conclude that epifauna are generally facilitated by *S. anglica* unless there is a shading effect on microalgae that serve as an important food resource.

## Comparison to *Spartina anglica* elsewhere in Australia

The contrasting findings between our study and Hedge & Kriwoken's (2000) are important, particularly because they are from 2 temperate sites in Australia and the comparisons to native saltmarsh are similar in that the marshes are both dominated by *Sarcocornia quinqueflora*. Hedge & Kriwoken (2000) found that total macrofaunal species richness and abundance were greater in *S. anglica* and native marsh than in mudflat. Furthermore, their multivariate analyses of assemblage structure revealed 2 groupings: one including the mudflat samples and the other combining both vegetated habitats. Essentially, Hedge & Kriwoken's (2000) results from the state of Tasmania suggested that invasion of *S. anglica* into mudflat raises the invertebrate richness and abundance and converts the macrofaunal species assemblage into the equivalent of that in native saltmarsh. Our results in the neighbouring state of Victoria indicate a different and potentially more consequential impact, i.e. that invasion by *S. anglica* creates a unique macrofaunal assemblage, different from both mudflat and native saltmarsh, with reduced species richness, diversity, and abundance.

Possible reasons for the differing findings are apparent in Table 7. In comparing *Spartina anglica* patches to mudflat, we found indices for total macrofauna to decline, whereas Hedge & Kriwoken (2000) found increases, but the discrepancy is mainly due to

the epifauna. As explained above, our declines of epifauna were likely caused by a shading effect, whereas Hedge & Kriwoken (2000) found no evidence for shading (no difference in porewater salinity). Furthermore, Hedge & Kriwoken (2000) found no differences in modal grain size among habitats, whereas, although we found no differences in median grain size, we did find increased mud content in *S. anglica* patches. These comparisons of grain size measurements indicate that *S. anglica* at our site caused more of a shift to a depositional environment than it did at Hedge & Kriwoken's (2000) site. Together, these observations of shading and depositional environment suggest that *S. anglica* at our site was denser and/or taller (i.e. more mature) than at Hedge & Kriwoken's (2000) site. No measures of above-ground plant structure were given by Hedge & Kriwoken (2000), but the below-ground biomass in *S. anglica* patches at our site was ca. 4-fold greater than at their site, suggesting a corresponding difference in above-ground density. Such a difference in *S. anglica* canopy size between the 2 studies could account for the differences in shading and the impacts on epifauna. For example, Sullivan & Currin (2000) investigated the relationship between *Spartina* spp. canopy size and shading, and found that microalgal production was lower underneath a tall form of *S. alterniflora* than under a short form. Therefore, whereas the epifauna at our site were likely inhibited by shading in the patches of relatively dense/tall *S. anglica*, the epifauna at Hedge & Kriwoken's (2000) site may have merely benefitted from the aerial habitat provided by *S. anglica* that was less dense/tall.

In comparing *Spartina anglica* patches to native *Sarcocornia quinqueflora* marsh, we found indices for total macrofauna to decline, whereas Hedge & Kriwoken (2000) found no differences (Table 7). Our declines were due to both epifauna and infauna, whereas Hedge & Kriwoken's (2000) show no patterns for either group. The differing responses of epifauna can be explained along the same lines as the arguments above (reduced microalgal food resources at our site caused by shading from the larger *Spartina anglica* canopy), because Hedge & Kriwoken (2000) found no differences in salinity or grain size between *S. anglica* patches and native marsh, whereas we did (Table 7). The fact that Hedge & Kriwoken (2000) found epifauna to be facilitated by *S. anglica* compared to mudflat, but not compared to native marsh, may reflect that the epifauna benefitted from aerial structure of both plants (*S. anglica* and *Sarcocornia quinqueflora*) equally compared to

unvegetated sediment. Regarding infauna and their differing responses in the 2 studies, we found greater below-ground plant biomass in *Spartina anglica* patches compared to native marsh, whereas Hedge & Kriwoken (2000) did not (Table 7). This suggests that burrowing in *S. anglica* sediment was inhibited relative to native marsh at our site, but not at Hedge & Kriwoken's (2000) site.

Differing responses to invasion could also be related to differences in the resident macrofaunal assemblages in the uninvaded habitats. Only 4 of the 20 species we identified were also reported by Hedge & Kriwoken (2000). Two of these species (*Helograpsus haswellianus* and *Nephtys australiensis*) responded similarly to invasion at both locations, showing some consistency between the studies, but the species that occurred at only one or the other location may simply have different inherent responses to invasion. In considering only the uninvaded habitats, Hedge & Kriwoken (2000) found higher total macrofaunal species richness and higher abundance in the native saltmarsh compared to mudflat, whereas we found each of these measures to be equal between the 2 habitats. Perhaps this comparison reflects an important difference between the native marsh systems in the 2 locations that caused differing responses to invasion.

A caveat for comparing these studies is that each is based on samples collected in a single season. One might argue that comparing Victoria in autumn (present paper) to Tasmania in winter (Hedge & Kriwoken 2000) is not appropriate, but the separation is only 3 mo, and it is unlikely that these 2 considerably different systems normally converge to the same characteristics during the same season. Indeed, Cottet et al. (2007) found high seasonal stability of the macrofaunal community in habitats invaded by *Spartina anglica*.

## Predictable impacts of *Spartina anglica*

Based on our results and literature analysis (Table 7), we present 2 general predictions about the impacts of *S. anglica* on macrofauna. (1) When sufficiently dense, the below-ground biomass of *S. anglica* excludes infauna due to dense roots/rhizomes and sediment compaction (van Wesenbeeck et al. 2007, Bouma et al. 2009, present study), whereas below some threshold density there is no impact (cf. Hedge & Kriwoken 2000). The impact relative to a habitat of native vegetation depends on the relative abundance of below-ground biomass in the 2 habitats. (2) The aerial portion of *S. anglica* promotes epi-

fauna by providing habitat complexity and possibly protection (most references in Table 7), except when the plant is so dense that it reduces microalgal productivity due to shading (present study). The impact relative to native vegetation again depends on the relative densities of the plants, and perhaps their above-ground architectures. Finally, because of the differing predicted impacts on infauna and epifauna, the overall impact of *S. anglica* on the total macrofaunal assemblage is not possible to predict (see the highly variable findings in Table 7).

Note that the density of *Spartina anglica* infestation is a critical factor in both of our predictions. Density is often related to age of infestation, and other authors have emphasized the importance of invasion age or maturity for the impacts of various *Spartina* spp. (Levin & Talley 2000, Neira et al. 2005, 2007, Bouma et al. 2009).

Two other factors that might have predictive value are the areal extent of an invasion and the hydrodynamic regime. We included these factors in Table 7 when information was available, but such details are rarely published. Bouma et al. (2009) found that meadows of *Spartina anglica* generally had greater impacts than small patches, presumably because of less influence from edge effects. Also, effects of aerial plant architecture on hydrodynamics and sediment deposition are unlikely to be fully developed in a small patch (Bouma et al. 2005, Neira et al. 2006, Peralta et al. 2008). Therefore, some of the variability in findings among other studies in Table 7 might be due to their being done mostly on small patches of *S. anglica*. Furthermore, the impacts of *S. anglica* at our site might have been stronger if the plants had developed into a large meadow rather than being small patches. Exposure to currents and waves can also have further complex effects. Hydrodynamic regime proved an important factor in the results of Millard & Evans (1984), with the overall impacts of *S. anglica* on total macrofauna indices being opposite at exposed and sheltered sites. Also, Swales et al. (2004) showed that growth and sediment-trapping effects of *S. anglica* are influenced by local wave energy. We recommend that future studies report information on age and areal extent of infestations, density of above- and below-ground biomass, and hydrodynamic regime.

## Implications for food webs

The reduced richness, diversity, and abundance of macrofauna in areas invaded by *Spartina anglica* in Anderson Inlet may result in less diversity and biomass of higher trophic levels and reduced food resources for coastal birds and fishes. These degenerative impacts on the coastal ecosystem are of particular concern where *S. anglica* has invaded wetlands of international importance (e.g. those recognized by the Ramsar Convention), such as ones in southeastern Australia that are habitat for rare and endangered species, including the eastern curlew, eastern great egret, and royal spoonbill. These birds feed on crustaceans in Anderson Inlet during nesting and migration (Blood 1995). Colonization of mudflat by *S. anglica* reduces not only the density of prey but also the extent of foraging ground for these birds. Furthermore, the biomass of *S. anglica* does not necessarily enter the food web. Stable-isotope studies of macrofaunal communities in San Francisco Bay and neighbouring estuaries showed that the native and hybrid *Spartina* spp. do not contribute significantly to the nutrition of surface-feeding molluscs and crustaceans (Brusati & Grosholz 2009). Stable-isotope studies in Anderson Inlet also indicated that *S. anglica* does not contribute significantly to the nutrition of benthic crustacean detritivores (Hindell 2008), although it was found to be a major nutritional contributor to estuary perch *Macquaria colonorum* (Hindell & Warry 2010).

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