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Evidence for effects of *Spartina anglica* invasion on benthic macrofauna in Little Swanport estuary, Tasmania

PAUL HEDGE[1]* AND LORNE K. KRIWOKEN[2]

[1]*Marine Resources Division, Department of Primary Industries, Water and Environment, GPO Box 192B, Hobart, Tasmania 7001, Australia (Email: paul.hedge@dpiwe.tas.gov.au) and*
[2]*Centre for Environmental Studies, University of Tasmania, Hobart, Tasmania, Australia*

Abstract *Spartina anglica* is an exotic perennial grass that can rapidly colonise the intertidal zone of temperate estuaries and lagoons. Consequently, there is considerable concern about its impact on estuarine flora and fauna. This study provides the first investigation of ecological impacts by *S. anglica* in Australia. The objective was to investigate the impacts of *S. anglica* on benthic macroinvertebrate communities inhabiting mudflat and native saltmarsh habitats at Little Swanport estuary, Tasmania. The null hypothesis that species richness and species abundance of benthic macroinvertebrates in exotic *S. anglica* marsh does not differ from adjacent native saltmarsh and mudflat habitats was tested. Eighteen species and 3716 macroinvertebrates were collected from 60 intertidal core samples in three habitats. Species richness, total abundance of invertebrates, crustacean abundance and mollusc abundance of mudflat communities were significantly ($P < 0.05$) lower when compared to those inhabiting adjacent *S. anglica* marsh and native saltmarsh. However, species richness and total abundance of invertebrates of native saltmarsh and *S. anglica* marsh did not differ significantly. Ordination of macroinvertebrate data clearly separated mudflat sites from vegetated sites but showed remarkable similarity between exotic and native vegetated sites.

Key words: benthic macrofauna, coastal, estuaries, invasion, mudflat, saltmarsh, *Spartina anglica*, wetlands.

INTRODUCTION

During the last decade, introduced marine species have received considerable attention on a global scale (Carlton 1989, 1994; Leppakoski 1993; Nolan 1993; 1996a; 1996b; Hewitt & Martin 1996). One of the major concerns for ecologists has been the effect of these invaders on existing indigenous habitats and communities (Carlton 1989, 1994). Although many introduced marine species appear to have relatively benign effects on existing habitats (Nolan 1993), the invasion of others can lead to dramatic environmental change. *Spartina anglica* provides a good example of an introduced marine species that can cause dramatic environmental change to indigenous habitats.

Spartina anglica, commonly referred to as rice grass, is an emergent saltmarsh grass that colonises the intertidal zone of temperate estuaries and waterways. Typically, *S. anglica* infestations form dense aggregations of culms, rhizomes and roots that promote sediment accretion, eventually leading to the formation of intertidal terraces or saltmarsh islands. The vast majority of infestations have been found to occur in intertidal mudflat habitat, although it also occurs in native saltmarsh, seagrass, mangrove and intertidal seagrass habitats (Thompson 1991; Blood 1995; Hedge 1997). Prostrate or stout species, such as *Salicornia quinqueflora* and *Samolus repens* or white mangrove seedlings, *Avicennia marina*, appear to be particularly prone to competitive exclusion by *S. anglica* (Hedge, 1999, personal observation).

Mudflat, saltmarsh, seagrass and mangrove habitats are valued for the roles they play in estuarine processes and the provision of habitat for mammals, birds, fish and many invertebrates (Adam 1985, 1990, 1995; Saenger 1994, 1995; Inglis 1995; Morrisey 1995). These habitats also provide important nursery and feeding habitats for economically important fish species (Pollard 1981; Saenger 1994, 1995; Connolly *et al.* 1997). Not surprisingly, there has been considerable concern and speculation about environmental change associated with the progressive invasion of *S. anglica* in temperate Australia (Bell 1995; Bishop 1995; Blood 1995; Bridgewater 1995; Fotheringham *et al.* 1995; Gibbs & Phillips 1995; Simpson 1995; Wells 1995; Williamson 1995).

There have been no comprehensive studies examining the ecological impact of *S. anglica* to Australia's estuaries. Most studies have focused on its distribution (Pringle 1975, 1988 [Condition and distribution of *Spartina anglica* (rice grass) in selected estuaries and inlets along the Bass Strait coast, Tasmania. Unpublished report for Department of Lands, Parks and Wildlife, Hobart, Tasmania, Australia], 1993), or

*Corresponding author.
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on controlling the spread of *S. anglica* (Wells *et al.* 1991 [Herbicide trials for the control of *Spartina Anglica* (rice grass) at Port Sorell, Tasmania. Internal unpublished report, Department of Parks, Wildlife and Heritage, Hobart, Tasmania, Australia]; Bishop 1995; Pritchard 1995). Furthermore, the ecology of habitats threatened by *S. anglica* invasion in temperate Australia, particularly mudflat and saltmarsh, has received little scientific attention and is poorly understood (Adam 1990, 1995; Robertson 1994; Saenger 1994; Fairweather & Quinn 1995).

In some cases, the environmental change caused by *S. anglica* invasion is clearly visible, providing a relatively sound basis on which to speculate about the impacts associated with invasion. For example, at Duck Bay and Little Swanport estuary in Tasmania, the spread of *S. anglica* has transformed intertidal mudflats to *S. anglica* saltmarsh and to a lesser extent displaced native saltmarsh species (Hedge 1997a). In Anderson Inlet, Victoria, bird observers note that the vast majority of wader birds avoid *S. anglica* (Simpson 1995). The authors have also observed wader birds avoiding infestations in Tasmania. In other cases, however, the ecological effects of *S. anglica* invasion may be cryptic or difficult to detect. For example, changes to benthic macroinvertebrate communities of mudflats are difficult to determine from field observations. Reise (1985) points out that benthic macroinvertebrates are an integral component of mudflat habitats and their biomass is considerably greater than in other tidal flat communities.

Studies by Jackson (Long & Mason 1983) on benthic macroinvertebrate communities in the River Sour, UK, found species richness to be higher in mudflat communities than in adjacent *S. anglica* marsh. Similar studies by Luiting *et al.* (1997) examining impacts of a closely related species, *Spartina alterniflora*, in Willapa Bay, WA, USA, found significant differences between mudflat and vegetated communities; however, strong seasonal effects on community structure were apparent in each habitat type. To the contrary, a brief pilot study by Hedge in the Little Swanport estuary, Tasmania (1997: Ecology, impact and control of rice grass (*Spartina anglica*) in the Little Swanport estuary. Unpublished technical report submitted to Fishcare, Australia and the Rice Grass Advisory Group, Hobart) found benthic macroinvertebrate communities associated with *S. anglica* marsh to have higher species richness and total abundance of invertebrates when compared with adjacent mudflat communities.

Spartina anglica invasion of native saltmarsh may also lead to changes in the structure of resident invertebrate communities. Capehart & Hackney (1989) examined the effect of three saltmarsh plant structures on densities of the Carolina saltmarsh clam, *Polymesoda caroliniana*. Results showed that invertebrate densities were inversely related to root and rhizome density, suggesting that dense root and rhizome aggregrations may inhibit burrowing animals.

The aim of the study was to examine the effect of *S. anglica* invasion on species richness and species abundance of benthic macroinvertebrate communities in the Little Swanport estuary, Tasmania. The null hypothesis was that species richness and species abundance of benthic macroinvertebrates in exotic *Spartina anglica* marsh do not differ significantly when compared

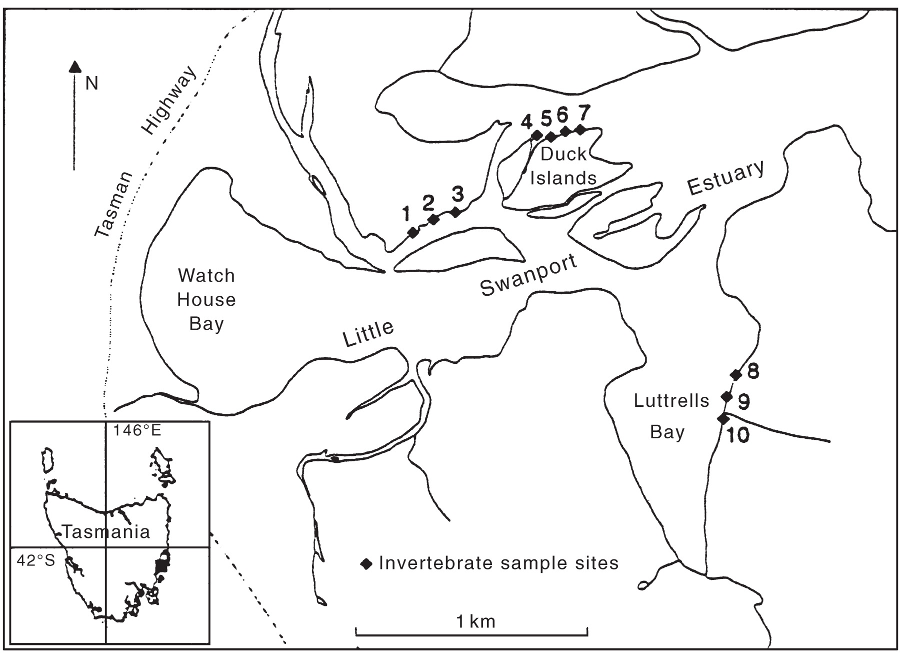

Fig. 1. Location of Little Swanport estuary, Tasmania, and selected macroinvertebrate sampling sites.

with adjacent mudflat and native saltmarsh habitats. The study also provided new ecological information on benthic macroinvertebrate communities inhabiting mudflat and saltmarsh habitat in a temperate Australian estuary.

Data on environmental variables were collected to provide additional information to account for observed community differences between habitats. For example, variations in underground biomass (Osenga & Coull 1983; Capehart & Hackney 1989), sediment particle size distribution (Whitlatch 1977, 1981; Edgar & Shaw 1995; Mannino & Montagna 1997) and organic content of sediments (Whitlatch 1981; Lana & Guiss 1991; Mannino & Montagna 1997) have been shown to influence the structure of benthic macroinvertebrate communities. Furthermore, invasion of mudflat habitat by *Spartina* spp. has been shown to alter pre-existing pH (Chung 1990), salinity (Chung 1990) and oxygen levels (Osenga & Coull 1983; Lana & Guiss 1991). Collection of environmental data from a poorly understood habitat also provided a comparative basis for future studies in this area.

Temporal and spatial variation in the structure of benthic macroinvertebrate communities inhabiting soft-bottom habitats are well documented (Whitlatch 1977; Rainer 1981; Thrush 1991; Mannino & Montagna 1997). Ideally, impact studies on benthic communities should be designed to accommodate interannual, interseasonal and spatial variation. Nonetheless, a snapshot study, such as this one, can provide valuable insight into environmental change associated with an invasive species.

METHODS

Location

The Little Swanport estuary is situated on Tasmania's east coast (148°00′ east, 42°20′ south) (Fig. 1). The estuary has a single narrow outlet approximately 150 m wide at high tide but considerably narrower at low tide. Tidal exchange between the estuary and adjacent marine waters is diurnal with an amplitude of 0.7–1 m (Mitchell 1988). Salinity in the estuary varies considerably and is affected strongly by rainfall events (Mitchell 1988). The Little Swanport river is the main freshwater input to the estuary with mean annual discharge rates between 1971 and 1981 of approximately 72 188 m^3 (Mitchell 1988). Approximate annual rainfall in the region is 500–625 mm with most rain occurring in winter and spring. Major habitat types in the estuary include mudflat, saltmarsh, sandflat, seagrass, reef and rocky shores. In the upper reaches of the estuary, saltmarsh and mudflat habitats dominate the intertidal zone. The majority of *S. anglica* occurs in the upper reaches of the estuary.

Invertebrate sampling

To investigate the effect of *S. anglica* invasion on macroinvertebrate infaunal communities, 10 sites were randomly selected from three regions of the *S. anglica* infestation within the estuary (Fig. 1). Regions were selected on the basis that they contained a mosaic of mudflat, native saltmarsh and *S. anglica* marsh habitats at the same tidal height. This stratified random sampling approach was adopted to represent any mesoscale spatial variation (distances greater than hundreds of metres) that may occur within different areas of infestation. The number of sites was distributed evenly between each of the three regions. Core samples in vegetated habitats were taken approximately 2 m in from the leading edge of saltmarsh. Native saltmarsh flora was dominated by *Sarcocornia quinqueflora* with sparse tussocks of *Juncus krausii*.

Between 22 and 25 August 1997, macroinvertebrate infaunal communities were sampled by taking two sediment cores (100 × 150 mm diameter) from each of the three habitat types at each of the 10 sites. Raffaelli & Hawkins (1996) point out that the diameter of the core should be bigger than the largest animal. Results from a pilot project in Little Swanport estuary (Hedge, 1997, unpublished data) show that polychaete worms may be up to 80 mm long; therefore the core size used in this study (150 mm diameter) was considered suitable.

Sediment samples were sieved in the field through 1 mm mesh to separate animals from roots/rhizomes, debris and sediments. Sieve contents were bagged and fixed, immediately after sieving, in 10% buffered formalin stained with rose bengal. In the laboratory, fixed invertebrates were systematically separated from debris in a sorting tray and preserved in 70% alcohol containing 2% glycerol. Invertebrates were classified to species level where possible using a dissecting microscope.

Environmental variables

A smaller 100 × 45 mm diameter core sample, located approximately 5–10 cm from each invertebrate core sample, was taken to determine sediment particle-size distribution and the proportion of organic materials and root/rhizome biomass in the sediments. To reduce processing effort, the paired cores (45 mm diameter) were amalgamated to provide one composite core per habitat type at each site. Edgar & Shaw (1993) and Edgar *et al.* (1994) have also amalgamated replicate core samples when determining measures of environmental variables in benthic habitats. Sediments were dried at 60°C for 3 days before sieving. Live roots and rhizomes were removed and dried separately at 60°C for 3 days.

Composite core samples from each habitat type at each site were subsampled to determine particle-size distribution and organic content of sediments. Sediment retained on sieve sizes –0.5, 0, 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4 and >4 phi was weighed and recorded as a percentage of the total weight to determine particle-size distribution. Approximately 30 g of dried sediment was ashed at 550°C for 30 min to determine the organic content of sediments. The differences in weight between before and after ashing (organic content) were expressed as a percentage of the total weight.

Salinity (ppt), pH and redox (mV) measurements of sediment water were collected from all invertebrate core locations. Salinity was measured with a WTW LF 320

Table 1. Summary data of benthic macroinvertebrate species sampled from three habitats in Little Swanport estuary, Tasmania, August 1997. (a) Total abundances; (b) summary statistics as medians with range in brackets based on individual core data

(a) Species	Mudflat	Native saltmarsh	*Spartina anglica*
Mollusca			
Hydrococcus brazieri	25	686	704
Tatea rufilabris	11	621	497
Arthritica semen	30	21	17
Austrocochlea brevis	0	0	6
Bembicium melanostromum	0	3	6
Salinator solida	0	13	5
S. fragilis	39	0	0
Xenostobus inconstans	0	18	4
X. securis	0	17	1
Crustacea			
Eorchestia palustris	16	219	226
Paracorophium sp.	48	2	10
Helograpsus haswellianus	0	7	6
Gnorimosphaeroma sp.	0	0	3
Sphaeroma sp.	0	1	
Annelida			
Nephtys australiensis	92	89	123
Perinereis vallata	10	19	8
Boccardia sp.	1	109	3
Abarenicola affinis	1	0	0
(b)	**Median (range)**	**Median (range)**	**Median (range)**
Species richness	3.2^a (0–7)	5.6^b (0–9)	5.8^b (0–10)
Species abundance	11^a (0–74)	53^b (38–414)	44^b (18–337)
Polychaetes	4.5^a (0–13)	7.5^a (0–33)	6^a (0–17)
Molluscs	4^a (0–23)	34.5^b (14–363)	32^b (4–312)
Crustacea	0^a (0–38)	4.5^b (0–45)	8.5^b (0–51)

Medians followed by the same letter are not significantly different at $P < 0.05$ (Student–Neumann–Keulls *posthoc* test).

Table 2. Mean (± SE) of environmental variables for each habitat type recorded from macroinvertebrate sampling sites during August 1997, in the Little Swanport estuary, Tasmania

Habitat	Temperature (°C)	pH	Salinity (ppt)	Redox (mV)	Biomass ($g\,m^{-2}$)	Organic content (% weight)	Sediment size (modal phi)
Mudflat ($n = 10$)							
mean	8.2	6.9	19.6	9.1	NA	6.75	2.9
SE	(0.36)	(0.02)	(2.45)	(29.2)	(2.14)	(0.20)	
Saltmarsh ($n = 10$)							
mean	8.1	6.4	19.8	246.9	1196.7	10	3.25
SE	(0.32)	(0.08)	(2.45)	(21.4)	(543.4)	(2.41)	(0.25)
Spartina ($n = 10$)							
mean	8.5	6.3	18.6	92.5	1257.9	7.43	2.9
SE	(0.37)	(0.05)	(2.55)	(29.7)	(207.5)	(1.90)	(0.19)

conductivity meter (Wissenschaftlich–Technische Werkstatten, Weilheim, Germany) fitted with a WTW Tetracon 325 probe; pH with a WTW pH 320 pH meter fitted with a WTW SenTix 97T probe; and redox with the pH meter fitted with a ACTIVON AEP511 Redox-Probe (Activon Scientific Products, Brighton, Victoria, Australia). All measurements were taken 5 cm below the sediment surface.

Data analyses

Analyses of invertebrate data were based on species richness and species abundance values. Species richness has been regarded as a practical and meaningful way to measure species diversity that also captures much of the essence of biodiversity (Margules & Usher 1981; Gaston 1996). A variety of univariate and multivariate techniques were used to examine invertebrate and environmental data. Non-parametric tests were used where data failed the normality test (SigmaStat Analyses Package; Jandel, San Rafael, CA, USA).

The Kruskal–Wallis one way ANOVA on ranks test was used to determine differences in species richness and species abundance among habitats. Spearman's rank order correlation was used to investigate the relationship between environmental and community variables.

Non-parametric multivariate analyses are an effective method with which to investigate changes in the community structure of marine benthic invertebrates (Clarke 1993). The PATN computer program (Manufacturer?, City?, Country?) was used to examine ecological relationships between habitats, sites and cores (Belbin 1991; Clarke 1993). Association between cores and sites, based on the Bray–Curtis measure of dissimilarity, was determined by constructing an association matrix (ASO). When community and environmental data were combined, data were standardised using the 'average rank' option. The ASO matrix of similarity was used to: (i) classify the sites or cores into groups by hierarchical polythetic agglomerative clustering and (ii) map the interrelationships between sites and cores in an ordination.

Inter relationships between sites and cores were mapped in an ordination using semistrong hybrid (SSH) multidimensional scaling (MDS). Data generated by this technique were expressed in three dimensions. However, only two of the three dimensions were chosen to map interrelationships. This is a commonly used and acceptable technique provided that the stress value of the ordination is sufficiently low (Clarke 1993). Ordination was accepted if stress values were less than 0.15. The stress value is a measure of goodness of fit for the data; values less than 0.15 are considered acceptable (Belbin 1991; Clarke 1993; Wong *et al.* 1993).

A Monte Carlo test (MCAO) was used to identify taxa and environmental variables significantly correlated with the ordination space. Results of ordination analyses were displayed as a scatterplot. Similarity between cores and sites is proportional to the distance between points (i.e. the smaller the distance between points the greater their similarity). Taxa and environmental variables considered to be significantly correlated with the ordination space, based on results of the MCAO test, were plotted as vectors in the same ordination space.

RESULTS

Diversity and abundance

A total of 18 species and 3716 individuals was collected from 60 intertidal core samples in three habitats. Ten species and 272 individuals were collected from mudflat habitat which was dominated by the annelid, *Nephtys australiensis*, the amphipod, *Paracorophium* sp., and the molluscs, *Salinator fragilis* and *Arthritica semen*. Thirteen species and 1824 individuals were collected from native saltmarsh. In *S. anglica* marsh, 16 species and 1620 individuals were collected. Both *S. anglica* marsh and native saltmarsh were dominated by the molluscs, *Hydrococcus brazieri* and *Tatea rufilabris*, and the amphipod *Eorchestia palustris*. *Salinator fragilis* was only found in mudflat habitats; conversely, *Salinator solida* was only found in vegetated habitat. The annelid, *Boccardia* sp., was common in native saltmarsh but rare in *S. anglica* and mudflat habitats. Table 1 provides a list of invertebrate species abundances in each habitat type.

Habitat characteristics

Mean ± SE values of environmental variables for each habitat sites are detailed in Table 2. Mean temperature and salinity of sediment water over the sampling period was similar for all habitat types. Redox values of sediment pore water differed significantly between habitats (ANOVA $F_{2,57} = 19.8$, $P < 0.001$). Student–Neumann–Keulls (SNK) comparisons showed that all habitats were significantly different when compared with each other.

Differences in the organic content of sediments between sites were not considered to be significant (Kruskal–Wallis ANOVA $H_2 = 1.59$, $P = 0.452$). Differences in the biomass of roots and rhizomes between vegetated sites were not considered to be significant (Student's *t*-test $t_{18} = 1.75$, $P = 0.098$). However, the power of the performed test (0.2604) is below the desired power (0.8) to exclude the possibility that a type II error has occurred. Modal sediment size varied considerably between sites but not between habitats. However, at sites 5–7, modal sediment size of native saltmarsh sediments (phi 4) was smaller than mudflat (phi 2.5) and *S. anglica* marsh (modal phi 2.5–3).

Univariate analyses

Total abundance of invertebrates per core sample differed significantly between habitats (Kruskal–Wallis ANOVA $H_2 = 34.5$, $P < 0.001$), with that of mudflats significantly lower (11) than in native saltmarsh (53) and *S. anglica* marsh (44), which did not differ (Table 1).

Species richness per core sample differed significantly between habitats (Kruskal–Wallis ANOVA $F_{2,57} = 12.5$, $P < 0.001$), with that of mudflat habitat (3.25) lower than in *S. anglica* marsh (5.85) and native saltmarsh (5.65), which did not differ (Table 1).

Mollusc abundance per core sample and crustacean abundance per core both differed significantly between habitats (Kruskal–Wallis ANOVA $H_2 = 35.3$, $P < 0.001$) and Kruskal–Wallis SNK comparisons showed that mollusc and crustacean abundance in mudflat habitat were lower than in native saltmarsh and *S. anglica* marsh. Native saltmarsh and *S. anglica* marsh were not different in either mollusc or crustacean abundance. Polychaete abundance per core between habitats did not differ significantly (Kruskal–Wallis ANOVA $H_2 = 2.92$, $P = 0.233$).

Total abundance of invertebrates was significantly correlated (Spearman rank order, $P < 0.05$) with the redox values, organic matter and silt content of sediments. Biomass of roots and rhizomes and total abundance of invertebrates were also significantly correlated (Spearman rank order $P < 0.001$). Species richness was significantly correlated with biomass (Spearman rank order $P < 0.001$), but not with organic matter, redox values or silt content of the sediments.

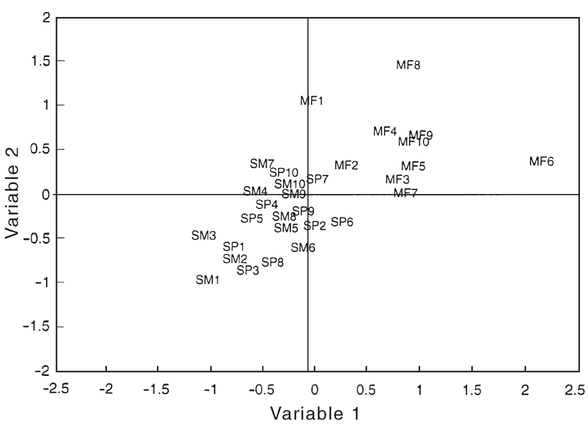

Fig. 2. Ordination (SSH MDS, three dimension, stress = 0.113) of 30 sites (MF, mudflat; SM, native saltmarsh; SP, *Spartina anglica* marsh) based on 18 benthic macroinvertebrate taxa from the Little Swanport estuary, Tasmania, during August 1997.

Multivariate analyses

Ordination (SSH MDS, three dimension, stress 0.113) of sites based on abundance of 18 taxa clearly separated mudflat communities (upper right sector of ordination space) from vegetated communities (Fig. 2). Sites from native saltmarsh and *S. anglica* marsh were generally grouped together on the left sector of the ordination space. Furthermore, vegetated sites were tightly grouped relative to mudflat sites. Ordination (SSH MDS, three dimension, stress = 0.143) of core samples also clearly separated mudflat from vegetated communities (ordination not shown).

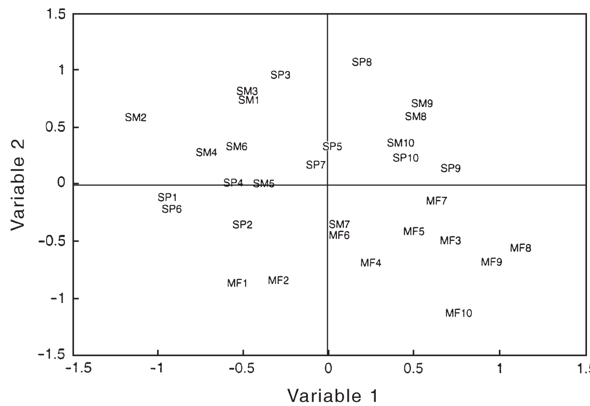

Fig. 3. Ordination (SSH MDS, three dimension, stress = 0.145) of 30 sites (MF, mudflat; SM, native saltmarsh; SP, *Spartina anglica* marsh) based on 18 benthic macroinvertebrate taxa and environmental characteristics from the Little Swanport estuary, Tasmania, during August 1997.

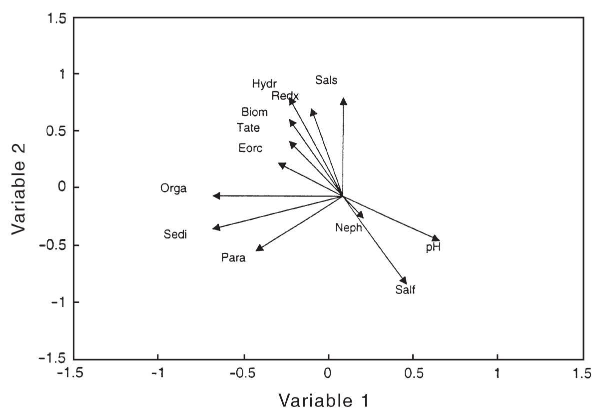

Fig. 4. Benthic macroinvertebrate taxa and environmental characteristics considered to be significantly correlated with the ordination space (see Fig. 3) on the basis of a Monte Carlo test. Salf, *Salinator fragilis*; Sals, *Salinator solida*; Hydr, *Hydrococcus brazieri*; Tate, *Tatea rufilabris*; Eorc, *Eorchestia palustris*; Para, *Paracorophium* sp.; Neph, *Nephtys australiensis*. Biom, root and rhizome biomass; Orga, organic content of sediments; Sedi, modal sediment size.

Table 3. Benthic macroinvertebrate taxa and environmental characteristics significantly correlated with the ordination space on the basis of a Monte Carlo test

Variable	Correlation (*r*)
Hydrococcus brazieri	0.9
Tatea rufilabris	0.82
Eorchestia palustris	0.8
Nephtys australiensis	0.75
Paracorophium sp.	0.67
Salinator solida	0.66
S. fragilis	0.6
Biomass	0.91
Organic matter	0.9
pH	0.76
Redox	0.71
Modal sediment size	0.68

$P < 0.01$. See Fig. 3 for details of ordination.

Ordination (SSH MDS, three dimension, stress = 0.145) of sites based on taxa and environmental characteristics separated mudflat sites from vegetated sites (Fig. 3). Although there is dissimilarity between vegetated sites, distinct differences between native saltmarsh and *S. anglica* sites were not apparent. Sites in Luttrells Bay (sites 8–10) showed some degree of similarity forming two main groups in the right sector of the ordination space: vegetated sites and mudflats. Seven taxa and five environmental characteristics were significantly ($P < 0.01$) correlated with the ordination space on the basis of a Monte Carlo test (Table 3). Figure 4 illustrates these variables as vectors in the same ordination space. Generally, *S. fragilis* and relatively high pH values are associated with mudflat habitat, while *S. solida*, *H. brazieri*, *E. palustris*, *T. rufilabris*, biomass and relatively high redox values are associated with vegetated habitats. Ordination (SSH MDS, three dimension, stress = 0.149) of core samples based on 18 benthic invertebrate taxa and environmental characteristics also separated mudflat from vegetated sites (ordination not shown).

DISCUSSION

With the exception of a pilot project conducted by Hedge (1997, unpublished data), this study provides the first detailed and comprehensive investigation of *S. anglica* impacts to intertidal fauna in Australia. Studies examining the impact of exotic *Spartina* on intertidal fauna in the River Sour, England (Jackson 1985) and Willapa Bay, WA, USA (Luiting *et al.* 1997) have been based on a two-way comparison between invaded mudflats and adjacent uncolonised mudflats. The design of this study, a three-way comparison of mudflat, native saltmarsh and *S. anglica* marsh habitat, appears to be unique.

Results indicate that during the winter in the Little Swanport estuary, species richness and species abundance of benthic macroinvertebrate communities associated with *S. anglica* marsh are significantly different when compared to that of adjacent mudflats. However, differences in species diversity and total abundance of invertebrates between *S. anglica* marsh and native saltmarsh were not statistically significant. Univariate analyses show that species richness, total abundance of invertebrates, crustacean abundance and mollusc abundance were all significantly higher in native saltmarsh and *S. anglica* marsh than in adjacent mudflats. Furthermore, multivariate analyses (ordination and cluster analyses) based on benthic macroinvertebrate taxa and habitat variables consistently separated sites and cores into two main groups: those representing mudflat habitat and those representing vegetated habitat. Thus, the results of this study provide evidence to suggest that the null hypothesis should be rejected in that species richness and species abundance of benthic macroinvertebrates in exotic *S. anglica* marsh does differ significantly when compared with adjacent uninvaded mudflat habitats. However, there are elements of the habitat for which this may not hold true. The study found that there were no significant differences between communities of native saltmarsh and exotic *S. anglica*.

The most abundant and widespread species inhabiting mudflat was *N. australiensis*, with this polychaete present in 95% of mudflat core samples. Other subdominant species, such as *Paracorophium* sp., *S. fragilis* and *A. semen* were patchy in their distribution, occurring in less than 45% of core samples. *Salinator fragilis*, a widespread estuarine mollusc (Edgar 1997), was the only species to occur exclusively in mudflat habitat, all other mudflat species inhabited *S. anglica* marsh. Macroinvertebrate assemblages of native saltmarsh and *S. anglica* marsh showed a remarkable degree of similarity, particularly with regard to abundance of dominant species (e.g. *H. brazieri*, *T. rufilabris*, *E. palustris* and *N. australiensis*). However, the spionid polychaete, *Boccardia* sp. was more abundant in native saltmarsh than in *S. anglica* marsh.

Differences in benthic macroinvertebrate assemblages between habitat types may be attributed to a variety of factors. When *S. anglica* invades mudflat or native saltmarsh, subterranean habitat structure is altered. In the case of mudflats, the presence of dense networks of culms, rhizomes and roots after *Spartina* invasion increases habitat complexity and heterogeneity (Lana & Guiss 1991; Flynn *et al.* 1996). *Spartina* invasion may also alter habitat complexity and heterogeneity of native saltmarshes (Capehart & Hackney 1989). However, our results did not find significant differences in species richness and total abundance of invertebrates between vegetated habitats. Begon *et al.* (1996) point out that increases in spatial heterogeneity may correspond with increases in species richness and effects on species abundance (Pickett & Cadenasso 1995; Begon *et al.* 1996).

Spartina roots and rhizomes can actively contribute to sediment oxygenation, encouraging faunal colonisation (Teal & Wieser 1966; Osenga & Coull 1983; Lana & Guiss 1991). Results of this study show that sediment redox values were significantly higher ($P < 0.05$) in *S. anglica* marsh than adjacent mudflats and that redox and total abundance of invertebrates were positively correlated ($r_s = 0.39$, $P = 0.01$). Thus, higher species richness and invertebrate abundance of macrofaunal communities inhabiting *S. anglica* marsh, relative to those inhabiting mudflats, may be attributed to increases in habitat complexity, spatial heterogeneity and sediment oxygenation resulting from *S. anglica* invasion.

Other factors that may influence macrofaunal assemblages are resource availability and predation pressure. *S. anglica* is a highly productive saltmarsh plant (Long & Mason 1983; Adam 1990). Although studies in the temperate northern hemisphere show that only a small percentage of its biomass is grazed by herbivores (Long & Mason 1983), its contribution to the detrital food web is substantial and may be directly linked to increased secondary production. Chung (1990) and Doody (1990) claim that mudflat and estuarine productivity is increased after *S. anglica* invasion. Furthermore, Lana & Guiss (1991) point out that *S. alterniflora* detritus promotes the abundance of macroinvertebrates. Results of our study show that species abundances of benthic macroinvertebrates inhabiting *S. anglica* marsh are almost six times that of adjacent mudflats. Furthermore, total abundance of invertebrates was positively correlated ($r_s = 0.69$, $P < 0.001$) with the root and rhizome biomass of vegetated sites.

Spartina anglica marsh may also provide a refuge for resident fauna by providing protection from abiotic stresses or predation. For example, the dense aggregation of *S. anglica* culms may provide shade and reduce wind velocities thus mitigating the effects of desiccation on epibenthic fauna. Fish and wader birds are prominent predators on mudflats. Minello & Zimmerman (1983) examined the effects of simulated *Spartina* on predation rates of estuarine fish. They found that vegetative structure reduced predation rates of pinfish, *Lagodon rhomboides*, and Atlantic croaker, *Micropogonias undulatus*. Furthermore, resident and migratory wader birds exert heavy predation pressure on mudflat macroinvertebrate communities (Long & Mason 1983; Reise 1985; Inglis 1995). Reports from Victoria, Australia (Simpson 1995) and England (Evans 1986; Goss-Custard & Moser 1990) state that wader birds avoid *S. anglica* infested mudflats. Thus, invasion of mudflats by *S. anglica* may promote species abundance and species richness of macroinvertebrates by providing a refuge from abiotic stresses and reducing predation pressure.

Comparison with similar studies

In the preceding summer (February 1996) Hedge (1997, unpublished) conducted a similar study on macroinvertebrate communities of *S. anglica* marsh and adjacent mudflats in a nearby region of the Little Swanport estuary. Species richness and total abundance of invertebrates were significantly higher in *S. anglica* marsh. Furthermore, multivariate analyses based on macroinvertebrate taxa of core samples produced two main groupings: cores taken from mudflats and cores taken from *S. anglica* marsh. There are notable differences in macrofaunal assemblages reported by Hedge (1997, unpublished) and the assemblages reported in this study. Seasonal and temporal fluctuations in benthic macrofaunal assemblages are well documented (Reise 1985; Lana & Guiss 1991; Thrush 1991; Edgar & Shaw 1993; Mannino & Montagna 1997; Wilson *et al.* 1999). Higher species richness is likely to have been influenced by increased sampling effort (increased number of core samples).

Research in the UK (Long & Mason 1983; Jackson *et al.* 1985), the USA (Luiting *et al.* 1997) and in Brazil (Lana & Guiss 1991) have compared the structure of benthic invertebrate communities inhabiting mudflat and adjacent vegetated communities. Results from these studies indicate that there are significant differences in species richness and species abundance between habitat types. However, differences are variable between habitats and appear to be strongly influenced by seasonality. Furthermore, when comparing studies of these different regions, the responses of resident faunal assemblages to invasion are inconsistent.

In conclusion, the results of this study provide evidence suggesting that *S. anglica* invasion of mudflat habitat in Little Swanport estuary may significantly promote a more species rich and abundant macrobenthos. Of notable interest, however, was that communities associated with *S. anglica* marsh are remarkably similiar to those associated with native saltmarsh occurring at a similar tidal height. In the light of these results, it is tempting to speculate that *S. anglica* invasion may not necessarily constitute a major ecological threat to Australia's temperate estuaries. However, the results of this study should be considered to be a snapshot only, and due consideration should be made for the temporal and spatial variation that characterizes benthic communities of soft-bottom habitats. Furthermore, this study has only examined a relatively small component of a complex estuarine system. Unfortunately, there are no other known empirical studies examining the effects of *S. anglica* invasion on the flora or fauna of Australia's temperate estuaries.

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