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Justin G. McKinnon
University of Wollongong

Paul E. Gribben
University of New South Wales

Andrew R. Davis
University of Wollongong, andy_davis@uow.edu.au

Dianne F. Jolley
University of Wollongong, djolley@uow.edu.au

Jeffrey T. Wright
University of Wollongong, jeffw@uow.edu.au

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

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.

Keywords

Differences, soft, sediment, macrobenthic, assemblages, invaded, Caulerpa, taxifolia, compared, uninvaded, habitats

Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

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DIFFERENCES IN SOFT-SEDIMENT MACROBENTHIC ASSEMBLAGES INVADED BY *CAULERPA TAXIFOLIA* COMPARED TO UNINVADED HABITATS

Running head: Macrofaunal assemblages associated with *Caulerpa taxifolia*

Justin G. McKinnon[1], Paul E. Gribben[2, 3], Andrew R. Davis[1], Dianne F. Jolley[4] and Jeffrey T. Wright[1,5 *]

[1] Institute for Conservation Biology and School of Biological Sciences, University of Wollongong, Wollongong 2522, Australia

[2] Centre for Marine Biofouling and Bio-Innovation and School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney 2052, Australia

[3] Present Address: Institute of Water and Environmental Management, and Department of Environmental Sciences, University of Technology, Sydney, 2007, Australia

[4] GeoQuest, School of Chemistry, University of Wollongong, Wollongong 2522, Australia

[5] Present address: National Centre for Marine Conservation and Resource Sustainability, Australian Maritime College, The University of Tasmania, P.O. Box 986, 7250, Launceston, Australia

[*]Corresponding Author, Email: jeff.wright@amc.edu.au

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 there is little known about its effects on soft-sediment invertebrate assemblages. We compared soft-sediment macroinvertebrate assemblages in estuaries in southeastern Australia invaded by *C. taxifolia* to examine two main predictions: (1) *C. taxifolia* will have very different assemblages compared to unvegetated sediment because infauna are inhibited but epifauna are facilitated and, (2) *C. taxifolia* will have different assemblages compared to 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 seagrass, in *C. taxifolia* epifauna were more abundant than in *H. ovalis* but less abundant than in *Z. capricorni* 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 are consistent with invasion by *C. taxifolia* causing 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 organics and sediment chemistry which all have potentially important implications for native fauna (Posey 1988, Chisholm and 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 and consequently, similar faunal assemblages (Hedge & Kriwoken 2000) or assemblages differing in some species or functional groups and consequently different faunal assemblages (e. g. fewer infaunal surface feeders; Levin et al. 2006, Neira et al. 2005). The reasons why some infauna are negatively affected by habitat-forming invasive species is unresolved but it 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* (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 & Davies 2006) and modifies chemical and physical sediment properties (Chisholm and Moulin 2003, Gribben et al. In press). *C. taxifolia* outperforms native seagrasses in the Mediterranean (Ceccherelli & Cinelli 1997), although seagrass beds in southeastern Australia do not appear to be readily invaded (Glasby and 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 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 and Gribben 2008, Gribben et al. In press) there is little known about how soft-sediment macroinvertebrate assemblages are affected by *C. taxifolia* invasion.

In estuaries invaded by *C. taxifolia* in southeastern Australia there may be two main predictions of its impact. First, compared to unvegetated sediment *C. taxifolia* will 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* will have different assemblages because infauna are inhibited by changes to the sediment even though epifauna are not. However, there may be some similarities between *C. taxifolia* and seagrasses if they are functionally similar or indeed, there may be stronger differences than expected, if epifauna (e.g. herbivores, Gollan and Wright 2006) are also inhibited. We tested our predictions by examining patterns of macrobenthic invertebrate assemblages associated with *C. taxifolia*, two seagrass species and unvegetated sediment at sites in two estuaries in southeastern Australia. Specifically, we asked the following questions. 1) Do macrobenthic invertebrate assemblages differ among habitats and sites? 2) Does 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?

METHODS

Study Organisms and locations

In southeastern Australia, *C. taxifolia* has invaded 14 estuaries since its discovery in 2000. Our study was conducted from May to June 2006 in two of these estuaries where *C. taxifolia* is locally abundant (St Georges Basin, 150°36'E 35°11'S, and Burrill Lake 150°27'E 35°24'S). *C. taxifolia* was first described in Burrill Lake in 2001 and 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 was 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*; unvegetated sediment only occurred as very small patches (< 1 m diam.) at invaded sites and appeared to have been caused by disturbance to vegetated native habitat. Consequently, we did not sample unvegetated habitat in Burrill Lake. *Zostera capricorni* and *H. ovalis* differ in ways that may be important for invertebrate assemblages. *Z. capricorni* has long densely packed leaves and thick rhizomes compared to *H. ovalis* which 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

To investigate differences in sediment redox potential, pH and silt fraction among habitats, replicate (N=5/habitat/site) sediment cores were collected from 1-5m water depth at each site in each estuary. Samples were collected from patches of approximately 100% cover in the habitat sampled. In St Georges Basin, cores were taken to a depth of 20 cm using a stainless steel wedge (dimensions of top of wedge: 20 x 10 cm) which gave a vertical profile of the core from which measurements could be taken. We sampled a sediment profile to understand changes in redox potential with sediment depth. Three redox readings were taken per core at profile depths of 0-2 cm, 2-5 cm and 5-10 cm. For pH, a single reading was taken between 2-5 cm depth as the probe did not allow resolution at smaller scales. In Burrill Lake, the wedge could not be used as the sediment was a thin layer (~ 5 cm) overlying very coarse shell grit and the 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, in sediment cores from Burrill Lake both redox potential and pH were only measured once (between 2-5 cm depth). Redox potential was measured using a Metrohm AG 9109 Herisau Combined Pt-wire electrode with Ag/AgCl reference electrode. The instrument was calibrated using Orion Application Solution ORP Standard 967961 and all redox readings corrected for $EH_{Ref} = -210 \pm 3$ mV, i. e. reported redox potentials are versus 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 five replicate cores). Silt fraction in the sediment samples was determined from the top 5cm from the same cores used to measure redox and pH. Initially laser diffraction using an X-ray Diffraction instrument (Mastersizer, Malvern Instruments Inc) of sediment samples (50 mL) was done. Following this, sub-samples (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 determined.

Water dissolved oxygen (DO) was measured using a YSI 95 DO and Temperature Microelectrode Array Model #95/25 Ft and all other water quality parameters measured using a Yeo-Kal multiparameter water instrument, YSI 460 MSD. For consistency, water measurements in all habitats were taken between 10 and 15cm above the sediment.

Macrobenthic invertebrate assemblages

To compare differences in macrobenthic invertebrate assemblages among habitats within estuaries, faunal core samples were collected from 1-1.5 m water depth using a handheld, stainless steel corer (22 cm diam. x 10 cm deep) from two sites in both St Georges Basin (Smiths Bay and Pats Bay) and Burrill Lake (Kings Point and Broadwater). Replicate (N=10 per habitat) cores were collected from intermingling patches in *C. taxifolia, H. ovalis* and unvegetated sediment at both sites in St Georges Basin, and *C. taxifolia* and *Z. 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 1 mm sieve. 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.

Most invertebrates were identified to species level, except for polychaetes and some other rare taxa, which were only identified to family, and counted. Taxa were further defined by (1) whether they were epifauna or infauna 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 *C. 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 source (i.e. suspended material vs. detritus or microorganisms in the sediment), and feeding function 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 arrangement with ontogeny (i.e. post-settlement recruits are epifaunal and adults are infaunal, Gribben & Wright 2006a, Wright et al. 2007). 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 is only one replicate of each habitat x depth combination within each core there is no test for the factor block and interactions including the block factor in this analysis (Quinn and Keough 2002).

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 between the same habitat between sites. We did not consider comparisons of different habitat types between sites relevant so they were not compared. Two-factor ANOVAs (habitat x 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 x 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 four functional groups. We used proportional abundance of each feeding group to understand their relative abundance within assemblages.

For 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 ANOVAs are robust to deviations from heterogeneity when balanced designs are employed (Quinn & Keough 2002). Tukey's tests were used to assess for 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 four 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 values of redox and the invertebrate categories for each habitat at each site (n=7 habitat means for each analyses).

RESULTS

Sediment properties and water quality

Silt content was higher in *C. taxifolia* compared to seagrass in Smiths Bay and at both sites in Burrill Lake, although differences were not statistically significant in 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 *C. taxifolia* compared to unvegetated sediment at Smiths Bay in St Georges Basin (Fig. 1B; Table 1) and lower in *C. taxifolia* compared seagrasses in both estuaries (Fig. 1B, E; Table 1). There was no difference between *H. ovalis* and unvegetated sediment in Smiths Bay. Sediment pH was relatively neutral across all sites but was significantly lower in *C. taxifolia* and *H. ovalis* compared to unvegetated sediment in Pats Bay (Fig. 1C; Table 1), but not at Smiths Bay. Sediment pH was significantly higher in *C. taxifolia* compared to *H. ovalis* in Smiths Bay. All other habitat comparisons within sites in St Georges Basin were non-significant.

Generally, habitats in St Georges Basin and Burrill Lake were broadly similar in water quality parameters. Pooled results across sites were: water pH (mean ± SE, 8.0 ± 0.2 in *C. taxifolia*, 7.8 ± 0.0 in *H. ovalis*, 8.0 ± 0.1 in *Z. capricorni,* and 8.1 ± 0.2 in unvegetated); salinity (ppt: mean ± SE, 30 ± 2 in *C. taxifolia*, 30.4 ± 0.1 in *H. ovalis*, 28 ± 2 in *Z. capricorni* and 30 ± 1 in unvegetated); DO (mg/L: mean ± SE, 13 ± 3 in *C. taxifolia*, 12.4 ± 0.4 in *H. ovalis*, 11 ± 4 in *Z. capricorni*, and 13 ± 2 in unvegetated); temperature (°C: mean ± SE, 14 ± 1 in *C. taxifolia*, 13.4 ± 0.2 in *H. ovalis*, 13 ± 1 in *Z. capricorni* and 14 ± 1 in unvegetated);

and turbidity (NTU: mean ± SE, 3 ± 6 in *C. taxifolia*, 4 ± 7 in *Z. capricorni*, below detection in *H. ovalis* and unvegetated).

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 pair wise comparisons between *C. taxifolia* and unvegetated sediment were most dissimilar ($R=0.840$ and 0.890 in Smiths Bay and Pat's Bay, respectively) while within-site pair wise comparisons between *C. taxifolia* and *H. ovalis* were most similar ($R=0.252$ and 0.433 in Smiths Bay and Pat's Bay, respectively). In Burrill Lake, pair wise ANOSIM tests were significantly different within and between sites (all $P<0.05$) in all but one 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 *A. 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 three families of infaunal polychaete (Cirratulidae, Capitellidae and Maldanidae) and in Burrill Lake due to the infaunal bivalve *Tellina deltoidalis*.

The epifaunal gastropods, *B. australis* and *N. burchardi* were significantly more abundant in *C. taxifolia* than unvegetated sediment but not *H. ovalis* in St Georges Basin (Table 3). In contrast, the infaunal polychaetes; Cirratulidae, Capitellidae and Maldanidae were less abundant in *C. taxifolia* compared to unvegetated sediment, although differences were not statistically significant for Cirratulidae (both sites) and Maldanidae (Smiths Bay, Table 3). In Burrill Lake, *B. australis* (Kings Point) and *N. burchardi* were significantly less abundant in *C. taxifolia* compared to *Z. capricorni* as were the infaunal bivalves *A. trapezia* (Broadwater) and *T. deltoidalis*.

The total abundance of invertebrates was significantly higher in *C. taxifolia* and *H. ovalis* compared to unvegetated sediment but there was no significant difference in total abundance between *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* compared to *Z. capricorni,* although these differences were not significant (Fig. 3E; Table 4).

Species richness was significantly higher in seagrass compared to *C. taxifolia* in both estuaries and higher in *C. taxifolia* compared to unvegetated sediment 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 sediment.

Infaunal abundance was significantly lower in *C. taxifolia* compared to unvegetated sediment in St Georges Basin (Fig. 3C; Table 4). In both estuaries infaunal abundance was also lower in *C. taxifolia* compared to seagrass, although at Kings Point the difference between *C. taxifolia* and *Z. capricorni* was not significant (Fig. 3C, G; Table 4). Infaunal polychaetes (St Georges Basin) and bivalves (Burrill Lake) were the species at notably lower densities in *C. taxifolia*. Infaunal abundance was significantly higher in *H. ovalis* compared to unvegetated sediment in St Georges Basin.

Epifaunal abundance was significantly higher in *C. taxifolia* and *H. ovalis* compared to unvegetated sediments, and significantly higher in *C. taxifolia* compared to *H. ovalis* in St Georges Basin (Fig. 3D; Table 4). Epifaunal *A. trapezia* recruits, gastropods and one ascidian (at Smiths Bay) were the species at high abundance in *C. taxifolia*. By contrast, in Burrill Lake, epifaunal abundance was lower in *C. taxifolia* compared *Z. capricorni* at both sites although differences were not statistically significant in Broadwater (Fig. 3H; Table 4). Epifaunal gastropods were the species at high abundance in *Z. capricorni*. There was a significant difference between sites at St. Georges Basin.

Functional groups

Surface detritus feeding was the most abundant 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 *C. taxifolia* compared to unvegetated sediment in St Georges Basin (Fig. 4A; Table 5). In contrast, the proportional representation of suspension feeders, sub-surface deposit feeders, and predators/omnivores were higher in unvegetated sediment compared to *C. taxifolia*, although differences between habitats were not significant (Fig. 4B-F; Table 5). Similar patterns of lower but non-significant differences between habitats were observed in the proportion of feeding groups between the seagrass *H. ovalis* and unvegetated sediment (Fig. 4B-D; Table 5). In both estuaries, the proportional representation of feeding groups in *C. taxifolia* and seagrasses were very similar (Fig. 4A-H; Table 5).

Habitats/sites with low average redox potential (e.g. the three *C. 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 *C. taxifolia*, seagrass and unvegetated sediment. More specifically, when compared to unvegetated sediment, *C. taxifolia* had a higher abundance of epifauna but a lower abundance of infauna and when compared to seagrass, *C. taxifolia* also had a lower abundance of infauna but the epifaunal response depended on seagrass species. Epifauna were less abundant in *C. taxifolia* compared to *Z. capricorni* but more abundant in *C. taxifolia* compared to *H. ovalis*. The consistently lower infaunal abundance in *C. taxifolia* compared to all 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 epifauna suggests that general predictions for them will be difficult to make because their response depends on the habitat they invade (vegetated or unvegetated sediment) and native seagrass species.

The higher total and epifaunal abundance in *C. taxifolia* (and *H. ovalis*) compared to unvegetated sediment were due to the numerical dominance of the gastropods *B. australis* and *N. burchardi.* Although we only described patterns, possible mechanisms facilitating epifauna in *C. taxifolia* compared to unvegetated sediment include decreased 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 is widely reported (Crooks 2002, Rodriguez 2006). Indeed, Gribben and Wright (2006a) found that *C. taxifolia* provided a refuge from predation for *A. trapezia* recruits. Alternatively, increased detrital food supply following invasion may be important. For example, invasion of a macroalga to sand flats appears responsible for a greater abundance of an epifaunal gastropod (Bolam & Fernandes 2002) and the invasion of *Spartina*-hybrid to an unvegetated tidal flat has positive effects on sub-surface deposit feeders which 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 *A. trapezia* recruits.

Differences in epifaunal abundance between *C. taxifolia* and native seagrass also appeared driven by the relatively high abundance of the gastropods, *B. australis* and *N. burchadi* in *C. taxifolia* vs. *H. ovalis*, and a lower abundance of these two species in *C. taxifolia* vs. *Z. capricorni*. Although we cannot directly compare epifaunal abundances between *H. ovalis* and *Z. capricorni* in the different estuaries, these differences may be related to differences between the two seagrass species in structural complexity or above and below-ground biomass, 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 greater time *C. taxifolia* has been present at sites (five years at Burrill Lake vs. two years 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 three out of the four sites (Fig. 2), differences in traits between the seagrass species may explain the observed patterns of epifaunal abundance.

Despite the lower infaunal abundance in *C. taxifolia* compared to both unvegetated sediment and seagrass, 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 affect infauna generally. Indeed, the abundance of most polychaete and bivalve taxa was lower in *C. taxifolia* compared to unvegetated and native seagrass habitats in both estuaries irrespective of feeding mode – even detritus and/or deposit feeding infauna (Cirratulidae and *Tellina*) were at lower abundance. 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.

The lower densities of infauna in *C. taxifolia* may be related to changes in environmental characteristics following invasion. In our study, redox potential varied consistently among habitats (i.e. unvegetated > *H.* ovalis > *C. taxifolia*, *Z. capricorni* > *C. taxifolia*) and the correlation between mean redox potential and mean infaunal abundance indicated that redox 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 1983, Laudian 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 (Gribben et al. In press) and increased levels of H_2S (Chishlom & Moulin 2003) have also been recorded in *C. taxifolia* compared to unvegetated sediment. Low dissolved oxygen within *C. taxifolia* compared to unvegetated sediment (Wright et al. In review) may also contribute to the low abundance of surface feeding infauna. The reasons for differences in infaunal composition between *C. taxifolia* and native seagrasses in this study are less clear but may also be linked to differences in anoxia, sulphur or the degree of structural complexity of *C. taxifolia* vs. seagrasses and its subsequent effects on flow regimes, dissolved oxygen and food supply. The mechanisms of impact on infauna by *C. taxifolia* and other habitat-forming invasive species 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 *C. taxifolia* were very similar across sites and estuaries (Fig. 2). Multivariate analyses also indicated no difference in assemblages in *C. taxifolia* between sites in Burrill Lake and the lowest difference for assemblages in *C. taxifolia* 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*-hybrid 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 *C. taxifolia* causing important changes to soft-sediment macroinvertebrate assemblages. The low abundance of infauna compared to unvegetated sediment and native vegetated habitats is similar to results for several other habitat-forming invasive species into soft-sediments (Levin et al. 2006, Neira et al. 2005) although other species show weak or positive effects on infaunal abundance (Posey 1988, Hedge & Kriwoken 2000). Thus, generalisations about changes associated with invasion of marine habitat-forming species may be difficult to make. Overall, our conclusions are tempered as we have no information on 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 determine if it is indeed causing the observed changes in 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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LITERATURE CITED

Anderson LW (2005) California's reaction to *Caulerpa taxifolia*: a model for invasive species rapid response. Biol Inv 7:1003-1006

Bolam SG, Fernandes TF (2002) The effects of macroalgal cover on the spatial distribution of macrobenthic invertebrates: The effect of macroalgal morphology. Hydrobiologia 475/476:437-448

Bruno JF, Bertness MD (2001) Habitat modification and facilitation in benthic marine communities. In: Bertness M, Gaines S, Hay M (eds) Marine Community Ecology. Sinuaer Associates Inc, Sunderland, Massachusetts, p 201-218

Ceccherelli G, Cinelli F (1997) Short-term effects of nutrient enrichment of the sediment and interactions between the seagrass *Cymedocea nodosa* and the introduced green alga *Caulerpa taxifolia* in a Mediterranean bay. J Exp Mar Biol Ecol 217:165-177

Chisholm JRM, Moulin P (2003) Stimulation of nitrogen fixation in refractory organic sediments by Caulerpa taxifolia (Chlorophyta). Limnol Oceanogr 48:787-794

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117-143

Creese RG, Davies AR, Glasby TM (2004) Eradicating and preventing the spread of the invasive alga *Caulerpa taxifolia* in NSW. NSW Fisheries Final Report Ser 64:110

Crooks JA (1998) Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. Mar Ecol Prog Ser 162:137-152

Crooks JA (2002) Characterizing eco-system consequences of biological invasions: the role of ecosystem engineers. Oikos 97:137-152

Crooks JA, Khim HS (1999) Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. J Exp Mar Biol Ecol 240:53-75

Edgar GJ (2000) Australian marine life: the plants and animals of temperate waters. Reed New Holland, Sydney

Fauchald K, Jumars P (1979) The diet of worms; a study of polychaete feeding guilds. Oceanogr Mar Biol Ann Rev 17:193-284

Gale SJ, Hoare PG (1991) Quaternary sediments: petrographic methods for the study of unlithified rocks. Belhaven, London

Glasby TM, Creese RG (2007). Invasive marine species management and research. In: ‘Marine Ecology’ (eds S. D. Connell & B.M. Gillanders). Oxford University Press, Melbourne, pp. 569-594

Gribben PE, Wright JT (2006a) Invasive seaweed enhances recruitment of a native bivalve: roles of refuge from predation and habitat choice. Mar Ecol Prog Ser 318:177-185

Gribben PE, Wright JT (2006b) Sublethal effects on reproduction in native fauna: are females more vulnerable to biological invasion? Oecologia 149:352-361

Gribben PE, Wright JT, O’Connor W, Doblin M, Eyre B, Steinberg PD. Reduced performance of native infauna following recruitment to a habitat-forming invasive marine alga. Oecologia In press.

Gutierrez JL, Jones CG, Strayer DL, Iribarne OO (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101:79-90

Hacker SN, Dethier MN (2006) Community modification by a grass invader has differing impacts for marine habitats. Oikos 113:279–286

Hedge P, Kriwoken LK (2000) Evidence for effects of *Spartina anglica* invasion on benthic macrofauna in Little Swanport Estuary, Tasmania. Austral Ecology 25:150-159

Laudian J, Schiedek D, Brey T, Portner H-O, E. AW (2002) Survivorship of juvenile surf clams *Donax serra* (Bivalvia, Donacidae) exposed to severe hypoxia and hydrogen sulphide. J Exp Mar Biol Ecol 271:9-23

Levin PS, Coyer JA, Petrik R, Good TP (2002) Community-wide effects of nonindigenous species on temperate rocky reefs. Ecology 83:3182-3193

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species. ICUN, http://www.issg.org/booklet.pdf

Meinesz A, Belsher T, Thibaut T, Antolic B, Ben Mustapha K, Bourdouresque C-F, Chiaverini D, Cottalorda J-M, Djellouli A, El Abed A, Orestano C, Grau AM, Ivesa l, Jaklin L, Langar H, Massuti-Pascual E, Peirano A, Tunesi L, de Vaugelas J, Zavodnik N, Zuljevic A (2001) The introduced marine alga *Caulerpa taxifolia* in the Medtiterranean. Biol Inv 38:499-508

Neira C, Grosholz ED, Levin LA, Blake R (2006) Mechanisms generating modification of benthos following tidal flat invasion by a *Spartina* hybrid. Ecol Appl 16:1391-1404

Neira C, Levin LA, Grosholz ED (2005) Benthic macrofaunal communities of three sites in San Francisco Bay invaded by hybrid Spartina, with comparison to uninvaded habitats. Mar Ecol Prog Ser 292:111-126

Posey MH (1988) Community changes associated with the spread of an introduced seagrass, Zostera japonica. Ecology 69:974-983

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. University Press, Cambridge

Reusch TBH, Williams SL (1999) Macrophyte canopy structure and the success of an invasive marine bivalve. Oikos 84:398-416

Rodriguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biol Inv 8:927-939

Shumway SE, Scott TM (1983) The effects on anoxia and hydrogen sulphide on survival, activity and metabolic rate in the coot clam, *Mulinia lateralis*. J Exp Mar Biol Ecol 71:135-146

Underwood AJ (1997) Experiments in Ecology. Cambridge University Press, Cambridge

Williams SL, Heck KLJ (2001) Seagrass community ecology. In: Bertness MD, Gaines SD, Hay ME (eds) Marine community ecology. Sinuaer Associates, Inc., Massachusetts, p 317-338

Winer BJ (1991) Statistical principles in experimental design. McGraw-Hill, New York

Wright JT (2005) Differences between native and invasive *Caulerpa taxifolia:* a link between asexual fragmentation and abundance in invasive populations. Mar Biol 147:559-569

Wright JT, Davies AR (2006) Demographic feedback between clonal growth and fragmentation in an invasive seaweed. Ecology 87:1744-1754

Wright JT, Gribben PE (2008) Predicting the impact of an invasive seaweed on the fitness of native fauna. J Appl Ecol 45:1540-1549

Wright JT, McKenzie LA, Gribben PE (2007) A decline in the density and health of a native bivalve associated with *Caulerpa taxifolia* invasion. Mar Freshwater Res 58:263-277

York PH, Booth DJ, Glasby TM, Pease BC (2006) Fish assemblages in habitats dominated by *Caulerpa taxifolia* and native seagrasses in south-eastern Australia. Mar Ecol Prog Ser 312:223-234

Table 1. ANOVAs of sediment silt fraction (SFF), redox potential 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 Kings Point (KP) and Broadwater (B) in Burrill Lake. At St Georges Basin, analysis of redox potential among habitats was only be performed on the data from Smiths Bay, as the results for Pats Bay were unreliable due to malfunctioning redox probe. Interaction terms *P*>0.25 removed from analyses. For Redox at Smiths Bay, main effect of block and higher order interactions containing the factor block not shown (see methods). Results of Tukey's tests examining differences between habitats are presented only.

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)							

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

Taxa				**St Georges Basin**						**Burrill Lake**			
Class	**Family (species)**	**Living arrangement**	**Trophic group**	**Pats Bay**			**Smiths Bay**			**Broadwater**		**Kings Point**	
				Caulerpa	Unvegetated	*H. ovalis*	*Caulerpa*	Unvegetated	*H. ovalis*	*Caulerpa*	*Zostera*	*Caulerpa*	*Zostera*
Bivalvia	Arcidae *(Anadara trapezia)*	infauna	suspension	28	27	32	18	26	25	4	35	4	12
Bivalvia	Arcidae *(Anadara trapezia* recruit)	epifauna	suspension	14	0	0	33	0	0	0	2	4	2
Bivalvia	Laternulidae *(Laternula marilina)*	infauna	suspension	2	2	11	6	0	5	0	0	0	1
Bivalvia	Tellinidae *(Tellina deltiodalis)*	infauna	deposit	0	0	0	1	2	2	8	39	12	27
Bivalvia	Mactridae *(Spisula trigonella)*	infauna	suspension	1	1	4	1	2	2	0	0	0	0
Bivalvia	Psammobiidae *(Solotellina alba)*	infauna	deposit	0	0	0	0	1	0	0	0	0	0
Bivalvia	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
Gastropoda	Nassariidae *(Nassarius burchadi)*	epifauna	surface detritus	19	0	6	23	4	8	22	39	6	16
Gastropoda	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
Polychaeta	Capitellidae	infauna	deposit	0	7	18	8	22	23	0	0	0	0
Polychaeta	Maldanidae	infauna	suspension	0	17	48	2	5	7	0	0	0	0
Polychaeta	Nereididae	infauna	predator/detritus	0	1	0	0	1	1	0	0	0	0
Polychaeta	Eunicidae	epifauna	predator/detritus	2	4	2	0	1	7	0	0	0	0
Polychaeta	Glyceridae	infauna	predator	0	1	2	0	1	1	0	0	0	0
Polychaeta	unidentified			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
Ascidiacea	Pyuridae *(Pyura stolonifera)*	epifauna	suspension	0	0	0	0	1	3	0	1	0	0
Ascidiacea	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
Malacostraca	Palamonidae (*Palaemon intermedius*)	epifauna	suspension	1	0	0	6	0	0	6	5	1	4
Malacostraca	Hymenosomatidae (*Amarinus paralacustris*)	epifauna	predator/detritus	0	0	0	3	0	0	0	0	0	0
Malacostraca	Grapsidae (*Paragrapsus laevis*)	epifauna	predator/detritus	0	0	0	0	0	0	0	1	0	0
Malacostraca	Diogenidae spp.	infauna	surface detritus	0	0	0	0	0	0	0	0	0	1
Malacostraca	Ampithoidae (*Cymadusa setosa*)	infauna	not known	0	0	0	0	0	0	1	0	0	0
Malacostraca	Aoridae spp.	infauna	not known	0	0	1	0	0	0	0	0	0	0
	Species richness			**10**	**11**	**13**	**13**	**15**	**16**	**9**	**12**	**7**	**9**

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 Kings Point (KP) and Broadwater (B) in Burrill Lake. Interaction terms where P>0.25 were removed from analyses. Results of Tukey's tests examining differences between habitats are presented only.

St Georges Basin			
Source	***df***	**F**	***P***
Anadara trapezia			
Site (Si)	1	2.32	0.1337
Habitat (Ha)	2	0.67	0.5183
Residual	54		
Batillaria australis			
Site (Si)	1	23.27	**<0.001**
Habitat (Ha)	1	69.38	**0.0142**
Si × Ha	2	2.18	0.1224
Residual	54		
Tukey's; H=C>U			
Nassarius burchardi			
Site (Si)	1	2.03	0.1601
Habitat (Ha)	2	22.53	**<0.001**
Residual	54		
Tukey's; H=C>U			
***Cirratulid* spp.**			
Site (Si)	1	19.97	**<0.001**
Habitat (Ha)	2	23.43	**<0.001**
Residual	54		
Tukey's; H>U=C			
***Capitellid* spp.**			
Site (Si)	1	6.59	**0.0130**
Habitat (Ha)	2	7.04	**<0.002**
Residual	54		
Tukey's; H=U>C (SB and PB)			
***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)			

Burrill Lake			
Source	***df***	**F**	***P***
Anadara trapezia			
Site (Si)	1	4.28	**0.0458**
Habitat (Ha)	1	5.60	0.2546
Si × Ha	1	4.28	**0.0458**
Residual	36		
Tukey's; Z>C (B), Z=C (KP)			
Batillaria australis			
Site (Si)	1	10.49	**0.0026**
Habitat (Ha)	1	3.47	0.3137
Si × Ha	1	6.19	**0.0176**
Residual	36		
Tukey's; Z>C (KP), Z=C (B)			
Nassarius burchardi			
Site (Si)	1	14.86	**<0.001**
Habitat (Ha)	1	6.67	**0.0140**
Residual	36		
Tukey's; Z>C			
Tellina deltoidalis			
Site (Si)	1	0.30	0.5894
Habitat (Ha)	1	9.81	**0.0034**
Residual	36		
Tukey's; Z>C			

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 Smiths Bay (SB) and Pats Bay (PB) in St Georges Basin, and unvegetated sediment, *C. taxifolia* and *Zostera capricorni* (Z) at Kings Point (KP) and Broadwater (B) in Burrill Lake. Interaction terms where *P*>0.25 were removed from analyses. Results of Tukey's tests examining differences between habitats are presented only.

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'; 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)			

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 Smiths Bay (SB) and Pats Bay (PB) in St Georges Basin, and unvegetated sediment, *C. taxifolia* and *Zostera capricorni* (Z) at Kings Point (KP) and Broadwater (B) in Burrill Lake. Interaction terms *P*>0.25 removed from analyses. Results of Tukey's tests examining differences between habitats are presented only.

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		

Figure legends

Figure 1. Mean (±SE) sediment silt fraction (SFF), redox and pH, (N=5/habitat/site) in *Caulerpa taxifolia* (Ctax), unvegetated sediment (unveg) and *Halophila ovalis* (Hal) at Smiths Bay and Pats Bay, St Georges Basin (A-C), and *C. taxifolia* (Ctax) and *Zostera capricorni* (Zostera) at Kings Point and Broadwater, Burrill Lake (D-F). N=10 cores/habitat/site. ND: no data for redox potential at Pats Bay due to a malfunctioning probe.

Figure 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 for each habitat at each site. A) St Georges Basin where P = Pats Bay site, S = Smiths Bay site, c = *C. taxifolia*, u = unvegetated sediment, H = *Halophila ovalis*. B) Burrill Lake where B = Broadwater site, K = Kings Point site, c = *C. taxifolia*, z = *Zostera capricorni*

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

Figure 4. Mean percentage (±SE) representation of surface detritus feeders (SDR), suspension feeders (SF), sub-surface deposit feeders (SSDF) and predadors/omnivores (P/O) per core in *Caulerpa taxifolia* (Ctax), unvegetated sediment (unveg) and *Halophila ovalis* (Hal) at Smiths Bay and Pats Bay, St Georges Basin (A-D), and *C. taxifolia* (Ctax) and

Zostera capricorni (Zostera) at Kings Point and Broadwater, Burrill Lake (E-H). N=10 cores/habitat/site.

Figure 5 Correlations between mean redox potential and mean total invertebrate abundance, species richness, infaunal abundance and epifaunal abundance per core in all habitats sampled at Smiths Bay, St Georges Basin, and Broadwater and Kings Point, Burrill Lake.

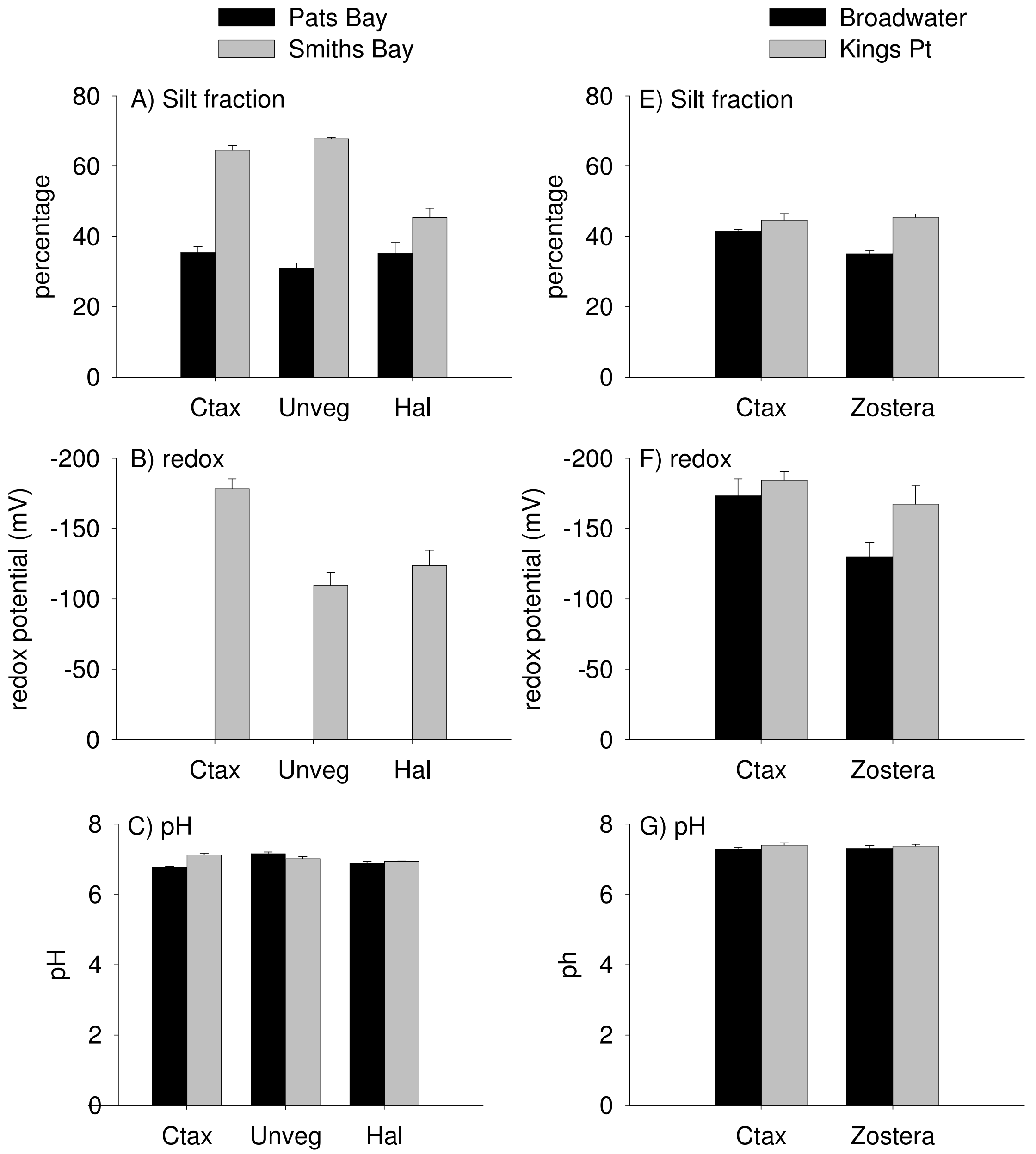

Pats Bay
Smiths Bay
Broadwater
Kings Pt
A) Silt fraction
percentage
80
60
40
20
0
Ctax
Unveg
Hal
E) Silt fraction
percentage
80
60
40
20
0
Ctax
Zostera
B) redox
redox potential (mV)
-200
-150
-100
-50
0
Ctax
Unveg
Hal
F) redox
redox potential (mV)
-200
-150
-100
-50
0
Ctax
Zostera
C) pH
pH
8
6
4
2
0
Ctax
Unveg
Hal
G) pH
ph
8
6
4
2
0
Ctax
Zostera

Figure 1.

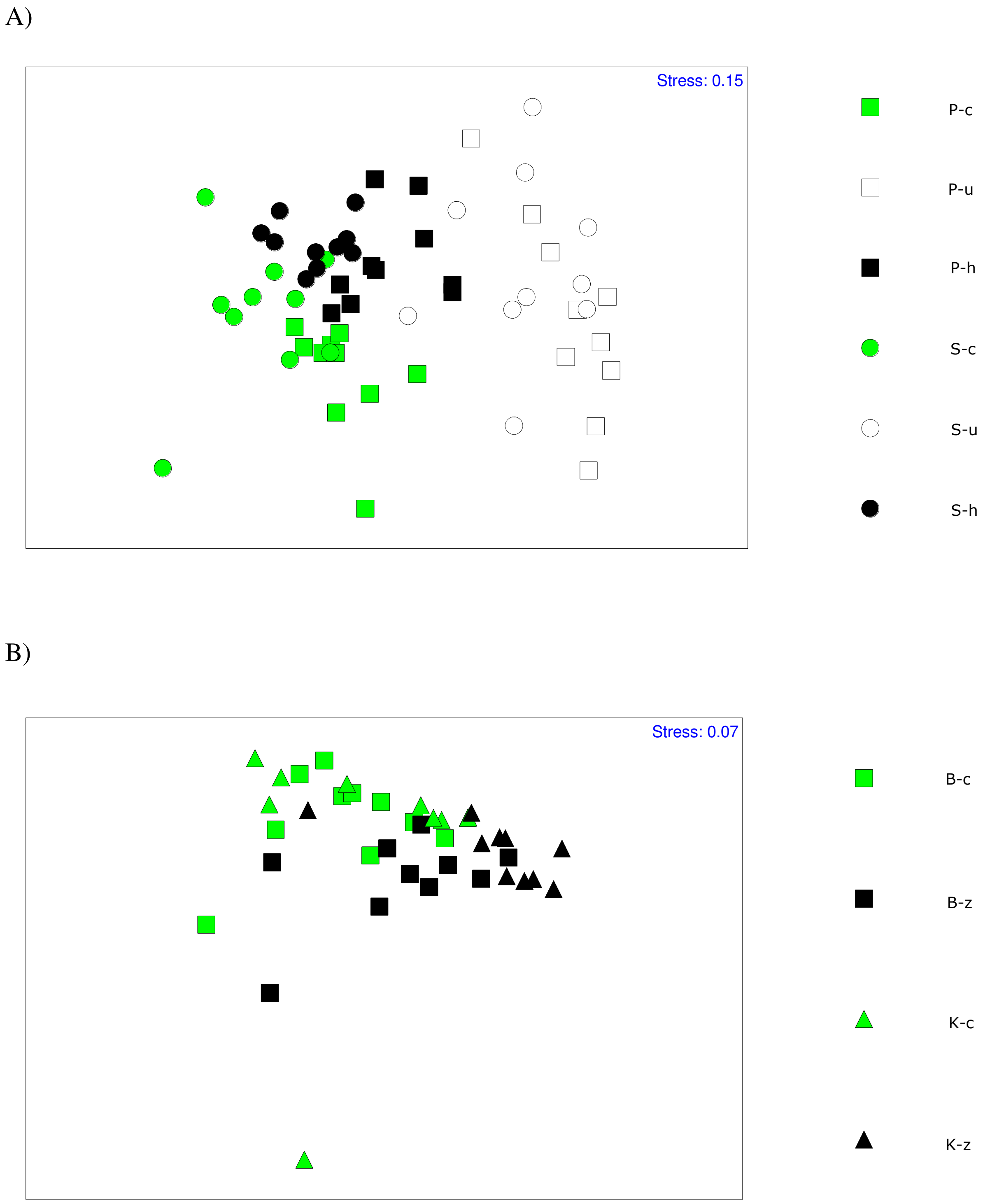


Figure 2.

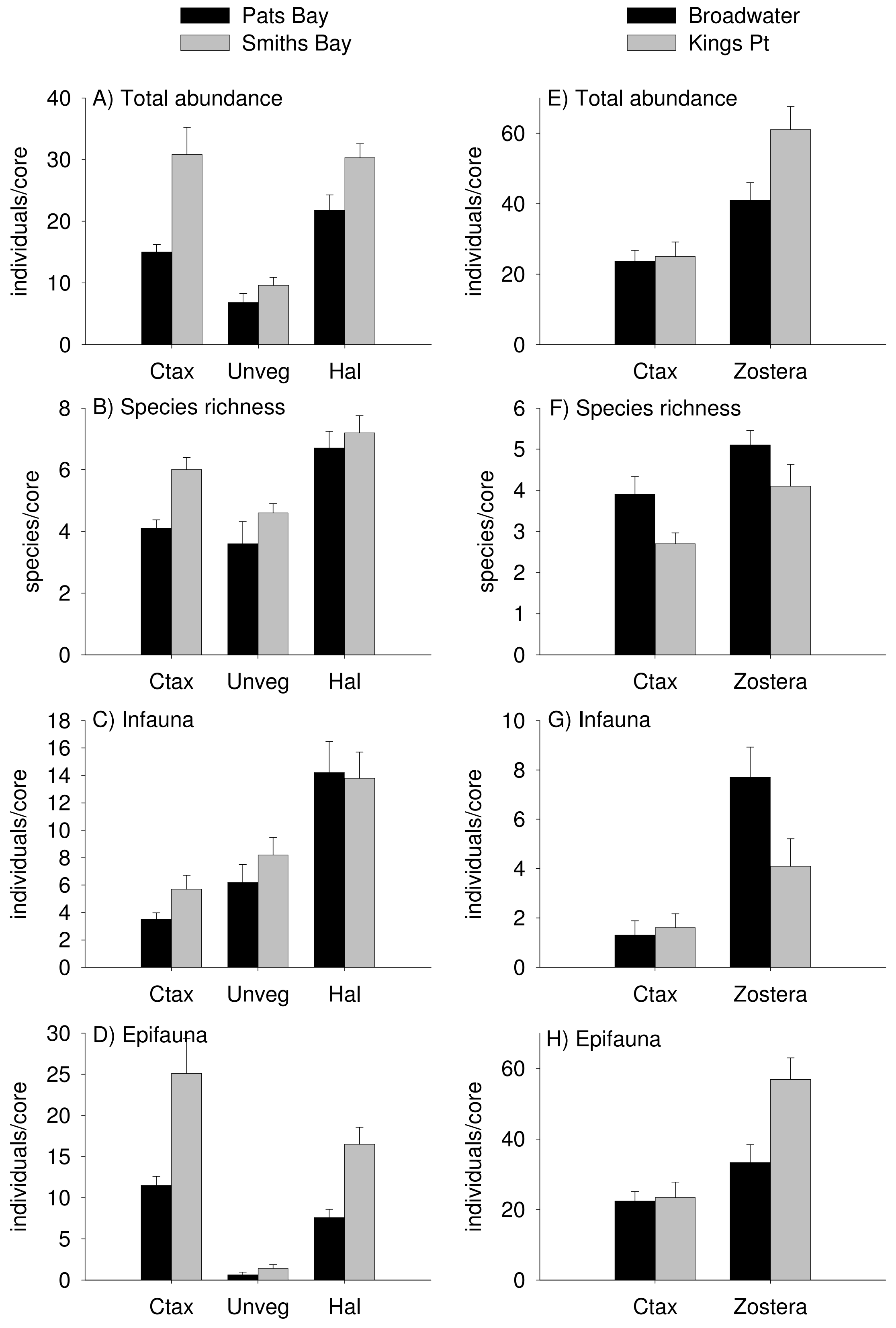
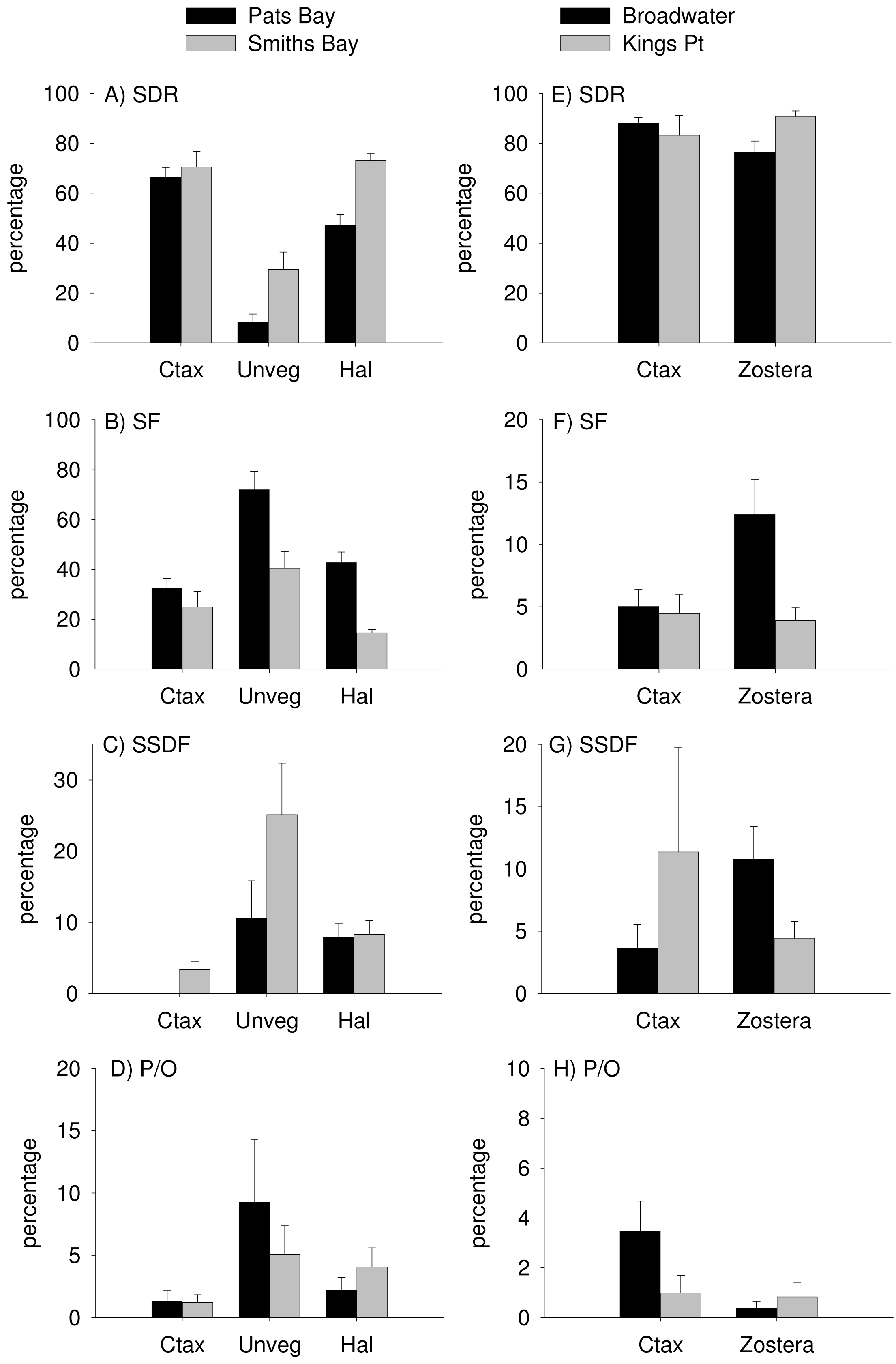

Pats Bay
Smiths Bay
Broadwater
Kings Pt
A) Total abundance
individuals/core
40
30
20
10
0
Ctax
Unveg
Hal
B) Species richness
species/core
8
6
4
2
0
C) Infauna
individuals/core
18
16
14
12
10
8
6
4
2
0
D) Epifauna
individuals/core
30
25
20
15
10
5
0
E) Total abundance
individuals/core
60
40
20
0
Ctax
Zostera
F) Species richness
species/core
6
5
4
3
2
1
0
G) Infauna
individuals/core
10
8
6
4
2
0
H) Epifauna
individuals/core
60
40
20
0

Figure 3



Pats Bay
Smiths Bay
Broadwater
Kings Pt
A) SDR
B) SF
C) SSDF
D) P/O
E) SDR
F) SF
G) SSDF
H) P/O
percentage
Ctax
Unveg
Hal
Zostera
0
5
10
15
20
30
40
60
80
100
2
4
6
8

Figure 4

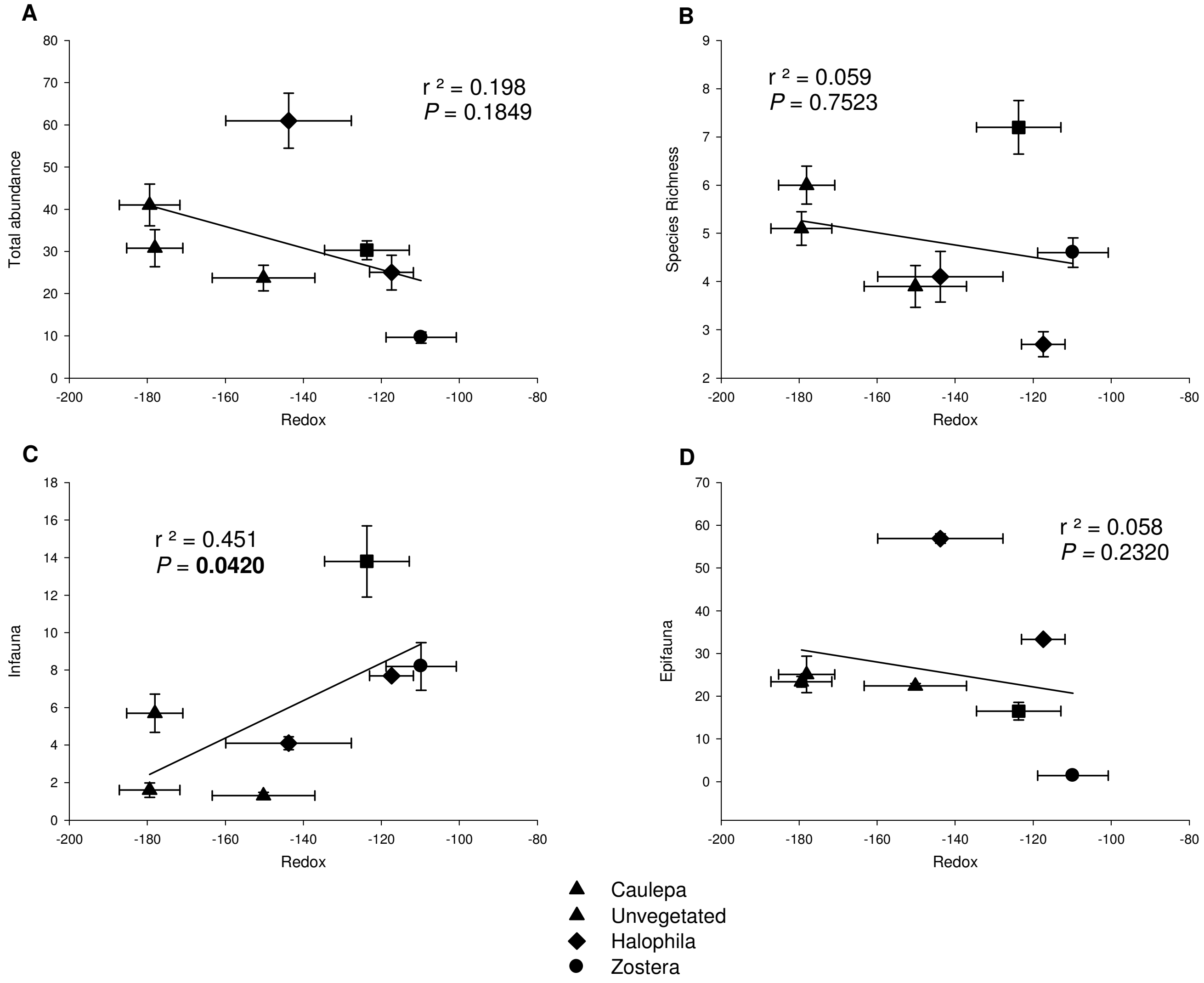

A
Total abundance
r ² = 0.198
P = 0.1849
Redox
B
Species Richness
r ² = 0.059
P = 0.7523
Redox
C
Infauna
r ² = 0.451
P = 0.0420
Redox
D
Epifauna
r ² = 0.058
P = 0.2320
Redox
-200
-180
-160
-140
-120
-100
-80
▲ Caulepa
▲ Unvegetated
◆ Halophila
● Zostera

Figure 5