Differences in soft-sediment macrobenthic assemblages invaded by *Caulerpa taxifolia* compared to uninvaded habitats

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ABSTRACT: *Caulerpa taxifolia* is a habitat-forming green alga that has invaded several temperate regions worldwide. Although *C. taxifolia* covers large areas of soft-sediment habitat, little is known about its effects on soft-sediment invertebrate assemblages. We compared soft-sediment macroinvertebrate assemblages in 2 estuaries in southeastern Australia invaded by *C. taxifolia* to examine 2 main predictions: (1) areas covered with *C. taxifolia* will have different assemblages compared to unvegetated sediment because infauna are inhibited but epifauna are facilitated, and (2) areas with *C. taxifolia* will have different assemblages compared to those with native seagrasses (*Halophila ovalis* and *Zostera capricorni*) because infauna are inhibited but epifauna are not. Multidimensional scaling and ANOSIM showed differences in invertebrate assemblages between all habitats. In *C. taxifolia*, infauna were less abundant and epifauna were more abundant compared to unvegetated sediment. However, when compared to native seagrasses, epifauna in *C. taxifolia* were more abundant than in *H. ovalis* in one estuary but less abundant than in *Z. capricorni* in another estuary, while infauna in *C. taxifolia* were less abundant than in both seagrass species. The consistently low infaunal abundance in *C. taxifolia*, irrespective of infaunal feeding mode, suggests *C. taxifolia* impacts infauna generally. Examination of environmental factors potentially responsible for the low abundance of infauna indicated that differences in redox potential (and associated chemical changes) may explain patterns in abundance of infauna among habitats. Our findings indicate that invasion by *C. taxifolia* causes important changes to soft-sediment macroinvertebrate assemblages and suggest that infauna may be particularly vulnerable to invasion because of changes to sediment chemistry.

KEY WORDS: *Caulerpa taxifolia* · Community composition · Ecosystem engineers · Facilitation · Habitat-forming species · Inhibition · Invasion biology · Seagrass

INTRODUCTION

Marine and estuarine habitat-forming invasive species have major effects on native communities. In soft-sediment marine systems, they modify a range of abiotic factors, including water flow, food availability, the deposition of organic material and sediment chemistry, which all have potentially important implications for native fauna (Posey 1988, Chisholm & Moulin 2003, Neira et al. 2005, 2006, Hacker & Dethier 2006). However, their effects on soft-sediment fauna are complex and appear to depend on the habitat invaded (unvegetated vs. native habitat-forming species) and whether fauna live in or above the sediment (infauna vs. epifauna). Compared to unvegetated sediment, habitat-forming invasive species typically have a higher abundance of epifauna, but a

lower abundance of certain infaunal species or functional groups and, consequently, very different faunal assemblages (Crooks 1998, Crooks & Khim 1999, Hedge & Kriwoken 2000, Neira et al. 2005, 2006, Levin et al. 2006). An exception to this general pattern is the invasive seagrass *Zostera japonica*, which had a higher abundance of infauna compared to unvegetated sediment (Posey 1988). Compared to native habitat-forming species, invasive habitat-forming species have a similar abundance of epifauna and infauna, leading to similar faunal assemblages (Hedge & Kriwoken 2000), or assemblages differing in some species or functional groups, which leads to different faunal assemblages (e.g. fewer infaunal surface feeders; Neira et al. 2005, Levin et al. 2006). The reasons why some infauna are negatively affected by habitat-forming invasive species is unresolved, but they may relate to changes to the sediment quality following invasion. For example, sediment pore water sulphides and anoxia have been linked to poor survivorship of infauna beneath invasive *Spartina* spp. (Neira et al. 2006).

Caulerpa taxifolia is a habitat-forming green alga considered one of the worst 100 invasive species in the world (Lowe et al. 2000). It has invaded several temperate regions worldwide where it covers large areas of soft-sediment habitat (Meinesz et al. 2001, Creese et al. 2004, Anderson 2005). *C. taxifolia* spreads rapidly across unvegetated sediment, reaches very high densities, forms a thick, vegetated mat above the sediment (Wright 2005, Wright & Davis 2006) and modifies the chemical and physical properties of sediments and water (Chisholm & Moulin 2003, Gribben et al. 2009). *C. taxifolia* has variable impacts on native seagrass in the Mediterranean (Ceccherelli & Cinelli 1997, Ceccherelli & Sechi 2002), while seagrass beds in southeastern Australia do not appear to be readily invaded (Glasby & Creese 2007). Consequently, invaded estuaries in southeastern Australia may become a mosaic of different habitat-forming macrophytes (invasive *C. taxifolia* and native seagrasses) and unvegetated sediment. Although *C. taxifolia* covers large areas of soft-sediment habitat and fish assemblages differ between *C. taxifolia* and native seagrass (York et al. 2006), with the exception of studies of a dominant estuarine bivalve species in southeastern Australia (Gribben & Wright 2006a,b, Wright et al. 2007, Wright & Gribben 2008, Gribben et al. 2009), little is known about how soft-sediment macroinvertebrates are affected by *C. taxifolia* invasion.

Invasion of estuaries by *Caulerpa taxifolia* may have 2 main impacts on soft-sediment macrobenthic assemblages. First, compared to unvegetated sediment, *C. taxifolia* may have very different assemblages because epifauna are facilitated by the addition of structure, but infauna are inhibited by changes to the sediment. Second, compared to native seagrasses, *C. taxifolia* may have different assemblages, because infauna are inhibited by changes to the sediment even though epifauna are not. We tested our predictions by examining patterns of macrobenthic invertebrate assemblages associated with *C. taxifolia*, 2 seagrass species and unvegetated sediment at sites in 2 estuaries in southeastern Australia. Specifically, we asked the following questions. (1) Do macrobenthic invertebrate assemblages differ among habitats and sites? (2) Do the total species richness, total faunal abundance, epifaunal abundance and infaunal abundance differ among habitats and sites? (3) Does the abundance of different feeding groups differ among habitats and sites? (4) Do environmental characteristics potentially important for fauna (sediment properties and water quality) differ among habitats and sites, and are they correlated with any differences in faunal assemblages?

MATERIALS AND METHODS

Study organisms and locations. In southeastern Australia, *Caulerpa taxifolia* has invaded 14 estuaries since its discovery in 2000. Our study was conducted from May to June 2006 in 2 of these estuaries where *C. taxifolia* is locally abundant (St Georges Basin, 35° 11' S, 150° 36' E, and Burrill Lake, 35° 24' S, 150° 27' E). *C. taxifolia* was first described in Burrill Lake in 2001 and in St Georges Basin in 2004 (Creese et al. 2004). As of June 2006, approximately 0.1 km^2 (<1%) of the soft-sediment benthos of St Georges Basin and approximately 0.5 km^2 (~12%) of the soft-sediment benthos of Burrill Lake were affected by *C. taxifolia*. In St Georges Basin, *C. taxifolia* co-occurs primarily with the seagrass *Halophila ovalis* and unvegetated sediment. In Burrill Lake, *C. taxifolia* co-occurs primarily with the seagrass *Zostera capricorni* while unvegetated sediment only occurred in very small patches (<1 m diameter) at invaded sites and appeared to have been caused by disturbance to *Z. capricorni*. Consequently, we did not sample unvegetated habitat in Burrill Lake. *Z. capricorni* and *H. ovalis* differ in ways that may be important for invertebrate assemblages: *Z. capricorni* has long, densely packed leaves and thick rhizomes, while *H. ovalis* has short leaves and thin rhizomes (Edgar 2000). The greater above- and below-ground biomass of *Z. capricorni* might influence sediment properties or water flow (e.g. Reusch & Williams 1999). In St Georges Basin, *Z. capricorni* was sparse or absent from the sites invaded by *C. taxifolia*.

Sediment properties and water quality. Differences in sediment redox potential, pH and silt fraction among habitats were determined using replicate (N = 5 per habitat and site) sediment cores collected from 1 to 1.5 m water depth at 2 sites in St Georges Basin (Smiths Bay and Pats Bay) and Burrill Lake (Kings

Point and Broadwater). Samples were collected from patches of approximately 100% cover of each habitat at each site. In St Georges Basin, cores were taken to a depth of 20 cm using a stainless steel wedge (dimension of the top of the wedge: 20×10 cm), which gave a vertical profile of the core from which measurements could be taken. Three redox readings were taken per core at profile depths of 0–2, 2–5 and 5–10 cm. We sampled a sediment profile to understand changes in redox potential with sediment depth as this provides insights into changes in chemistry within the sediment. For pH, a single reading was taken between 2 and 5 cm depth as the probe was too large to sample the depth profile. In Burrill Lake, the sediment was a thin layer (~5 cm) overlying very coarse shell grit and the wedge corer could not be pushed in deeply enough to obtain a depth profile. Instead, a shovel was used to carefully scoop up sediment with care taken to ensure the core was kept intact. The presence of the rhizoids or rhizomes maintained the integrity of the profile. Subsequently, both redox potential and pH were only measured once (between 2 and 5 cm depth) in sediment cores from Burrill Lake. Redox potential was measured using a Metrohm AG 9109 Herisau Combined Pt-wire electrode, with an Ag/AgCl reference electrode. The instrument was calibrated using Orion Application Solution ORP Standard 967961, and all redox readings were corrected for $EH_{Ref} = -210 \pm 3$ mV, i.e. reported redox potentials are versus that of the hydrogen electrode, $EH_0 = 0$ mV. A Sensorex Combination pH electrode (450C) with a Rex pH meter (Model pHβ-4) was used for all pH measurements and was calibrated against standardised pH 4 and 7 NIST buffers before use. The electrode was rinsed with deionised water before and after each measurement. Instruments were recalibrated after sampling each habitat (i.e. after 5 replicate cores). The silt fraction in the sediment samples was determined from the top 5 cm of the same cores used to measure redox and pH. Initially, laser diffraction using an x-ray diffraction instrument (Mastersizer, Malvern Instruments) of sediment samples (50 ml) was done. Following this, subsamples (of approximately 1 g) were taken from each sample using thief sampling (Gale & Hoare 1991). Samples were then added to a tap water dispersant and the proportion of silt and clay was determined.

For consistency, water measurements in all habitats were taken between 10 and 15 cm above the sediment. The dissolved oxygen (DO) of water was measured using a YSI 95 DO and temperature microelectrode array, Model No. 95/25 Ft, and water pH, salinity and temperature were measured using a Yeo-Kal multiparameter water instrument, YSI 460 MSD.

Macrobenthic invertebrate assemblages. To compare differences in macrobenthic invertebrate assemblages among habitats, faunal core samples were collected from 1 to 1.5 m water depth using a handheld, stainless steel corer (22 cm diameter, 10 cm length) at the 2 sites in St Georges Basin (Smiths Bay and Pats Bay) and in Burrill Lake (Kings Point and Broadwater). Replicate (N = 10 per habitat) cores were collected from intermingling patches of *Caulerpa taxifolia*, *Halophila ovalis* and unvegetated sediment at both sites in St Georges Basin, and in *C. taxifolia* and *Zostera capricorni* at both sites in Burrill Lake. All cores were collected from patches of approximately 100% cover in the habitat sampled. Core contents were sieved on site through a sieve of 1 mm mesh size. After sieving, all invertebrates were placed into individually labelled Ziplock bags. Samples were fixed in 5% formalin and stored in 70% ethanol for further identification.

Except for polychaetes and some other rare taxa, which were only identified to family level, most invertebrates were identified to species level and counted. Taxa were further defined by (1) whether they were epifaunal or infaunal and (2) their feeding mode (suspension feeders, surface detritus feeders, sub-surface deposit feeders and predators/omnivores; according to Fauchald & Jumars 1979) to analyse potential effects of *Caulerpa taxifolia* invasion on specific functional groups. Although other studies have placed suspension feeders and surface deposit feeders into the same group (Neira et al. 2005, Levin et al. 2006), we analysed these groups separately, as their food sources (i.e. suspended material vs. detritus or microorganisms in the sediment) and feeding functions are different. We also placed *Anadara trapezia* adults and recruits into separate categories for both multivariate analyses and univariate analyses of epifaunal abundance and infaunal abundance, as they change their living arrangements with ontogeny (i.e. postsettlement recruits are epifaunal and adults are infaunal; Gribben & Wright 2006a). This distinction was not made for analysis of species richness.

Statistical analyses. Because different habitats were sampled at each estuary, estuaries were analysed separately. Two-factor analyses of variance (ANOVA) with the factors Habitat (fixed) and Site (random) were used to determine differences in sediment silt fraction, pH and redox. In St Georges Basin, redox potential data for Pats Bay could not be collected due to a malfunctioning probe. Consequently, redox in Smiths Bay was analysed with a 3-factor ANOVA with Habitat (fixed), Block (=core; random) and Sediment depth (fixed). Because there was only 1 replicate of each Habitat × Depth combination within each core, there is no test for the factor block or the interactions including the block factor in this analysis (Quinn & Keough 2002).

Non-metric multidimensional scaling (nMDS; Clarke 1993) was used to illustrate the patterns of variability in macrobenthic invertebrate assemblages in invaded

and native habitats within and between sites. For each estuary, differences in the composition of macrobenthic invertebrate assemblages between habitats and sites were investigated using analysis of similarities (ANOSIM) using the Bray-Curtis measure of similarity (Clarke 1993). Similarity percentage (SIMPER) analysis was used to determine the percentage contribution of each taxon to the Bray-Curtis measure of dissimilarity among habitats within sites, and within the same habitat between sites. We did not consider comparisons of different habitat types between sites to be relevant, so they were not compared. Two-factor ANOVAs (Habitat × Site) were then used to determine differences in the abundance of individual taxa that contributed >75% of the dissimilarities among assemblages in the SIMPER analyses. Two-factor ANOVAs (Habitat × Site) were also used to determine differences in total faunal abundance, species richness, infaunal abundance, epifaunal abundance and the proportional representation of each of the 4 functional groups. We used proportional abundance of each feeding group to understand their relative abundance within assemblages.

For the ANOVAs, data were tested for homogeneity of variance using Cochran's test (Winer 1991) and transformed as appropriate. When transformations did not remove heterogeneity analysis proceeded as ANOVA is robust to deviations from heterogeneity when balanced designs are employed (Quinn & Keough 2002). Tukey's tests were used to assess differences between habitats within sites when interaction terms were significant and when a significant difference was detected between habitats. Non-significant interaction terms in ANOVAs were removed if p > 0.25 (Underwood 1997).

Because anoxia negatively affects many marine invertebrates and sediment redox potential differed among habitats in a reasonably consistent way across sites and estuaries (see 'Results'), correlations were used to explore relationships between redox potential and the 4 major macrobenthic invertebrate indicator categories: total abundance, species richness, infaunal abundance and epifaunal abundance. Because separate cores were used to collect redox potential and invertebrate data, we performed correlations using mean redox values and the invertebrate categories for each habitat at each site (N = 7 habitat means for each analysis).

RESULTS

Sediment properties and water quality

Silt content was higher in areas with *Caulerpa taxifolia* compared to those with seagrass in Smiths Bay

and at both sites in Burrill Lake, although differences were not statistically significant at Kings Point (Fig. 1A, D, Table 1). Silt content did not differ between seagrass and unvegetated sediment in St Georges Basin. Sediment redox potential was extremely reducing in all sediments. Redox potentials were lower in sediment with *C. taxifolia* compared to unvegetated sediments at Smiths Bay in St Georges Basin (Fig. 1B, Table 1) and lower in sediment with *C. taxifolia* compared to sediments with seagrasses in both estuaries (Fig. 1B, E, Table 1). There was no difference in sediment redox between *Halophila ovalis* and unvegetated sediment in Smiths Bay. Sediment pH was relatively neutral across all sites, but was significantly lower in areas with *C. taxifolia* and *H. ovalis* compared to those with unvegetated sediment in Pats Bay (Fig. 1C, Table 1), but not in Smiths Bay. Sediment pH was significantly higher in *C. taxifolia* compared to *H. ovalis* areas in Smiths Bay. All other habitat comparisons within sites in St Georges Basin were non-significant.
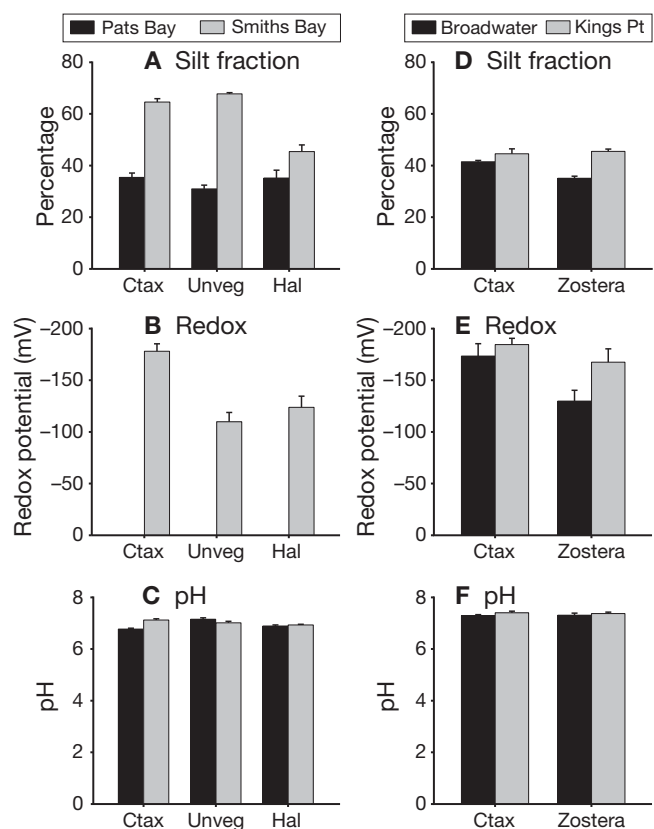

Fig. 1. Mean (±SE) sediment silt fraction, redox and pH (N = 5 habitat^{-1} site^{-1}) in (A to C) *Caulerpa taxifolia* (Ctax), unvegetated sediment (Unveg) and *Halophila ovalis* (Hal) at Pats Bay and Smiths Bay, in St Georges Basin, and (D to F) *C. taxifolia* (Ctax) and *Zostera capricorni* (Zostera) at Broadwater and Kings Point, in Burrill Lake (N = 5 cores habitat^{-1} site^{-1}). There were no data collected for redox potential at Pats Bay due to a malfunctioning probe

Table 1. ANOVAs of sediment silt fraction (SFF), redox potential (Redox) and pH among *Halophila ovalis* (H), unvegetated sediment (U) and *Caulerpa taxifolia* (C) at Smiths Bay (SB) and Pats Bay (PB) in St Georges Basin, and *C. taxifolia* and *Zostera capricorni* (Z) at Broadwater (B) and Kings Point (KP) in Burrill Lake. At St Georges Basin, analysis of redox potential among habitats was only performed on the data from Smiths Bay, as the results for Pats Bay were unreliable due to a malfunctioning redox probe. Interaction terms for which p > 0.25 were removed from analyses. For Redox at Smiths Bay, the main effect block and higher order interactions containing the factor block are not shown (see 'Materials and methods'). Only results of Tukey's tests examining differences between habitats are presented

| —— St Georges Basin —— | | | | —— Burrill Lake —— | | | |
Source	df	*F*	p	Source	df	*F*	p
SFF				**SFF**			
Site (Si)	1	242.3	**<0.001**	Site (Si)	1	36.48	**<0.001**
Habitat (Ha)	2	0.63	0.613	Habitat (Ha)	1	0.57	0.587
Si × Ha	2	23.32	**<0.001**	Si × Ha	1	12.45	**0.003**
Residual	24			Residual	16		
Tukey's; C > H = U (SB); C = H = U (PB)				Tukey's; C > Z (B); C = Z (KP)			
Redox				**Redox**			
Habitat (Ha)	2	11.838	**0.004**	Site (Si)	1	5.92	**0.027**
Depth (D)	2	0.312	0.740	Habitat (Ha)	1	8.96	**0.009**
Residual				Residual	17		
Tukey's; U = H > C (SB)				Tukey's; Z > C			
pH				**pH**			
Site (Si)	1	4.79	**0.0387**	Site (Si)	1	2.85	0.111
Habitat (Ha)	2	0.49	0.6702	Habitat (Ha)	1	1.15	0.299
Si × Ha	2	14.29	**<0.001**	Residual	17		
Residual	24						
Tukey's; U > C = H (PB); C = U, C > H, U = H (SB)							

Generally, habitats in St Georges Basin and Burrill Lake were broadly similar in water quality parameters. Pooled results (means ± SE) across sites were: water pH, 8.0 ± 0.2 in *Caulerpa taxifolia*, 7.8 ± 0.0 in *Halophila ovalis*, 8.0 ± 0.1 in *Zostera capricorni* and 8.1 ± 0.2 in unvegetated sediments; salinity, 30 ± 2 in *C. taxifolia*, 30.4 ± 0.1 in *H. ovalis*, 28 ± 2 in *Z. capricorni* and 30 ± 1 in unvegetated sediments; DO (mg l^{-1}), 13 ± 3 in *C. taxifolia*, 12.4 ± 0.4 in *H. ovalis*, 11 ± 4 in *Z. capricorni* and 13 ± 2 in unvegetated sediments; temperature (°C), 14 ± 1 in *C. taxifolia*, 13.4 ± 0.2 in *H. ovalis*, 13 ± 1 in *Z. capricorni* and 14 ± 1 in unvegetated sediments; and turbidity (NTU), 3 ± 6 in *C. taxifolia*, 4 ± 7 in *Z. capricorni*, below detection in *H. ovalis* and unvegetated sediments.

Macrobenthic invertebrate assemblages

Multivariate comparisons

A total of 28 benthic invertebrate taxa were recorded: 25 taxa at St Georges Basin and 15 taxa at Burrill Lake (Table 2). In both estuaries, nMDS plots indicated differences in invertebrate assemblages between habitats (Fig. 2A,B). In St Georges Basin, all pair-wise ANOSIM analyses showed significant within- and between-site variation in assemblages between habitats (all p < 0.002). Within-site pairwise comparisons showed areas with *Caulerpa taxifolia* and

unvegetated sediment to be most dissimilar (*R* = 0.840 and 0.890 in Smiths Bay and Pats Bay, respectively), while areas with *C. taxifolia* and *Halophila ovalis* were most similar (*R* = 0.252 and 0.433 in Smiths Bay and Pats Bay, respectively). In Burrill Lake, pairwise ANOSIM tests showed significant differences within and between sites (all p < 0.05) in all but 1 case: assemblages in *C. taxifolia* at Broadwater and Kings Point were not significantly different (*R* = 0.043, p = 0.166).

Univariate comparisons

In both estuaries, the epifaunal gastropod *Batillaria australis* contributed most to dissimilarity between assemblages (>55%). The bivalve *Anadara trapezia* (both infaunal adults and epifaunal juveniles) and the epifaunal gastropod *Nassarius burchardi* also contributed significantly to dissimilarities between assemblages. In addition, significant dissimilarities between assemblages occurred in St Georges Basin due to contributions from 3 families of infaunal polychaetes (Cirratulidae, Capitellidae and Maldanidae) and in Burrill Lake due to the infaunal bivalve *Tellina deltoidalis*.

The epifaunal gastropods *Battlaria australis* and *Nassarius burchardi* were significantly more abundant in *Caulerpa taxifolia* areas than in unvegetated sediment, but not in areas with *Halophila ovalis* in St Georges Basin (Table 3). In contrast, infaunal poly-

Table 2. Total abundance and species richness of macrofauna of all taxa in cores sampled from *Caulerpa taxifolia*, unvegetated sediment and *Halophila ovalis* at Pats Bay and Smiths Bay, in St Georges Basin, and *C. taxifolia* and *Zostera capricorni* at Broadwater and Kings Point, in Burrill Lake

| Taxon (species) | Living mode | Trophic group | St Georges Basin — Pats Bay | | | — Smiths Bay | | | Burrill Lake — Broadwater | | – Kings Point | |
			C. tax.	Unveg.	H. oval.	C. tax.	Unveg.	H. oval.	C. tax.	Z. cap.	C. tax.	Z. cap.
Bivalvia												
Arcidae (*Anadara trapezia*)	Infauna	Suspension	28	27	32	18	26	25	4	35	4	12
Arcidae (*Anadara trapezia* recruit)	Epifauna	Suspension	14	0	0	33	0	0	0	2	4	2
Laternulidae (*Laternula marilina*)	Infauna	Suspension	2	2	11	6	0	5	0	0	0	1
Tellinidae (*Tellina deltiodalis*)	Infauna	Deposit	0	0	0	1	2	2	8	39	12	27
Mactridae (*Spisula trigonella*)	Infauna	Suspension	1	1	4	1	2	2	0	0	0	0
Psammobiidae (*Solotellina alba*)	Infauna	Deposit	0	0	0	0	1	2	0	0	0	0
Veneridae (*Tapes watlingi*)	Infauna	Suspension	0	0	1	4	0	0	0	1	0	0
Gastropoda												
Battlariidae (*Battlaria australis*)	Epifauna	Surface detritus	71	1	66	168	7	144	186	283	220	542
Nassariidae (*Nassarius burchadi*)	Epifauna	Surface detritus	19	0	6	23	4	8	22	39	6	16
Muricidae (*Bedeva hanleyi*)	Epifauna	Predator	0	0	1	0	1	1	7	1	2	4
Polychaeta												
Cirratulidae	Infauna	Surface detritus	1	6	20	14	18	70	1	1	0	0
Capitellidae	Infauna	Deposit	0	7	18	8	22	23	0	0	0	0
Maldanidae	Infauna	Suspension	0	17	48	2	5	7	0	0	0	0
Nereididae	Infauna	Predator/Detritus	0	0	0	0	1	1	0	0	0	0
Eunicidae	Epifauna	Predator/Detritus	2	4	2	0	1	7	0	0	0	0
Glyceridae	Infauna	Predator	0	1	2	0	1	1	0	0	0	0
Unidentified	Infauna	Predator	3	0	6	3	4	2	0	1	0	0
Nemertea												
Unidentified	Epifauna	Predator	0	0	0	0	0	1	0	0	0	0
Ascidiacea												
Styelidae (*Styela plicata*)	Epifauna	Suspension	3	0	0	0	0	0	2	1	1	1
Pyuridae (*Pyura stolonifera*)	Epifauna	Suspension	0	0	0	0	1	3	0	1	0	0
Pyuridae (*Microcosmos* c.f. *squamiger*)	Epifauna	Suspension	0	0	0	18	0	0	0	0	0	0
Malacostraca												
Diogenidae (*Diogenes senex*)	Epifauna	Surface detritus	5	1	0	0	0	1	0	0	0	0
Palamonidae (*Palaemon intermedius*)	Epifauna	Suspension	1	0	0	6	0	0	6	5	1	4
Hymenosomatidae (*Amarinus paralacustris*)	Epifauna	Predator/Detritus	0	0	0	3	0	0	0	0	0	0
Grapsidae (*Paragrapsus laevis*)	Epifauna	Predator/Detritus	0	0	0	0	0	0	0	1	0	0
Diogenidae	Infauna	Surface detritus	0	0	0	0	0	0	0	0	0	1
Ampithoidae (*Cymadusa setosa*)	Infauna	Not known	0	0	0	0	0	0	1	0	0	0
Aoridae	Infauna	Not known	0	0	1	0	0	0	0	0	0	0
Species richness			**11**	**11**	**14**	**14**	**15**	**17**	**9**	**12**	**7**	**9**
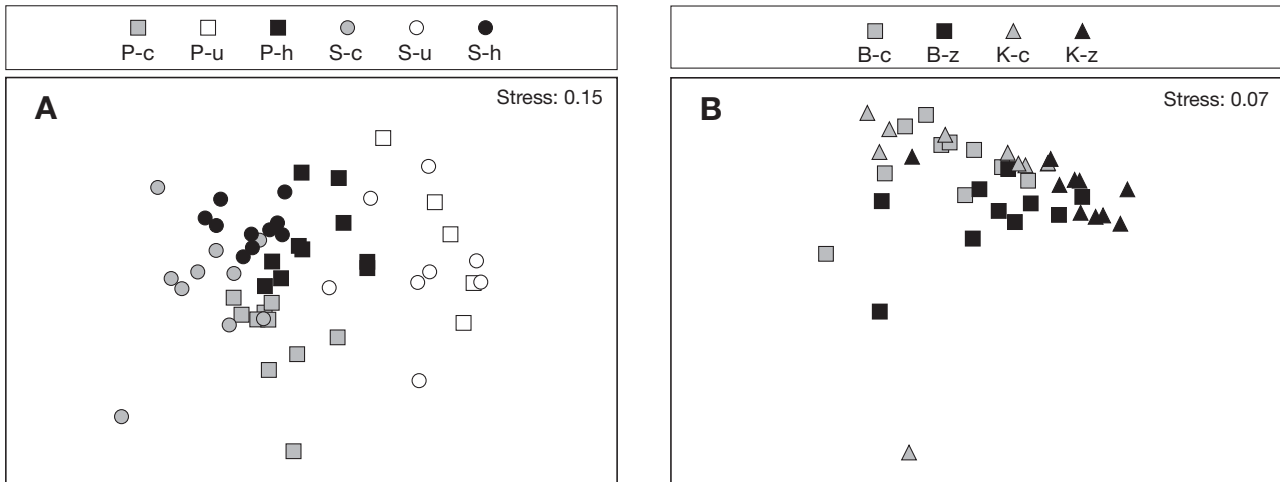
Fig. 2. nMDS plots illustrating patterns of difference of assemblages of invertebrates in different habitats and sites based on Bray-Curtis similarity on untransformed data (N = 10 habitat^{-1} site^{-1}). (A) St Georges Basin. P: Pats Bay site; S: Smiths Bay site; c: *Caulerpa taxifolia*; u: unvegetated sediment; h: *Halophila ovalis*. (B) Burrill Lake. B: Broadwater site; K: Kings Point site; c: *C. taxifolia*; z: *Zostera capricorni*

Table 3. Two-factor ANOVAs for the abundance of the taxa that contributed most to Bray-Curtis dissimilarities among assemblages in *Halophila ovalis* (H), unvegetated sediment (U) and *Caulerpa taxifolia* (C) at Smiths Bay (SB) and Pats Bay (PB) in St Georges Basin, and *C. taxifolia* and *Zostera capricorni* (Z) at Broadwater (B) and Kings Point (KP) in Burrill Lake. Interaction terms for which p > 0.25 were removed from analyses. Only results of Tukey's tests examining differences between habitats are presented

——————St Georges Basin——————				——————Burrill Lake——————			
Source	df	*F*	p	Source	df	*F*	p
Anadara trapezia				***Anadara trapezia***			
Site (Si)	1	2.32	0.1337	Site (Si)	1	4.28	**0.0458**
Habitat (Ha)	2	0.67	0.5183	Habitat (Ha)	1	5.60	0.2546
Residual	54			Si × Ha	1	4.28	**0.0458**
				Residual	36		
				Tukey's; Z > C (B), Z = C (KP)			
Batillaria australis				***Batillaria australis***			
Site (Si)	1	23.27	**<0.001**	Site (Si)	1	10.49	**0.0026**
Habitat (Ha)	1	69.38	**0.0142**	Habitat (Ha)	1	3.47	0.3137
Si × Ha	2	2.18	0.1224	Si × Ha	1	6.19	**0.0176**
Residual	54			Residual	36		
Tukey's; H = C > U				Tukey's; Z > C (KP), Z = C (B)			
Nassarius burchardi				***Nassarius burchardi***			
Site (Si)	1	2.03	0.1601	Site (Si)	1	14.86	**<0.001**
Habitat (Ha)	2	22.53	**<0.001**	Habitat (Ha)	1	6.67	**0.0140**
Residual	54			Residual	36		
Tukey's; H = C > U				Tukey's; Z > C			
***Cirratulid* spp.**				***Tellina deltoidalis***			
Site (Si)	1	19.97	**<0.001**	Site (Si)	1	0.30	0.5894
Habitat (Ha)	2	23.43	**<0.001**	Habitat (Ha)	1	9.81	**0.0034**
Residual	54			Residual	36		
Tukey's; H > U = C				Tukey's; Z > C			
***Capitellid* spp.**							
Site (Si)	1	6.59	**0.0130**				
Habitat (Ha)	2	7.04	**<0.002**				
Residual	54						
Tukey's; H = U > C							
***Maldanid* spp.**							
Site (Si)	1	7.97	**0.0107**				
Habitat (Ha)	1	2.42	0.2926				
Si × Ha	2	4.29	**0.0187**				
Residual	54						
Tukey's; H > U > C (PB), H = U = C (SB)							

chaetes from the families Cirratulidae, Capitellidae and Maldanidae were less abundant in *C. taxifolia* areas compared to unvegetated sediments, although differences were not statistically significant for Cirratulidae (both sites) or Maldanidae (Smiths Bay; Table 3). In Burrill Lake, *B. australis* (Kings Point) and *N. burchardi* were significantly less abundant in areas with *C. taxifolia* compared to those with *Zostera capricorni*, as were the infaunal bivalves *Anadara trapezia* (Broadwater) and *Tellina deltoidalis*.

The total abundance of invertebrates was significantly higher in *Caulerpa taxifolia* and *Halophila ovalis* areas compared to unvegetated sediments, but there was no significant difference in total invertebrate abundances between areas with *C. taxifolia* and *H. ovalis* in St Georges Basin (Fig. 3A, Table 4). In Burrill Lake, total abundance of invertebrates was lower in *C. taxifolia* areas compared to those with *Z. capricorni*, although these differences were not significant (Fig. 3E, Table 4).

Species richness was significantly higher in areas with seagrass compared to those with *Caulerpa taxifolia* in both estuaries and higher in *C. taxifolia* areas compared to unvegetated sediments in St Georges Basin, although differences were not statistically significant (Fig. 3B, F, Table 4). Species richness was also significantly higher in seagrass compared to unvegetated sediments.

Infaunal abundance was significantly lower in *Caulerpa taxifolia* compared to unvegetated sediments in St Georges Basin (Fig. 3C, Table 4). In both estuaries, infaunal abundances were also lower in areas with *C. taxifolia* compared to those with seagrass although, at Kings Point, the difference between *C. taxifolia* and *Zostera capricorni* was not significant (Fig. 3C,G, Table 4). Infaunal polychaetes (St Georges Basin) and bivalves (Burrill Lake) occurred in notably lower densities in *C. taxifolia* areas (Table 2). Infaunal abundance was significantly higher in areas with *Halophila ovalis* compared to unvegetated sediments in St Georges Basin.

Epifaunal abundance was significantly higher in *Caulerpa taxifolia* and *Halophila ovalis* compared to unvegetated sediments, and significantly higher in *C. taxifolia* compared to in *H. ovalis* in St Georges Basin (Fig. 3D, Table 4). Epifaunal *Anadara trapezia* recruits, gastropods and 1 ascidian (at Smiths Bay) showed high abundances in areas with *C. taxifolia* (Table 2). By contrast, in Burrill Lake, epifaunal abundance was lower in *C. taxifolia* compared to *Zostera capricorni* at both sites, although differences were not statistically significant in Broadwater (Fig. 3H, Table 4). Epifaunal gastropods occurred in high abundances in *Z. capricorni*.
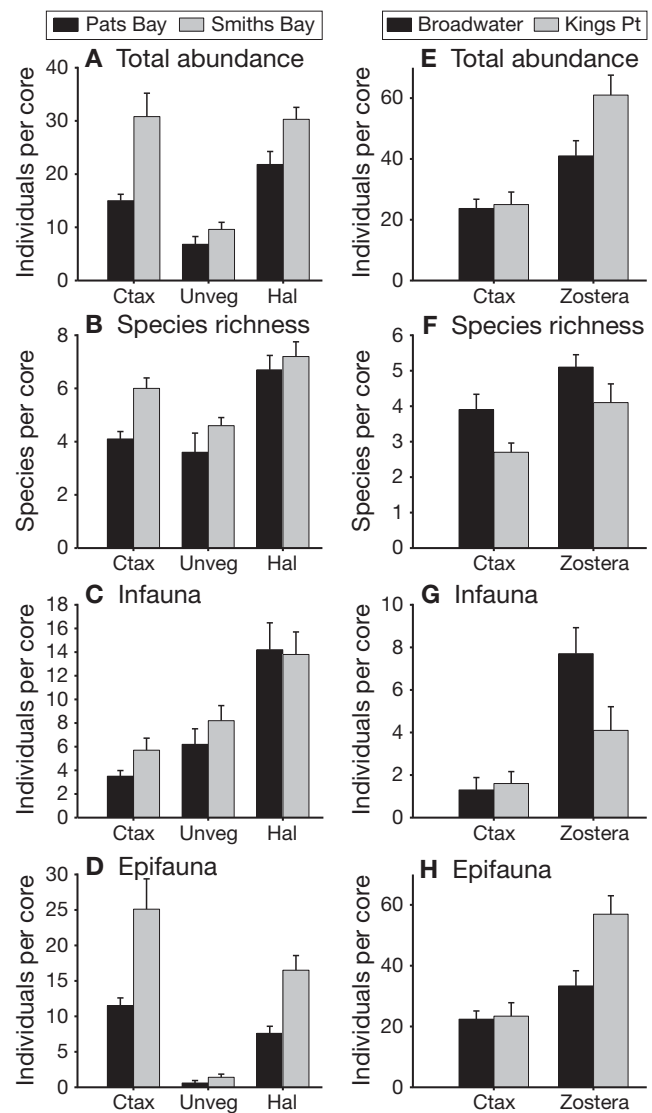

Fig. 3. Mean (±SE) total abundance, species richness, infauna and epifauna core^{-1} in *Caulerpa taxifolia* (Ctax), unvegetated sediment (Unveg) and *Halophila ovalis* (Hal) at Pats Bay and Smiths Bay, in St Georges Basin (A to D), and *C. taxifolia* (Ctax) and *Zostera capricorni* (Zostera) at Broadwater and Kings Point, in Burrill Lake (E to H) (N = 10 cores habitat^{-1} site^{-1})

Functional groups

Surface detritus feeding was the most common feeding mode observed in both estuaries (49.17 and 84.61% of all individuals in St Georges Basin and Burrill Lake, respectively).

The proportion of surface-feeding detritivores was significantly higher in *Caulerpa taxifolia* compared to unvegetated sediments in St Georges Basin (Fig. 4A, Table 5). In contrast, the proportional representations of suspension feeders, sub-surface deposit feeders and predators/omnivores were higher in unvegetated sedi-

Table 4. Two-factor ANOVAs of total abundance, species richness (SR), infaunal abundance and epifaunal abundance in *Halophila ovalis* (H), unvegetated sediment (U) and *Caulerpa taxifolia* (C) at Pats Bay (PB) and Smiths Bay (SB) in St Georges Basin, and unvegetated sediment, *C. taxifolia* and *Zostera capricorni* (Z) at Broadwater (B) and Kings Point (KP) in Burrill Lake. Interaction terms for which p > 0.25 were removed from analyses. Only results of Tukey's tests examining differences between habitats are presented

— St Georges Basin —				— Burrill Lake —			
Source	df	*F*	p	Source	df	*F*	p
Abundance				**Abundance**			
Site (Si)	1	24.14	**<0.001**	Site (Si)	1	4.85	**0.034**
Habitat (Ha)	1	19.02	0.105	Habitat (Ha)	1	8.12	0.215
Si × Ha	2	2.43	**0.032**	Si × Ha	1	3.74	0.061
Residual	54			Residual	36		
Tukey's; C = H > U (PB and SB)							
SR				**SR**			
Site (Si)	1	8.04	**0.006**	Site (Si)	1	7.41	**0.010**
Habitat (Ha)	2	17.58	**<0.001**	Habitat (Ha)	1		**0.003**
Residual	54			Residual	36		
Tukey's; H > C = U (SB and PB)				Tukey's; Z > C (B and KP)			
Infauna				**Infauna**			
Site (Si)	1	2.12	0.151	Site (Si)	1	3.23	0.081
Habitat (Ha)	2	24.67	**<0.001**	Habitat (Ha)	1	5.21	0.263
Residual	54			Si × Ha	1	4.51	**0.041**
Tukey's; U > H > C (SB and PB)				Residual	36		
				Tukey's; Z > C (B) Z = C (KP)			
Epifauna				**Epifauna**			
Site (Si)	1	28.91	**<0.001**	Site (Si)	1	6.83	**0.013**
Habitat (Ha)	2	155.99	**<0.001**	Habitat (Ha)	1	3.86	0.300
Residual	54			Si × Ha	1	5.76	**0.022**
Tukey's; C > H > U (SB and PB)				Residual	36		
				Tukey's; Z > C (KP), Z = C (B)			

ment compared to areas with *C. taxifolia*, although differences between habitats were not significant (Fig. 4B to D, Table 5). Similar non-significant patterns in the proportion of feeding groups were observed between *Halophila ovalis* and unvegetated sediment (Fig. 4A to D, Table 5). In both estuaries, the proportional representations of feeding groups in *C. taxifolia* and seagrasses were very similar (Fig. 4A to H, Table 5).

Habitats/sites with low average redox potential (e.g. the 3 *Caulerpa taxifolia* sites) had a significantly lower average abundance of infauna (Fig. 5). Relationships between redox potential and total abundance, species richness and epifauna were all non-significant (Fig. 5).

DISCUSSION

In line with our predictions, there were very different macroinvertebrate assemblages in areas with *Caulerpa taxifolia*, those with seagrass, and in unvegetated sediments. More specifically, when compared to unvegetated sediment, areas with *C. taxifolia* had a higher abundance of epifauna but a lower abundance of infauna and, when compared to seagrass, *C. taxifolia* areas also had a lower abundance of infauna, but the epifaunal response depended on the seagrass species or possibly the location. Epifaunal taxa were less abundant in areas with *C. taxifolia* compared to *Zostera capricorni*, but were more abundant in *C. taxifolia* compared to *Halophila ovalis* areas. The consistently lower infaunal abundances in *C. taxifolia* compared to those in all other habitats across multiple sites suggests that inhibition of infauna may be a general outcome of invasion by *C. taxifolia*. In contrast, differences in the response of epifaunal taxa suggest that general predictions will be difficult to make because their relative response may depend on the habitat *C. taxifolia* is being compared with (different seagrasses or unvegetated sediments).

The higher total and epifaunal abundance in *Caulerpa taxifolia* (and *Halophila ovalis*) areas compared to unvegetated sediments were due to the numerical dominance of the gastropods *Battlaria australis* and *Nassarius burchardi.* Although we only described patterns, possible mechanisms facilitating epifauna in areas with *C. taxifolia* compared to unvegetated sediments include decreased risk of predation, increased food supply, reduced physical stress and enhanced propagule supply and/or retention (Bruno & Bertness 2001, Rodriguez 2006). The provision of a refuge from predation for fauna associated with invasive macrophytes has been widely reported (Crooks
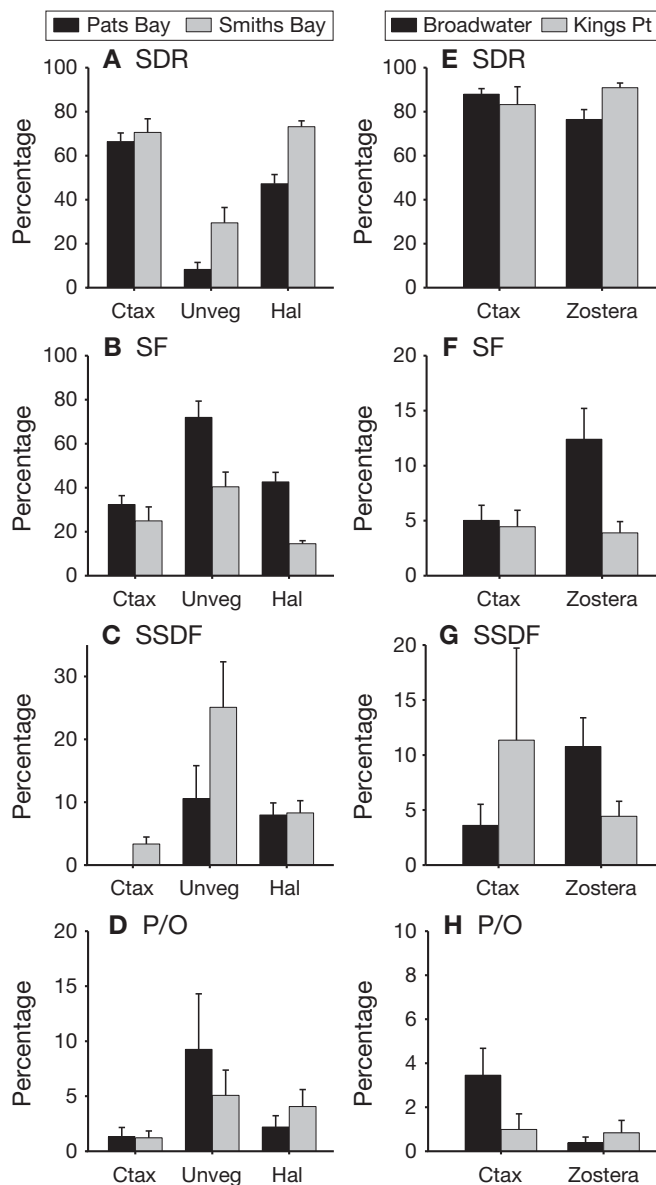
Fig. 4. Mean percentage (±SE) representation of surface detritus feeders (SDR), suspension feeders (SF), sub-surface deposit feeders (SSDF) and predators/omnivores (P/O) core^{-1} in *Caulerpa taxifolia* (Ctax), unvegetated sediment (Unveg) and *Halophila ovalis* (Hal) at Pats Bay and Smiths Bay, in St Georges Basin (A to D), and *C. taxifolia* (Ctax) and *Zostera capricorni* (Zostera) at Broadwater and Kings Point, in Burrill Lake (E to H) (N = 10 cores habitat^{-1} site^{-1})

2002, Rodriguez 2006). Indeed, Gribben & Wright (2006a) found that *C. taxifolia* provided a refuge from predation for *Anadara trapezia* recruits. Alternatively, increased detrital food supply following invasion may be important. For example, invasion of a *Spartina*-hybrid to an unvegetated tidal flat has positive effects on sub-surface deposit feeders that use *Spartina* detritus as a food resource (Neira et al. 2005, Levin et al.

2006). The relative importance of decreased predation or increased food supply may vary depending on the facilitated epifaunal species: increased detritus may be important for the epifaunal gastropods *B. australis* and *N. burchardi*, but not for *A. trapezia* recruits.

Differences in epifaunal abundance between *Caulerpa taxifolia* and native seagrasses also appeared to be driven by the relatively high abundance of the gastropods *Battlaria australis* and *Nassarius burchadi* in areas with *C. taxifolia* compared to those with *Halophila ovalis*, and a lower abundance of these 2 species in *C. taxifolia* compared to *Zostera capricorni* areas. Although we cannot directly compare epifaunal abundances between *H. ovalis* and *Z. capricorni* in the different estuaries, these differences may be related to differences in structural complexity or above- and below-ground biomass between the 2 seagrass species, both of which could influence predation and detrital food supply (Bruno & Bertness 2001, Williams & Heck 2001). However, whether differences in epifaunal abundance between native seagrasses and *C. taxifolia* are related to differences in traits of the seagrasses or simply reflect differences between estuaries unrelated to seagrass species remains to be determined. For example, a potentially important factor not taken into account by our sampling is the amount of time *C. taxifolia* has been present at the different sites (5 yr at Burrill Lake vs. 2 yr at St Georges Basin). However, given that the traits of ecosystem engineers can have strong effects on facilitation (Bruno & Bertness 2001, Gutierrez et al. 2003), and the mean abundance of epifauna in *C. taxifolia* was similar at 3 out of the 4 sites (Fig. 3), differences in traits between the seagrass species may explain the observed patterns of epifaunal abundance.

Despite the lower infaunal abundance in *Caulerpa taxifolia* areas compared to both unvegetated sediments and native seagrasses, there was no effect of habitat on the proportional representation of different infaunal functional groups (suspension feeders and sub-surface deposit feeders). This finding suggests that any impacts of *C. taxifolia* on infauna may not be restricted to specific functional groups, but may affect infauna generally. Indeed, the abundance of most polychaete and bivalve taxa were lower in areas with *C. taxifolia* compared to unvegetated sediments and habitats with native seagrasses in both estuaries, irrespective of feeding mode — even detritus- and/or deposit-feeding infauna (Cirratulidae and *Tellina*) occurred at lower abundances. Levin et al. (2006) and Neira et al. (2005) found lower abundances of surface-feeders, but no difference in sub-surface deposit feeders in sediments underlying the invasive *Spartina*-hybrid compared to nearby unvegetated tidal flats.

Table 5. Two-factor ANOVAs of mean percentage representation of surface detritus feeders (SDR), suspension feeders (SF), sub-surface deposit feeders (SSDF) and predators/omnivores (P/O) among *Halophila ovalis* (H), unvegetated sediment (U), *Caulerpa taxifolia* (C) at Pats Bay (PB) and Smiths Bay (SB) in St Georges Basin, and unvegetated sediment, *C. taxifolia* and *Zostera capricorni* (Z) at Broadwater (B) and Kings Point (KP) in Burrill Lake. Interaction terms for which p > 0.25 were removed from analyses. Only results of Tukey's tests examining differences between habitats are presented

| —— St Georges Basin ——				—— Burrill Lake ——			
Source	df	*F*	p	Source	df	*F*	p
SDR				**SDR**			
Site (Si)	1	19.29	**<0.001**	Site (Si)	1	0.04	0.841
Habitat (Ha)	2	21.71	**0.044**	Habitat (Ha)	1	0.01	0.947
Si × Ha	2	2.86	0.066	Si × Ha	1	2.85	0.100
Residual	54			Residual	36		
Tukey's; C = H > U							
SF				**SF**			
Site (Si)	1	25.44	**<0.001**	Site (Si)	1	6.02	**0.019**
Habitat (Ha)	2	5.98	0.143	Habitat (Ha)	1	0.97	0.505
Si × Ha	2	2.87	0.065	Si × Ha	1	3.40	0.074
Residual	54			Residual	36		
SSDF				**SSDF**			
Site (Si)	1	9.05	**0.004**	Site (Si)	1	0.41	0.528
Habitat (Ha)	2	5.81	0.147	Habitat (Ha)	1	0.98	0.503
Si × Ha	2	1.64	0.203	Si × Ha	1	3.58	0.067
Residual	54			Residual	36		
P/O				**P/O**			
Site (Si)	1	0.23	0.636	Site (Si)	1	1.71	0.199
Habitat (Ha)	2	1.99	0.147	Habitat (Ha)	1	1.09	0.486
Residual	54			Si × Ha	1	3.26	0.080
				Residual	36		
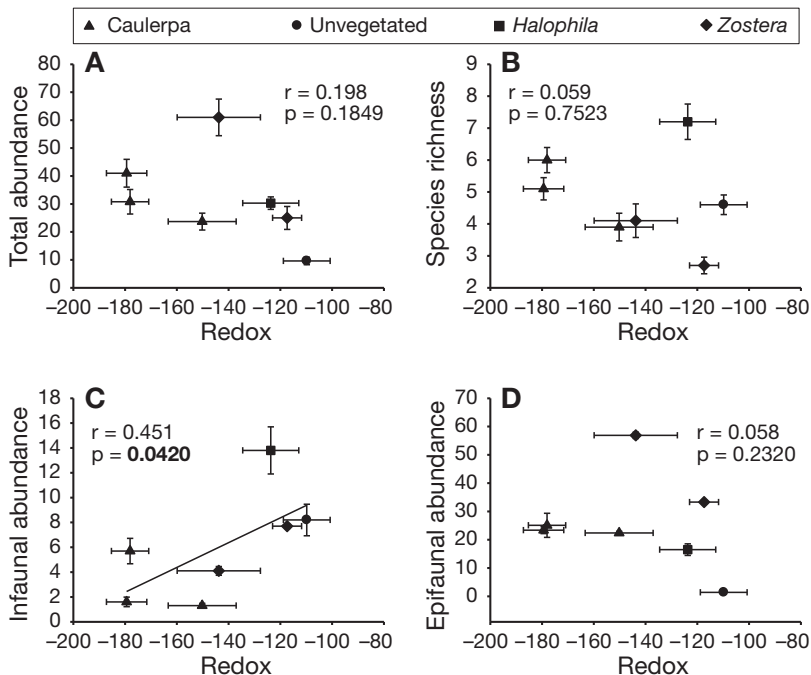
Fig. 5. Correlations between mean redox potential and mean (A) total invertebrate abundance, (B) species richness, (C) infaunal abundance and (D) epifaunal abundance per core in all habitats sampled at Smiths Bay, in St Georges Basin, and Broadwater and Kings Point, in Burrill Lake

The lower densities of infauna in *Caulerpa taxifolia* may be related to changes in environmental characteristics following invasion. In the present study, redox potential varied consistently among habitats (i.e. unvegetated > *Halophila* ovalis > *C. taxifolia*, *Zostera capricorni* > *C. taxifolia*), and the correlation between mean redox potential and mean infaunal abundance indicated that redox potential may be a strong structuring force among habitats at large spatial scales. Anoxia or hypoxia, resulting from reduced redox potential, has demonstrated negative effects on infauna (Shumway & Scott 1993, Laudien et al. 2002). Neira et al. (2006) showed that reduced water flow associated with the establishment of hybrid *Spartina* patches promoted the deposition of fine-grained, organic-rich sediments, which resulted in an increase in pore water sulfur and anoxia. Reduced flow, increased anoxia and increased levels of hydrogen sulphide (Chisholm & Moulin 2003, Gribben et al. 2009) have

also been recorded in *C. taxifolia* habitats compared to unvegetated sediments. In addition, low DO in the water column within the *C. taxifolia* canopy compared to unvegetated sediments (Gribben et al. 2009) may also contribute to the low abundance of surface-feeding infauna. The reasons for differences in infaunal composition between *C. taxifolia* and native seagrasses are less clear, but may also be linked to differences in anoxia, hydrogen sulphide, or the degree of structural complexity of *C. taxifolia* habitats versus seagrasses and its subsequent effects on flow regimes, sediment quality, DO and food supply. The mechanisms of how *C. taxifolia* and other habitat-forming invasive species affect infauna remain to be determined experimentally.

Despite the differences in community structure among habitats, the total abundance, species richness, and abundance of infauna and epifauna in *Caulerpa taxifolia* areas were very similar across sites and estuaries (Fig. 2). Multivariate analyses also indicated no differences in assemblages within *C. taxifolia* habitats between sites in Burrill Lake and the lowest differences for assemblages in *C. taxifolia* habitats between sites in St Georges Basin. Neira et al. (2005) present similar data, showing a reasonably consistent number of individuals and species per core in *Spartina*-hybrids at different sites, despite large differences in the same parameters in uninvaded habitats between sites. Homogenisation of communities in soft-sediment marine habitat-forming invasive species across large spatial scales may result from the strong consistent effects that these species have on environmental factors such as water flow and sediment quality. The potential effect of habitat-forming invasive species in decreasing ecological variation in assemblages at large scales is an important avenue for future research.

Our findings are consistent with invasion by *Caulerpa taxifolia* causing important changes in soft-sediment macroinvertebrate assemblages. The low abundance of infauna compared to that in unvegetated sediment and native vegetated habitats is similar to results for several other habitat-forming invasive species of soft sediments (Neira et al. 2005, Levin et al. 2006), although other species show positive effects on infaunal abundance (Posey 1988). Thus, generalisations about changes associated with the invasion of marine habitat-forming species may be difficult to make. Overall, our conclusions are tempered, as we have no information on macrofaunal assemblages at these sites before the invasion of *C. taxifolia*, nor have we determined effects using manipulative experiments. We have simply described patterns inside and outside of invaded areas. Future work should focus on experimental manipulations of *C. taxifolia* to deter-

mine if it is indeed causing the observed changes in macrofaunal assemblages. Moreover, manipulations of abiotic factors potentially affecting macroinvertebrate survivorship (sediment properties, water quality, food supply, larval supply and predator activity) will be important in identifying mechanisms causing impacts (e.g. Neira et al. 2006).

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