Spatial and temporal variation in the biodiversity of macroinvertebrates in Brisbane Water estuary and its relationship to environmental variation

FINAL REPORT OF THE BRISBANE WATER ESTUARY BIODIVERSITY STUDY

NOVEMBER 2006

Dr William Gladstone
Centre for Sustainable Use of Coasts and Catchments
University of Newcastle (Ourimbah Campus)

The University of Newcastle
AUSTRALIA

EXECUTIVE SUMMARY

A major aim of estuary management is to manage human uses so that the biodiversity of estuaries, and the ecological processes maintaining the biodiversity, are conserved. Estuary management therefore requires information on how biodiversity is distributed (i.e. the spatial variations) and the environmental factors and ecological processes responsible for the observed distribution. Maintenance of the environmental factors and ecological processes, via management practices, will ensure conservation of estuary biodiversity.

This report provides the results of the Brisbane Water Estuary Biodiversity Study. The goal of this study was to describe the spatial variation that occurs in the biodiversity of macroinvertebrates in Brisbane Water estuary and its relationship to environmental variables. Specifically, the objectives of this study were:
(1) to quantify patterns in the distribution and abundance of species and assemblages of benthic macroinvertebrates at a variety of spatial scales within the Brisbane Water estuary in *Zostera capricorni* seagrass beds and in subtidal unvegetated habitats;
(2) to identify the role of environmental variables in explaining the observed spatial and temporal variation in abundance of species of benthic macroinvertebrates;
(3) to identify the role of environmental variables in explaining the observed spatial and temporal variation in structure of assemblages of benthic macroinvertebrates.

Macroinvertebrates occurring in *Zostera capricorni* seagrass beds (~ 1 m depth) were sampled on 2 occasions (July 2004, January 2005) using a spatially hierarchical sampling design that included areas (separated by 3-5 km), locations within areas (separated by 1-2 km), sites within locations x areas (separated by 100s m) and replicate samples (separated by 1-2 m).

Macroinvertebrates occurring in subtidal, unvegetated sediments (~ 4-5 m depth) were sampled on 2 occasions (August 2004, February 2005) in a spatially hierarchical sampling design that included locations (separated by 3-5 km), sites within locations (separated by 100s m), and replicate samples (separated by 3-5 m).

A total of 138 species of macroinvertebrates were recorded, representing 121 species from seagrass and 67 species from unvegetated sediments.

Seagrass Habitat

Macroinvertebrate assemblages of seagrass were numerically dominated by polychaetes (57% of total abundance), molluscs (29% of total abundance), crustaceans (10% of total abundance). The greatest number of species in the seagrass habitat was recorded in the Koolewong-Yattalunga and St. Hubert's Island-Lintern Channel areas. Density of macroinvertebrates was greatest in the Woy Woy Bay area and biomass was greatest in the Erina Creek-Rocky Point and Koolewong-Yattalunga areas.

Spatial patterns in species richness, total density, total biomass, and density of a number of common and abundant species were not consistent through time, with most temporal variation occurring between locations (located 3-5 km apart) and between replicate samples (located metres apart).

Spatial patterns in species richness in both sampling times were related to variation in the concentration of photosynthetic pigments in sediment, near-bottom water velocity, and shear. Spatial patterns in total density of macroinvertebrates were related to variation in biomass of seagrass wrack, near-bottom water velocity, and shear in sampling time 1, and to seagrass biomass in sampling time 2. Spatial patterns in biomass of macroinvertebrates were related to variation in water column chlorophyll in sampling time 1 and to fetch in sampling time 2.

The spatial pattern of macroinvertebrate assemblages of seagrass consisted of four groups representing: the most northern location in the estuary (Fagan's Bay), two groups near the estuary entrance at Wagstaff and Hardy's Bay, and a large group of all other locations. This spatial pattern was consistent in both sampling times.

The spatial patterns of macroinvertebrate assemblages of seagrass in sampling time 1 were related (in order of importance) to: distance to estuary entrance, silt/clay content

of sediment, bottom velocity, wrack biomass, fetch ($\lambda = 0.06$), and water column chlorophyll. Spatial patterns of assemblages in time 2 were related to bottom velocity, distance to estuary entrance, fetch, silt/clay content of sediment, and wrack biomass.

Unvegetated Subtidal Sediment Habitat

Assemblages of unvegetated sediment were numerically dominated by polychaetes (53% of total abundance), molluscs (23% of total abundance), and crustaceans (19% of total abundance). The greatest numbers of species were recorded at Wagstaff (48 species) and St. Hubert's Island (43 species). Mean density and biomass of macroinvertebrates were both greatest at Wagstaff.

Six variables showed significant time x site(location) interactions in mean values: number of species, total density, total biomass, density of the polychaete worms *Owenia australis* and *Maldene sarsi*, and density of the amphipod *Limnoporeia kingi*. This interaction indicated that differences in mean values between sites were not consistent through time. Brittlestars of the family Ophiodermatidae exhibited a significant time x location interaction in mean density. Density of the bivalve mollusc *Dosinia sculpta* (Veneridae) declined significantly between sampling times 1 and 2 across the estuary.

The spatial pattern of assemblages in sampling times 1 and 2 coincided with the distribution of locations throughout the estuary. Assemblages at Koolewong and St Hubert's Is. differed from each other and from the assemblages at the other locations. Spatial patterns in assemblages in time 1 were related to the silt/clay content of sediment, bottom shear velocity, and turbidity. Spatial patterns in assemblages in time 2 were related to the silt/clay content of sediment and bottom shear velocity.

Management Implications

The results of this study have several important implications for the use of macroinvertebrates in estuarine monitoring programs and the assessment of the

impacts of human activities: (1) the number of replicate samples used in this study (n=6) was appropriate, as many significant differences were detected; (2) a limited number of places randomly chosen as controls cannot be regarded as sufficiently representative of other unsampled areas for the purposes of testing a significant change at a potentially impacted place. A large number of control locations need to be sampled in assessments of environmental impacts; (3) an impact will have to cause a very large change in a variable to be detected as a significant change in the difference between the impacted and controls places in their natural patterns of spatio-temporal variability; (4) measurement of variability at several smaller nested temporal scales (e.g. between days, weeks) may be required to ensure that differences between larger temporal scales (months, years) are not confounded by greater differences at smaller temporal scales; (6) the existence of significant variability at all of the spatial scales examined indicates that monitoring which targets several species will need to include several nested spatial scales and therefore represent a considerable sampling effort.

The implications of this study for management of Brisbane Water estuary include the following: (1) management should aim to maintain the existing estuary-wide variation in environmental variables; (2) environmental variables that appear to be of more importance for management (because they are potentially altered by human activities and are consistently and significantly associated with spatial variation in macroinvertebrates) include the silt/clay content of sediment, turbidity, wrack biomass, seagrass biomass, water column chlorophyll, and sediment photosynthetic pigments; (3) the greatest species richness of macroinvertebrates in seagrass occurred in the Koolewong-Yattalunga area; (4) the most distinctive assemblages of macroinvertebrates in seagrass occurred in Fagan's Bay and Hardy's Bay – Wagstaff; (5) the greatest species richness of macroinvertebrates in unvegetated subtidal sediments occurred in Wagstaff; and (6) the most distinctive assemblages of macroinvertebrates in unvegetated subtidal sediments occurred in Koolewong and St. Hubert's Is.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

LIST OF APPENDIXES

INTRODUCTION

Existing at the ocean-land interface, estuaries contain unique assemblages of animals and plants that support a range of human uses. Estuarine assemblages vary at a range of spatial and temporal scales (Morrisey et al., 1992a,b; Legendre et al., 1997; Kendall and Widdicombe, 1999; Edgar and Barrett, 2002; Ysebaert and Herman, 2002; Noren and Lindegarth, 2005). Determining the spatial and temporal scales at which assemblages vary is a necessary pre-requisite to understanding the environmental factors and processes that may be structuring assemblages (Underwood et al., 2000), the implications of anthropogenic changes to these environmental factors and processes, and the design requirements for surveys to assess and monitor the possible impacts of natural events and anthropogenic activities. In particular, the development of useful models relating environmental variables to spatial and temporal patterns in estuarine assemblages requires tests of these relationships in many different types of estuaries.

Investigations of the significant scales of spatial variation provide evidence of the possible types of environmental variables that may underlie the observed spatial patterns. Significant variation in the species richness and density of estuarine macroinvertebrates occurs at spatial scales of centimetres to kilometres (Volckaert et al., 1987; Thrush et al., 1989; Thrush, 1991; Morissey et al., 1992a; Ysebaert and Herman, 2002; Noren and Lindegarth, 2005). The relative importance of different spatial scales to total variability differs among species (Morissey et al., 1992a; Ysebaert and Herman, 2002). Environmental variables that underlie this spatial variation within estuaries include primary productivity (Heip et al., 1995); degree of flushing (Ardisson and Bourget, 1997); seagrass biomass (Howard et al., 1989; Heck et al., 1995), sediment particle size (Mannino and Montagro, 1997; Ysebaert and Herman, 2002; Dauvin et al., 2004); salinity (Ardisson and Bourget, 1997; Ysebaert and Herman, 2002), and chlorophyll a (Ysebaert and Herman, 2002).

Estuarine assemblages also vary significantly at a range of temporal scales and the relative importance of different temporal scales differs among species (Morissey et al. 1992b). The significant interactions that occur between temporal and spatial

scales indicate that patterns of spatial variability are not constant through time (Morissey et al. 1992b; Noren and Lindegarth, 2005). This has significant implications for considerations about the temporal stability or otherwise of these assemblages, for the detection of impacts associated with human activities, and for the realism of species-environment relationships based on studies conducted at a single point in time.

The goal of this study was to describe the spatial variation that occurs in the biodiversity of macroinvertebrates in Brisbane Water estuary and its relationship to environmental variables. Specifically, the objectives of this study were:

(1) to quantify patterns in the distribution and abundance of species and assemblages of benthic macroinvertebrates at a variety of spatial scales within the Brisbane Water estuary in *Zostera capricorni* seagrass beds and in subtidal unvegetated habitats;

(2) to identify the role of environmental variables in explaining the observed spatial and temporal variation in abundance of species of benthic macroinvertebrates;

(3) to identify the role of environmental variables in explaining the observed spatial and temporal variation in structure of assemblages of benthic macroinvertebrates.

METHODS AND MATERIALS

Study area

Variations in sediment type and sediment organic carbon content within Brisbane Water are associated with proximity to inflows. Sediments in the northern half of Brisbane Water, in both arms of Woy Woy Bay, and Kincumber Broadwater consist mostly of muds with a high organic carbon content. Salinity shows little variation throughout the estuary in dry periods but a distinct gradient exists in wet conditions from low salinity at the northern end of the estuary and adjacent to inflows, to near seawater at the southern end of the estuary. Turbidity is greater adjacent to inflows, at the northern end of the estuary, and in Kincumber Broadwater and parts of Woy Woy Bay. Concentrations of soluble ortho-phosphate and inorganic nitrogen in sediment pore water are high, and one to two orders of magnitude greater, respectively, than levels dissolved in the water column. The major spatial gradient in both nutrients is for levels to be greater in the northern and central sections of Brisbane Water, and in Woy Woy Bay, compared with values near Blackwall Point (Cheng, 1994). Elevated levels of dissolved nutrients and turbidity occur after storm events; however, they are transient increases. An important gap in understanding linkages between environmental variables and structure of macrobenthic assemblages is the absence of a validated hydrodynamic model for the estuary (SMEC/Umwelt (Australia), 2002).

Surveys by Cheng (1994) and NSW Fisheries in 1999 confirm the existence of extensive seagrass beds in the shallow waters of most parts of Brisbane Water. Seagrass distribution is extensive, but not continuous, adjacent to most shorelines. Deeper sections of Brisbane Water have a mud-sand substratum. The results of previous studies suggest a broad habitat composition of Brisbane Water that includes intertidal rock (natural and human), intertidal sediment, seagrass, mangroves, saltmarsh, wetlands, subtidal rocky reef, sandy beaches, and deep unvegetated sediments. The Brisbane Water Data Compilation Study reported declining extent of mangroves, seagrass, wetland, and saltmarsh (SMEC/Umwelt (Australia), 2002).

Cheng (1994) sampled benthic macroinvertebrates (5 mm mesh size) from 22 stations in Brisbane Water. However, specimens were identified to a coarse taxonomic level, relatively few specimens were collected, and sampling occurred on only one occasion, making detection and interpretation of spatial and temporal variation difficult.

Study sites and sampling design

Sampling occurred in 2 habitats: subtidal *Zostera capricorni* seagrass beds (1 m depth at low tidae) and unvegetated subtidal sediments (4–6 m depth at low tide). Samples were collected according to a spatially hierarchical sampling design. The largest spatial scale examined for the seagrass habitat was areas (7 levels, separated by 3-5 km) (Fig. 1). Areas progressed inward from the entrance to the estuary at the sea and included bays adjacent to the main estuary water. The boundaries of each area were arbitrarily determined and area is therefore a random factor in analyses. Two randomly selected locations (separated by 1-2 km) were sampled within each area and 2 sites of dimensions 5 x 5 m and separated by hundreds of metres were sampled within each location. Six replicate samples (separated by 1-2 m) were collected from within each site and sampling occurred on 2 occasions (August 2004 and January 2005). A pilot study conducted at the outset of the study found that 6 replicate samples (from either habitat) provided mean values with acceptable precision (standard error/mean < 0.10) for most variables (Andrew and Mapstone, 1987).

A different spatial hierarchy was used to sample unvegetated sediments because of the limited extent of this habitat occurring at 4-6 m depth in the estuary. Sampling was restricted to this depth range to eliminate depth as a possible source of variation. The largest spatial scale examined for unvegetated sediments was locations (5 levels, separated by approximately 5 km) (Fig. 2). Locations were selected in a similar way to areas of seagrass and were also treated as a random factor in analyses. Two randomly selected sites of dimensions 5 x 5 m and separated by hundreds of metres were sampled within each location. Six replicate samples (separated by 1-2 m) were collected from each site and sampling occurred on 2 occasions (October 2004 and March 2005).

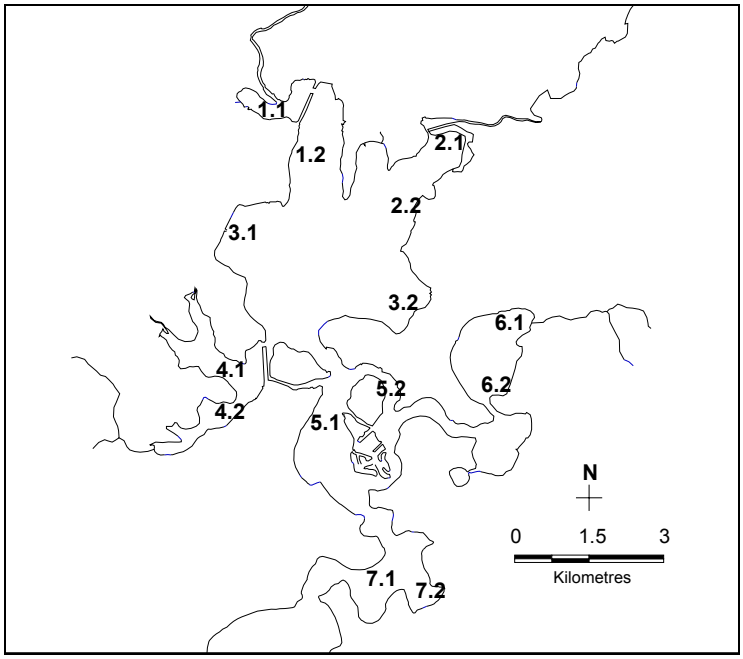

Fig. 1. Locations in Brisbane Water estuary where seagrass was sampled. 1.1 = Fagans Bay, 1.2 = Point Clare, 2.1 = Erina Creek (mouth), 2.2 = Rocky Point, 3.1 = Koolewong, 3.2 = Yattalunga, 4.1 = Woy Woy Bay, 4.2 = Woy Woy inlet, 5.1 = St Huberts Island, 5.2 = Lintern Channel, 6.1 = Kincumber creek (mouth), 6.2 = Bensville, 7.1 = Ettalong Beach, 7.2 = Hardy's Bay. The first number of each location number indicates the area i.e. 1.1 is location 1 in area 1. Two sites were sampled within each location. Sites 1 and 2 (as indicated in Fig. 3) are within location 1.1, sites 3 and 4 are within location 1.2 etc.

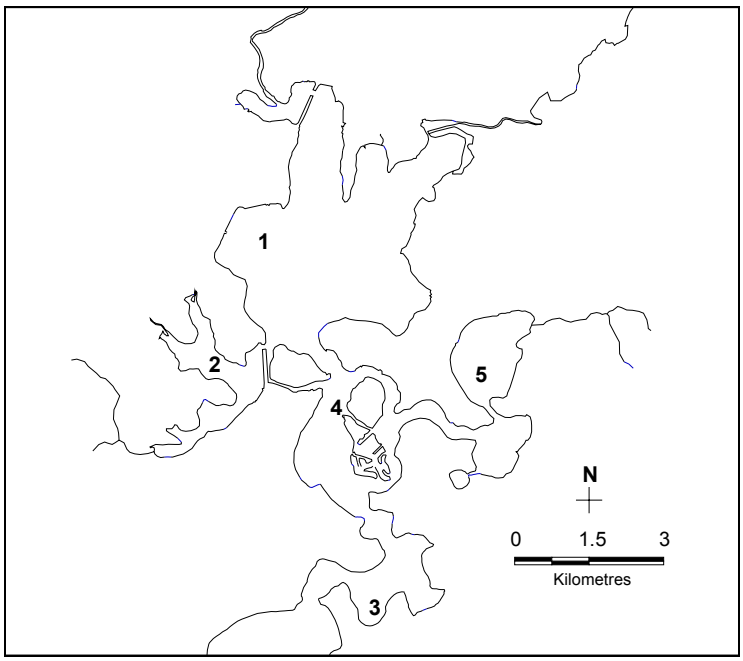

Fig. 2. Locations in Brisbane Water estuary where unvegetated sediment was sampled. 1 = Koolewong, 2 = Woy Woy, 3 = Wagstaff, 4 = St Huberts Island, 5 = Kincumber. Two sites were sampled within each location. Sites 1 and 2 (as shown in Fig.4) are within location 1, sites 3 and 4 are within location 2 etc.

Field sampling

Macroinvertebrate samples from *Zostera capricorni* seagrass beds were collected by hand with a 10 cm diameter PVC core to a depth of 10 cm. Samples from subtidal benthic sediments were collected from a boat using an Ekman benthic grab of dimensions 15 cm x 15 cm x 15 cm. Immediately after samples were collected they were washed through a 1 mm mesh sieve in the field and the retained specimens placed in plastic bags and fixed with 5% buffered formalin. All samples from each habitat type were collected within a 5 d period on each sampling occasion.

Additional samples for sediment grain size analysis were collected at the same time as the macroinvertebrate samples. Three replicate sediment cores (5 cm diameter x 10 cm depth) were taken in each *Z. capricorni* site and 3 additional benthic grab samples were retained from each subtidal sediment site.

Water column chlorophyll *a* (µg/L) and turbidity (ntu) were determined from surface waters in each seagrass with a calibrated field fluorometer (Turner Aquafluor). Both variables were also determined from surface (0-1 m) water and near-sediment (~4-6 m) water at each unvegetated sediment site. Three replicate readings were taken in each site. Secchi depth readings were taken at each subtidal sediment site (n=1 reading per site) to estimate the transparency of water, which correlates well with percentage of light transmission (Wetzel and Likens, 2000).

Biomass of benthic microalgae in seagrass beds was assessed from photosynthetic pigment analysis of samples from the top 5 mm of sediment, collected by hand using 13 mm diameter core tubes. Samples from subtidal sediment were sub-sampled from 80 mm diameter cores attached to a coring device on a 6 m pole (Plate 1). Five or six replicate samples, using 22 mm diameter cores, were taken at each site.

Plate 1. Field sampling for biomass of benthic microalgae showing the sediment corer being lowered into the water (upper photo) and retrieval of sediment sample in perspex corer (lower photo).

Organic matter content of the top 2 cm of sediment at each site in both habitat types was determined from sediment samples collected from 22 mm diameter cores. Three replicate cores were taken at each seagrass and subtidal sediment site. Samples from seagrass sites were collected by hand, and samples from subtidal sediment were sub-sampled from 80 mm diameter cores attached to a coring device on a 6 m length of pole.

Laboratory processing

Macroinvertebrate samples were rinsed of formalin and washed separately through a stacked series of sieves of mesh sizes 5.6 mm, 4 mm, 2.8 mm, 2 mm and 1 mm. Macroinvertebrates retained on each sieve were identified and counted. Individuals were identified to the finest level of taxonomic resolution possible and hereafter the identified taxa are referred to as 'species'. Identification was confirmed by staff from the Australian Museum, Sydney. Biomass (mg ash free dry weight) of all macroinvertebrates and of polychaetes, molluscs, and crustaceans was determined using the abundance of each group retained on each sieve and relevant equations in Edgar (1990).

Sediment samples were dried at 60^{o}C and separated, using an Endecotts EFL2000/2 vibrating shaker, into >1mm, 0.5-1 mm, 0.212-0.500 mm, 63-212 μm and <63 μm size fractions. Each fraction was weighed (to nearest 0.001 g) and expressed as a % of total sample weight. However, only the <63 μm fraction was used in analyses to avoid problems of non-independence when analysed together with other fractions and because this fraction has been shown to be the most relevant in explaining patterns of distribution and abundance of estuarine fauna (Edgar and Shaw, 1995).

Seagrass plants (*Zostera capricorni* and *Halophila ovalis*) collected in macroinvertebrate cores from seagrass sites were separated and enumerated and expressed as number of plants 1 m^{-1}. Biomass of each species of seagrass was determined by pooling plants of each species in each sample and weighing after being dried at 60^{o}C for 7 d. The biomass of wrack (dead and detached fragments of seagrass) in each sample was determined in the same way. Wrack biomass was expressed as g m^{-1}.

The total photosynthetic pigment content of the benthic microalgae in sediments (μg cm^{-3}) was determined from the sum of the chlorophyll *a* and phaeopigment *a* concentrations in 90% acetone extracted samples using a spectrophotometric assay technique (Pusceddu et al., 2004). Sediment samples

collected for organic matter content were dried at 60^{o}C for 2 d, weighed, and then combusted in a muffle furnace at approximately 500^{o}C for 2 hr. Weights of dry and ash material were used to determine % organic matter of sediment samples as follows: % organic matter = (1– ash wt/dry wt) x 100.

Two indicators of water movement were tested as potential explanatory environmental variables: near-bottom velocity and bed shear. Data for both was obtained from the hydrodynamic models developed for Brisbane Water as part of the Estuary Process Study (D Treloar personal communication).

Univariate analyses

Analysis of variance (ANOVA) was used to test the effects of time of sampling, three hierarchical spatial scales (area, location (area), site (location*area)), and their interactions on species richness, total density, total biomass, and density of the 5 most abundant species sampled in seagrass. ANOVA was also used to test the effects of time of sampling, 2 hierarchical spatial scales (location, site (location)), and their interactions on the same variables from unvegetated sediments. Prior to analyses data were checked for homogeneity of variances by Cochran's test and log-transformed to eliminate heterogeneous variances (Underwood, 1981). It should be noted that *F*-tests for the factors area and location (area) in the seagrass habitat and the factor location in the unvegetated sediment habitat were only possible when other sources of variation could be eliminated (i.e. when they were non-significant at $P > 0.25$) (Underwood, 1981). Table 1 provides the expected mean squares for these analyses and the rationale for requiring some sources of variation to be eliminated. We were also interested in understanding the relative importance of significant factors and the residual to variation in the dependent variables as the first step in developing explanatory hypotheses about processes underlying the observed spatial and temporal patterns (Underwood, 1997; Graham and Edwards, 2001). Variance estimates were calculated from the model of expected mean squares (Table 1). Negative estimates of variance were changed to zero and the remaining estimates re-calculated (Fletcher and Underwood, 2002). When significant interactions were recorded the results of

significance tests and the variance estimates for main effects were presented in the ANOVA summary table but not reported.

Table 1. Expected mean squares for the ANOVA for (a) seagrass using two times (T), seven areas (A), two locations (L) nested within each area, two sites (S) nested within each location, six replicate samples; and (b) unvegetated sediment using two times (T), five locations (L), two sites (S) nested within each location, six replicate samples.

(a) Seagrass

Source of variation	df	Expected mean squares
Time=T	1	$\sigma^2_R + 6\sigma^2(T \times S(L(A))) + 12\sigma^2(T \times L(A)) + 24\sigma^2(T \times A) + 168\sigma^2 T$
Area=A	6	$\sigma^2_R + 6\sigma^2(T \times S(L(A))) + 12\sigma^2(T \times L(A)) + 24\sigma^2(T \times A) + 12\sigma^2(S(L(A))) + 24\sigma^2(L(A)) + 48\sigma^2 A$
Location=L(A)	7	$\sigma^2_R + 6\sigma^2(T \times S(L(A))) + 12\sigma^2(T \times L(A)) + 12\sigma^2(S(L(A))) + 24\sigma^2(L(A))$
Site=S(L(A))	14	$\sigma^2_R + 6\sigma^2(T \times S(L(A))) + 12\sigma^2(S(L(A)))$
T x A	6	$\sigma^2_R + 6\sigma^2(T \times S(L(A))) + 12\sigma^2(T \times L(A)) + 24\sigma^2(T \times A)$
T x L(A)	7	$\sigma^2_R + 6\sigma^2(T \times S(L(A))) + 12\sigma^2(T \times L(A))$
T x S(L(A))	14	$\sigma^2_R + 6\sigma^2(T \times S(L(A)))$
Residual=R	280	σ^2_R

(b) Unvegetated sediment

Source of variation	df	Expected mean squares
Time=T	1	$\sigma^2_R + 6\sigma^2(T \times S(L)) + 12\sigma^2(T \times L) + 60\sigma^2 T$
Location=L	4	$\sigma^2_R + 6\sigma^2(T \times S(L)) + 12\sigma^2(T \times L) + 12\sigma^2 S(L) + 24\sigma^2 L$
Site=S(L)	5	$\sigma^2_R + 6\sigma^2(T \times S(L)) + 12\sigma^2 S(L)$
T x L	4	$\sigma^2_R + 6\sigma^2(T \times S(L)) + 12\sigma^2(T \times L)$
T x S(L)	5	$\sigma^2_R + 6\sigma^2(T \times S(L))$
Residual=R	100	σ^2_R

Multiple regression was used to model the relationships between biological variables (species richness, species density, total density of macroinvertebrates, total biomass of macroinvertebrates) and environmental variables in seagrass. The

variables used were the total number of species recorded in each site on each sampling occasion, total density, and total biomass and each environmental variable. Initial examination of environmental variables by Spearman rank correlation coefficients revealed a number of significant inter-correlations (see Results). Therefore, hierarchical partitioning (Chevan and Sutherland, 1991; MacNally, 2000; 2002; Walsh et al. 2004) was used to identify those variables that made a significant, independent contribution to explaining variation in the biological variables. This method of selecting variables was used in preference to stepwise selection of variables because the inter-correlations in the environmental variables meant that it would be impossible to determine whether the selected environmental variables contributed independently to variation in the response variable (Quinn and Keough, 2002). The statistical significance of each of the independent contributions was determined by randomizing (n=1000) the data matrix and comparing the observed value to the distribution of values obtained from the randomization. The observed independent contribution was significant if it exceeded 95% of the randomized values.

The environmental variables shown by hierarchical partitioning to have significant, independent effects on the biological variables were then used in a multiple regression model to explain the distribution of the biological variables (MacNally, 2002). The hier.part package in the R Statistical project was used for the hierarchical partitioning and statistical testing (Walsh and MacNally, 2004). Prior to analysis data characteristics were examined with box plots and scatter plots and, where necessary, $\log_{10}$-transformed to eliminate heterogeneous variances and to remove outliers. Environmental variables were standardized prior to hierarchical partitioning. This analysis was not done in the unvegetated subtidal sediment habitat because the small number of sites sampled (n=10) would have caused problems with over-fitting of environmental variables (n=7 variables).

Multivariate analyses

Multivariate statistics were used to analyse the significance of time and the hierarchical spatial scales as sources of variation in the assemblage structure. An examination of the multivariate data set of species and their abundances revealed

many species that occurred as single individuals and/or at a limited number of sites. To prevent these species exerting an undue influence species that were recorded only as single individuals in both sampling times (regardless of the number of sites where they were recorded) and species that were recorded at ≤ 2 sites in seagrass and at only 1 site in unvegetated sediment in both sampling times were removed from the data set prior to analysis. This screening resulted in the elimination of 44 taxa (4% of total individuals) from the seagrass data set and 23 taxa (1% individuals) from the unvegetated sediment data set. Although a pre-analysis screening is used commonly in multivariate analyses where a large number of rare species have been recorded (Chapman, 2002; Ysebaert and Herman, 2002), there are no generally accepted criteria for excluding or retaining species in analyses (Gaston, 1994; Manté et al., 2003). PERMANOVA (Anderson, 2001) was used to test the significance of time of sampling and the 3 nested spatial scales (areas, locations, sites) on assemblages from the seagrass habitat, and time of sampling and the 2 nested spatial scales (location, site) on assemblages from unvegetated sediments. The magnitude of the multivariate variability of each factor, interaction and the residual was calculated from the mean squares of the PERMANOVA using the same logic as the variance estimates calculated for the univariate data set (Table 1).

Spatial patterns in assemblage structure at each time of sampling were visualized with ordination diagrams using the program Canoco 4.5. Canonical correspondence analysis (CCA) was used to test for associations between assemblage patterns and the measured environmental variables in each habitat. Environmental variables were $\log_{10}$-transformed and standardized prior to analysis. A manual forward selection process in Canoco was used to select the subset of environmental variables that best explained the spatial patterns in assemblage structure. Environmental variables were ranked according to the proportion of total variance in the species data set they explained. The highest ranking environmental variable was selected and the remaining variables re-ordered according to the proportion of total variance they explained in conjunction with the variable already selected. The statistical significance of the variance explained by each of the environmental variables was tested by a Monte Carlo test (999 permutations) and variables that were significant at $P<0.05$ were added to the model.

RESULTS

Biodiversity of macroinvertebrates

A total of 138 species (13,772 individuals) were recorded, representing 6 phyla: Platyhelminthes (1 species), Nemertea (1 species), Annelida (48 species), Arthropoda (24 species), Mollusca (63 species), and Echinodermata (2 species).

Seagrass

General characteristics of the macroinvertebrate fauna of seagrass

A total of 121 species (12,881 individuals) were recorded from the *Z. capricorni* seagrass habitat with an average of 14 species (range=3-29) and 39 individuals (range=5-199) per replicate sample. Assemblages were numerically dominated by polychaetes (57% of total abundance), molluscs (29% of total abundance), crustaceans (10% of total abundance), and nemerteans (3% of total abundance). The most abundant species were the polychaetes *Barantolla lepete, Simplisetia aequisetis* and *Owenia australis*, the gastropod mollusc *Batillaria australis*, and the bivalve mollusc *Tellina deltoides*. In terms of biomass, the macroinvertebrate assemblage was dominated by molluscs (55% of total biomass), polychaetes (31% of total biomass), and crustaceans (5.5% of total biomass). Species contributing the most to total biomass included the gastropod molluscs *Batillaria australis*, *Prothalotia comtessie*, *Nassarius burchardi* and *Bittium lacertinium* (together representing 41% of total biomass) and the polychaetes *O. fusiformis*, *B. lepte* and *Notomastus chrysosetus* (14% of total biomass).

The greatest number of species in the seagrass habitat was recorded in the Koolewong-Yattalunga (92 species) and St. Hubert's Island-Lintern Channel (88 species) areas (Table 2a). Mean density of macroinvertebrates was greatest in the Woy Woy Bay area (54.13 ± 8.79 individuals per core) and mean biomass was

greatest in the Erina Creek-Rocky Point (166.22 ± 26.54 mg AFDW per core) and Koolewong-Yattalunga areas (164.56 ± 10.73 mg AFDW per core).

Table 2. Summary of number of species, mean density (± S.E.) and mean biomass (mg AFDW ± S.E.) recorded throughout Brisbane Water in each habitat. Area and location codes are shown in Fig. 1 and Fig. 2

(a) Seagrass

			Density		Biomass	
Area code	Area name	Species	Mean	SE	Mean	SE
1	Fagans Bay-Point Clare	71	34.88	4.41	94.74	9.24
2	Erina Creek-Rocky Point	69	42.35	6.23	166.22	26.54
3	Koolewong-Yattalunga	92	47.79	4.58	164.56	10.73
4	Woy Woy Bay	79	54.13	8.79	114.48	16.06
5	St Huberts-Lintern Channel	88	36.65	4.62	125.74	20.15
6	Kincumber Broadwater	62	31.31	4.96	112.84	12.39
7	Ettalong-Hardys Bay	85	31.13	5.00	121.91	27.13

			Density		Biomass	
Location code	Location name	Species	Mean	SE	Mean	SE
1.1	Fagans Bay	50	37.58	3.97	107.08	10.71
1.2	Point Clare	57	32.18	8.37	82.40	13.50
2.1	Erina Creek (mouth)	49	37.38	8.73	134.75	25.72
2.2	Rocky Point	61	47.33	9.40	197.69	44.34
3.1	Koolewong	71	51.88	7.52	166.37	10.28
3.2	Yattalunga	72	43.71	5.50	162.75	20.73
4.1	Woy Woy Bay	71	60.58	13.15	142.74	18.81
4.2	Woy Woy Inlet	66	47.67	12.63	86.22	17.82
5.1	St Huberts Island	65	35.92	3.70	139.46	24.41
5.2	Lintern Channel	71	37.38	9.26	112.02	34.27
6.1	Kincumber Creek (mouth)	50	33.38	5.64	121.68	12.97
6.2	Bensville	47	29.25	8.96	104.00	22.27
7.1	Ettalong	69	33.29	5.61	166.86	40.39
7.2	Hardys Bay	64	28.96	9.05	76.95	21.37

(b) Unvegetated sediment

			Density		Biomass	
Location code	Location name	Species	Mean	SE	Mean	SE
1	Koolewong	34	23.33	6.14	52.30	15.35
2	Woy Woy Bay	32	10.58	3.92	15.92	4.52
3	Wagstaff	48	53.54	16.99	150.36	65.85
4	St Huberts Island	43	11.67	4.36	31.18	11.06
5	Kincumber Broadwater	30	21.50	9.41	79.45	54.54

Two variables showed significant time x site(location(area)) interactions: total biomass of macroinvertebrates and density of the polychaete worm *Barantolla lepete* (Capitellidae) (Table 3). Total biomass declined significantly between sampling times at only 1 site within 5 locations, increased significantly between sampling times at only 1 site within 2 locations, decreased significantly at both sites within 4 locations, and did not change significantly at either site in 4 locations (Fig. 3c). The variance associated with this interaction (σ^2=0.04) was less than the variance between replicate samples (σ^2=0.21). The significant time x site(location(area)) interaction in density of *B. lepete* resulted from significant changes in mean density of *B. lepte* over time at only 1 site in 5 locations. Significant changes in both sites occurred at only one location. No significant changes over time were recorded at the remaining sites. The variance associated with this time x site(location(area)) interaction (σ^2=2.42) was less than the variance between replicate samples (σ^2=9.08).

Five variables showed significant time x location(area) interactions (Table 3): total number of species, and density of *Tellina deltoidalis, Batallaria australis, Simplisetia aequisetis,* and *Owenia australis*. The significant time x location(area) interaction indicates that mean values of these variables changed over time in different ways in locations separated by 1-2 km. The number of species declined significantly over time in both locations in 5 areas, did not change in either location in 1 area, and declined significantly in one location only in 1 area (Table 3) (Fig. 3a). Density of the bivalve mollusc *T. deltoidalis* (Tellinidae) (Fig. 3e) decreased over time at only 1 location in each of 2 areas, and increased at only 1 location in another area. Density did not change significantly in all other locations. Density of the gastropod mollusc *B. australis* (Batillariidae) (Fig. 3f) decreased at only 1 location in each of 2 areas and increased at only 1 location in 2 other areas.

Table 3. Summary of results of 4-factor ANOVA (see Table 1 for design) for species (untransformed), total density (ln(x) transformed), total biomass (ln(x) transformed) and density of *Barantolla lepete* (untransformed), *Tellina deltoidalis* (ln(x+0.1) transformed), *Batillaria australis* (ln(x+0.1) transformed), *Simplisetia aequisetis* (ln(x+0.1) transformed), and *Owenia australis* (ln(x+0.1) transformed) from seagrass samples.

		Species			Total density		
Source	*df*	MS	*F*	σ^2	MS	*F*	σ^2
Time=T	1	2497.19	85.06 ***[2]	14.57	31.07	77.53 ***[2]	0.18
Area=A	6	367.97	6.91 **[1]	5.89	2.54	4.02 *[1]	0.03
Location=L(A)	7	53.23	no test	0	0.63	no test	0
Site=S(L(A))	14	46.43	4.74 **	3.05	0.55	3.75 **	0.03
T x A	6	48.83	1.66 ns	0.81	0.64	1.61 ns	0
T x L(A)	7	29.36	3.00 *	1.63	0.40	2.71 ns	0.03
T x S(L(A))	14	9.80	1.11 ns	0.16	0.15	1.45 ns	0.01
Residual	280	8.83		8.83	0.10		0.10

		Total biomass			*B. lepte*		
Source	*df*	MS	*F*	σ^2	MS	*F*	σ^2
Time=T	1	18.76	16.39 **[2]	0.10	278.68	3.49 ns	1.14
Area=A	6	2.07	0.63 ns [1]	0	93.39	no test	0
Location=L(A)	7	3.28	no test	0.08	85.83	5.35 *[3]	2.27
Site=S(L(A))	14	0.70	1.67 ns	0.02	31.43	1.33 ns	0.65
T x A	6	1.02	0.89 ns	0	79.75	4.97 *	2.34
T x L(A)	7	1.14	2.74 ns	0.06	16.05	0.68 ns	0
T x S(L(A))	14	0.42	2.01 *	0.04	23.60	2.60 **	2.42
Residual	280	0.21		0.21	9.08		9.08

1 after eliminating T x A because non-significant at $P > 0.25$ and testing against L(A)

2 tested against T x L(A) after eliminating T x A

3 after eliminating S(L(A)) because non-significant at $P > 0.25$ and testing against T x L(A)

ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 3 cont'd. Summary of results of 4-factor ANOVA (see Table 1 for design) for species (untransformed), total density (ln(x) transformed), total biomass (ln(x) transformed) and density of *Barantolla lepete* (untransformed), *Tellina deltoidalis* (ln(x+0.1) transformed), *Batillaria australis* (ln(x+0.1) transformed), *Simplisetia aequisetis* (ln(x+0.1) transformed), and *Owenia fusiformis* (ln(x+0.1) transformed) from seagrass samples.

		T. deltoidalis			*B. australis*		
Source	*df*	MS	*F*	σ^2	MS	*F*	σ^2
Time=T	1	0.56	0.07 ns[2]	0	9.62	0.82 ns[2]	0
Area=A	6	8.97	1.57 ns[1]	0	43.27	1.30 ns[1]	0.21
Location=L(A)	7	5.72	no test	0	33.38	no test	0.68
Site=S(L(A))	14	4.63	1.81 ns	0.17	7.21	3.57 *	0.43
T x A	6	4.23	0.53 ns	0	8.21	0.77 ns	0
T x L(A)	7	8.00	3.14 *	0.45	11.80	5.85 **	0.82
T x S(L(A))	14	2.55	1.52 ns	0.14	2.02	1.47 ns	0.11
Residual	280	1.68		1.68	1.37		1.37

		S. aequisetis			*O. fusiformis*		
Source	*df*	MS	*F*	σ^2	MS	*F*	σ^2
Time=T	1	242.64	35.13 ***[2]	1.40	2.52	0.2 ns[2]	0
Area=A	6	14.22	1.23 ns[1]	0.05	41.43	3.88 *[1]	0.58
Location=L(A)	7	11.60	no test	0.14	10.68	no test	0
Site=S(L(A))	14	3.76	1.60 ns	0.12	2.91	2.32 ns	0.11
T x A	6	5.01	0.73 ns	0	8.29	0.67 ns	0
T x L(A)	7	6.91	2.93 *	0.38	12.33	9.82 ***	0.89
T x S(L(A))	14	2.36	1.51 ns	0.13	1.26	0.78 ns	0
Residual	280	1.56		1.56	1.60		1.60

1 after eliminating T x A because non-significant at $P > 0.25$ and testing against L(A)

2 tested against T x L(A) after eliminating T x A

3 after eliminating S(L(A)) because non-significant at $P > 0.25$ and testing against T x L(A)

ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

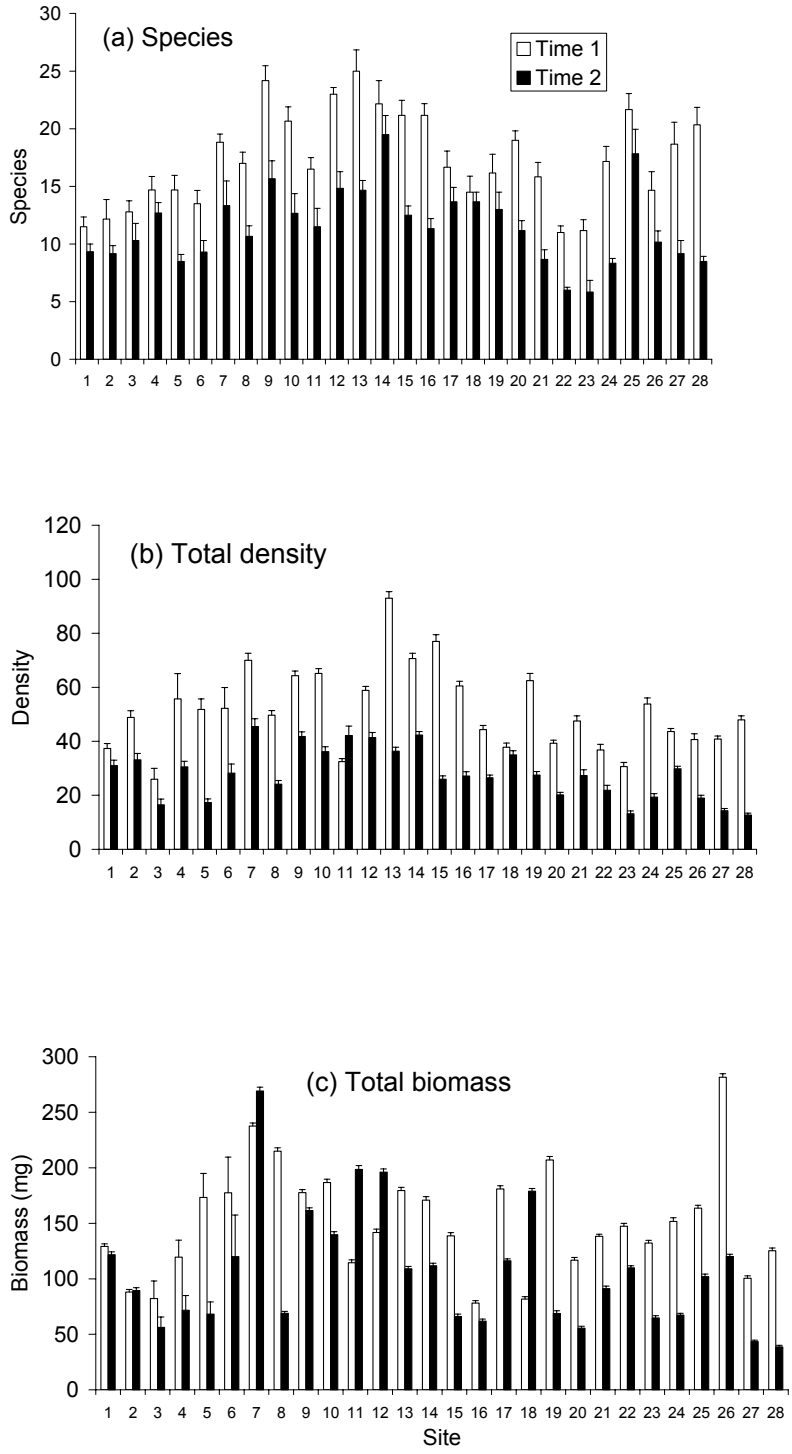

Fig. 3. Mean (± S.E., n = 6) values from seagrass for each site at each time of sampling.

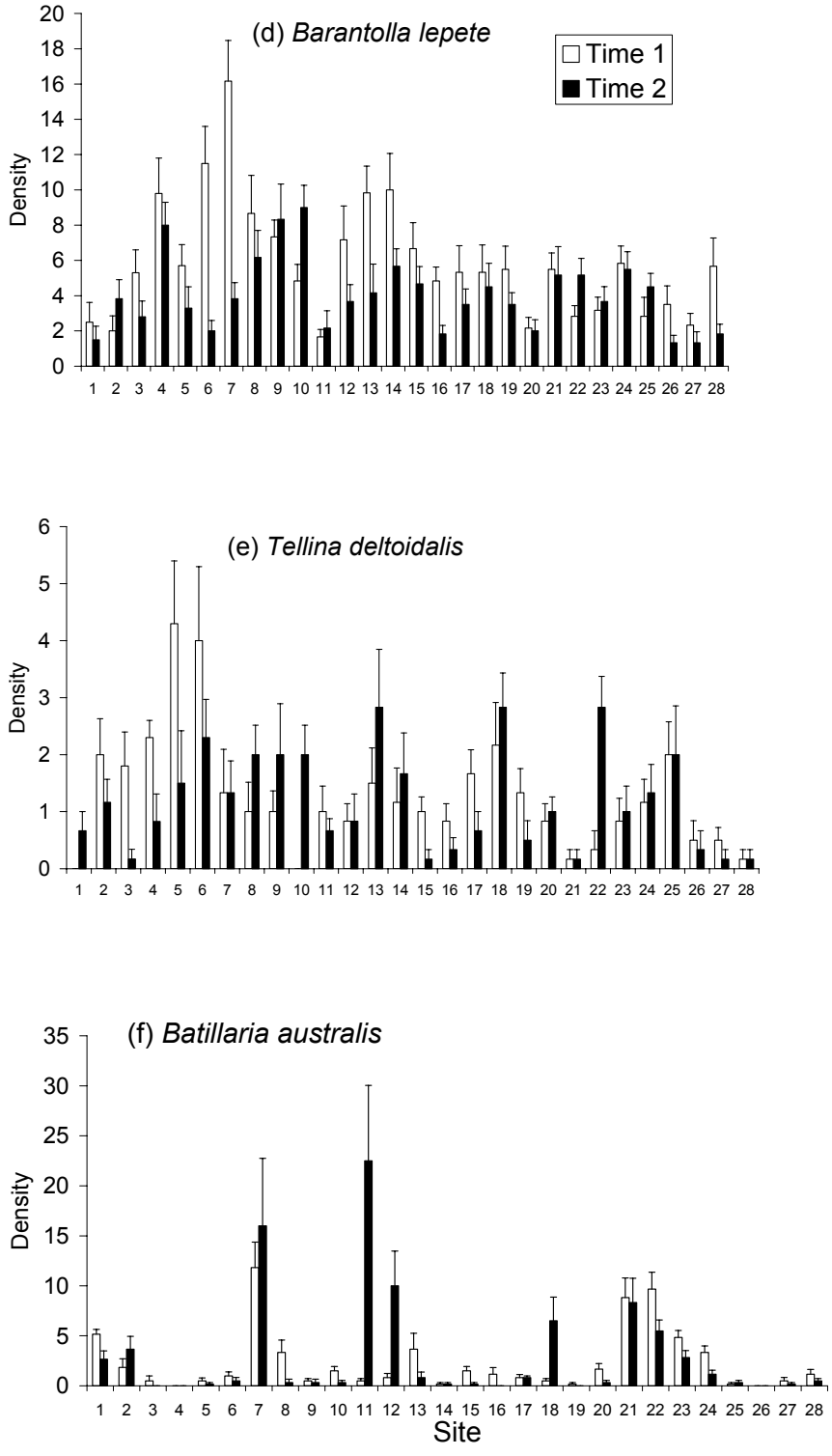

Fig. 3. Mean (± S.E., n = 6) values from seagrass for each site at each time of sampling.

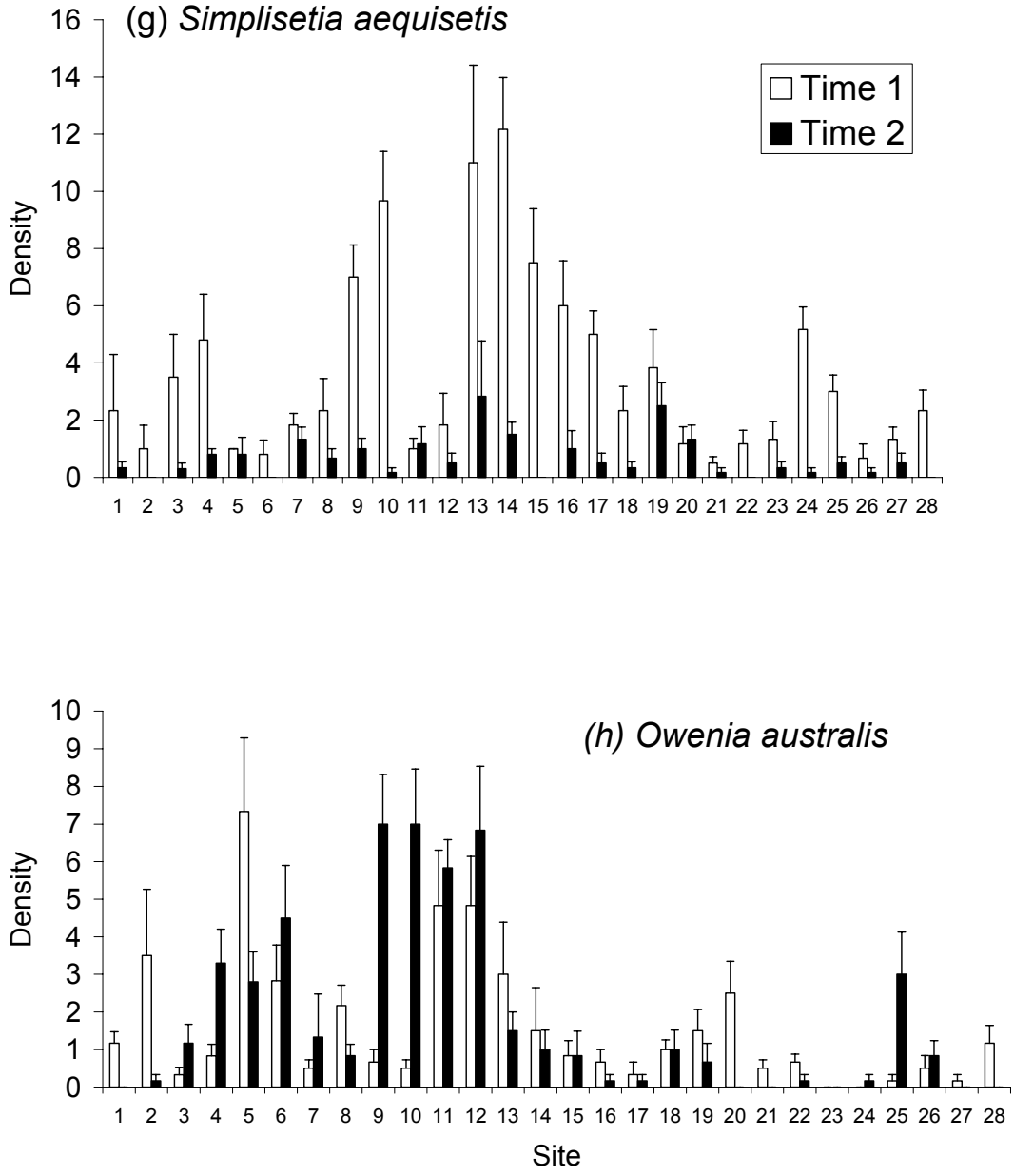

Fig. 3. Mean (± S.E., n = 6) values from seagrass for each site at each time of sampling.

Density of the polychaete worm *S. aequisetis* (Nereididae) (Fig. 3g) decreased only at 1 location in 5 areas and decreased at both locations in 2 areas. Density of the polychaete worm *O. australis* (Owenidae) (Fig. 3h) underwent complex patterns of change over time: density decreased at only 1 location in 2 areas, increased at only 1 location in one area, and increased at 1 location and decreased at the other location in 2 areas. These patterns of change over time were not spatially congruent between species. For example, within location 1 in area 1 density of *T. deltoidalis, B. australis*, and *S. aequisetis* did not change over time and density of *O. fusiformis* significantly declined. Within location 2 in area 1 density of *T. deltoidalis* and *S. aequisetis* significantly declined over time, density of *B. australis* did not significantly change, and density of *O. australis* significantly increased. The variance between replicate samples for these five variables was always greater than the variance associated with the significant interaction.

Only one variable (total density of macroinvertebrates) did not exhibit any significant interactions in its variation (Table 3). Total density (Fig. 3b) differed between times (declining between sampling times 1 and 2), areas, and sites(location(area)). Significant variation in total density between sites occurred only in one location in three areas (areas 1, 2 and 6). The magnitude of variation between replicate samples (σ^2=0.10) was exceeded only by the variation due to time (σ^2=0.18).

The spatial pattern of macroinvertebrate assemblages of seagrass (Fig. 4) consisted of four groups representing: the most northern location in the estuary (Fagan's Bay, sites 1 and 2), two groups near the estuary entrance at Wagstaff (sites 25 and 26) and Hardy's Bay (sites 27 and 28), and a large group of all other locations (Fig. 2). A similar spatial pattern was evident in sampling time 2, with the two locations closest to the estuary entrance being more similar to one another based on the closer positions on the ordination plot. A group of locations consisting of St. Hubert's Island (sites 17 and 18) and Kincumber Broadwater (sites 21-24) had similar assemblages. There was little difference in the assemblage at all other locations, as shown by the large overlap of sites on the ordination plot (Fig. 4).

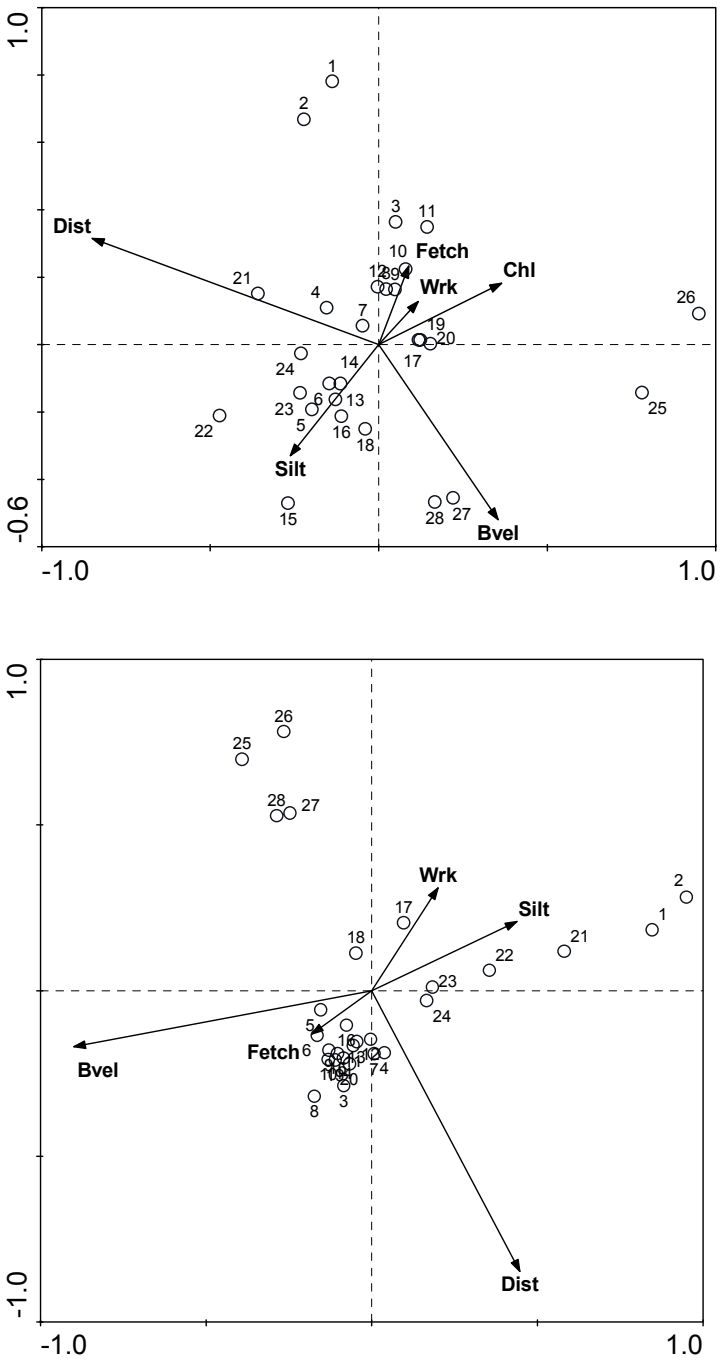

Fig. 4. Partial canonical correspondence analysis (CCA) ordination diagram of macroinvertebrates in seagrass based on the total abundance (square-root transformed) of macroinvertebrates in each site in sampling time 1 (upper) and sampling time 2 (lower). Sites are numbered from 1-28 (see Fig. 1). The first (horizontal) and second (vertical) CCA axes are shown. The environmental variables (shown by arrows) that explained a significant proportion of the spatial variation in the assemblages were selected by manual forward selection (Dist: distance to estuary entrance; Wrk: biomass of seagrass wrack; Chl: water column chlorophyll; Bvel: bottom velocity; Silt: silt/clay content of sediment).

Results of the PERMANOVA test reflected the temporal variation in spatial patterns revealed in the ordinations. Spatial variation in the assemblage exhibited complex and significant interactions with time at the spatial scale of sites (Table 4). Post-hoc examination of mean values for the significant time x site(location(area)) interaction showed the following results: sites that were not significantly different in time 1 were significantly different in time 2 (n=3 locations); sites that were not significantly different in time 1 were also not significantly different in time 2 (n=5 locations); sites that were significantly different in time 1 were also significantly different in time 2 (n=1 location); and sites that were significantly different in time 1 were not significantly different in time 2 (n=5 locations). However, the largest variation in assemblage structure occurred at the smallest spatial scale i.e. between replicate samples (σ^2=34.45).

Table 4. Results of permutational multivariate analysis of variance of macroinvertebrate assemblages in the seagrass habitat. Analysis was based on the Bray-Curtis dissimilarity measure of square-root transformed data. Variance (σ^2) estimates calculated from the MS values in this table and the same logic as in Table 1. Square-roots of the calculated variances are shown (Anderson et al., 2005)

Source	*df*	MS	*F*	σ^2
Time=T	1	45720.97	7.54 ***	15.36
Area=A	6	16173.01	1.42 ns[1]	9.93
Location=L(A)	7	11348.98	no test	13.48
Site=S(L(A))	14	2907.89	1.54 **	9.21
T x A	6	6067.06	1.03 ns	1.99
T x L(A)	7	5971.99	3.16 ***	18.44
T x S(L(A))	14	1891.04	1.59 ***	10.83
Residual	280	1187.10		34.45

[1] after eliminating T*A because non-significant at $P > 0.25$ and testing against L(A)

ns $P > 0.05$, ** $P < 0.01$, *** $P < 0.001$

Relationships with environmental variables

A number of the environmental variables in the seagrass habitat were significantly correlated (Table 5). Seagrass and wrack biomass, and sediment organic matter and total pigments, were significantly correlated in both sampling times. Bed shear was negatively correlated with distance to the estuary entrance and fetch. Bed shear and bottom velocity were significantly correlated. The other variables that were significantly correlated changed between sampling times.

Hierarchical partitioning identified 5 variables in time 1 (sediment photosynthetic pigments, wrack biomass, water column chlorophyll, bottom velocity, and bed shear) and 6 variables in time 2 (seagrass biomass, sediment organic matter, sediment photosynthetic pigments, fetch, bottom velocity, and bed shear) as having significant independent contributions to variation in the biological variables (Table 6).

The multiple regression models (Table 7) explained between 18 and 37% of total variation in the biological variables in time 1 and between 18 and 47% of total variation in time 2, suggesting that other unmeasured variables or combinations of variables were also important in explaining the observed variation. The environmental variables included in the models for total density and total biomass of macroinvertebrates differed between sampling times, whereas the same suite of environmental variables explained variation in species richness in both sampling times (with the exception of the addition of seagrass biomass and sediment organic matter in time 2).

Table 5. Spearman rank correlation coefficients (n=28) between the seagrass habitat environmental variables silt/clay content of sediment (% sample weight), seagrass biomass (g m^{-2}), wrack biomass (g m^{-2}), water column chlorophyll (Chlor.) (μg L^{-1}), distance to estuary entrance (Dist.) (km), fetch (km), % organic matter of sediment (Org.), concentration of photosynthetic pigments in sediment (Pigm.) (μg cm^{-3}), bottom velocity (Bvel) (m s^{-1}), and bed shear (Shear) (N m^{-2}). Unless stated otherwise correlations are not statistically significant at $\alpha = 0.05$ (* $P<0.05$, ** $P<0.01$). Results for each time have not been corrected for multiple comparisons so at $\alpha=0.05$ two of the significant correlations may have occurred by chance.

(a) Time 1

	Silt/clay	Seagrass	Wrack	Chlor.	Dist.	Fetch	Org.	Pigm.	Bvel
Seagrass	-0.20								
Wrack	0.08	**0.47***							
Chlor.	0.01	**-0.38***	**-0.43***						
Dist.	0.01	0.14	0.18	-0.12					
Fetch	-0.09	0.11	-0.30	**0.46***	0.06				
Org.	**0.42***	-0.19	0.30	0.14	0.22	-0.32			
Pigm.	0.24	-0.28	0.22	-0.07	**0.65****	-0.20	**0.50****		
Bvel	**-0.39***	0.12	0.18	0.29	-0.22	0.25	-0.20	-0.32	
Shear	-0.27	0.09	0.35	-0.37	**-0.42***	**-0.60****	-0.16	-0.27	**0.44***

(b) Time 2

	Silt/clay	Seagrass	Wrack	Chlor.	Dist.	Fetch	Org.	Pigm.	Bvel
Seagrass	0.25								
Wrack	0.23	**0.47***							
Chlor.	-0.15	0.23	-0.04						
Dist.	**0.43***	0.28	0.05	0.13					
Fetch	-0.09	-0.25	**-0.44***	0.31	0.06				
Org.	0.30	-0.22	0.27	-0.33	0.15	**-0.40***			
Pigm.	0.03	-0.19	0.29	-0.04	0.25	-0.25	**0.57****		
Bvel	-0.14	0.13	0.17	0.29	-0.22	0.25	**-0.48****	-0.30	
Shear	-0.10	0.29	**0.41***	-0.02	**-0.42***	**-0.60****	-0.18	-0.12	**0.44***

Table 6. Results of hierarchical partitioning for seagrass habitat for species richness, total density of macroinvertebrates, total biomass of macroinvertebrates (log_{10}-transformed) and the predictor variables silt/clay content of sediment (log_{10}-transformed), seagrass biomass (log_{10}-transformed), wrack biomass (log_{10}-transformed), water column chlorophyll (log_{10}-transformed), distance to estuary entrance, fetch (log_{10}-transformed), % organic matter of sediment (log_{10}-transformed), and pigment content of sediment (log_{10}-transformed). The value shown for each predictor variable is its % independent contribution to total variation in the response variables (rounded to 2 decimal places). * indicates the contribution of a predictor variable is significantly different from random (at α=0.05).

(a) Time 1

	Species	Density	Biomass
Silt/clay	5.58	4.37	20.29
Seagrass	1.38	1.74	4.14
Wrack	1.15	12.27*	1.77
Chlor.	1.44	2.34	42.98*
Dist.	6.58	10.42	11.39
Fetch	3.13	3.37	2.43
Org.	4.39	1.21	3.02
Pigm.	19.37*	2.15	3.30
Bvel	18.07*	12.84*	6.15
Shear	38.91*	49.29*	4.53

(b) Time 2

	Species	Density	Biomass
Silt/clay	2.95	4.02	3.42
Seagrass	14.86*	35.65*	12.00
Wrack	2.81	4.37	7.21
Chlor.	6.17	8.94	10.62
Dist.	8.38	14.92	3.10
Fetch	2.28	11.14	30.46*
Org.	12.78*	9.56	12.36
Pigm.	10.62*	1.94	2.20
Bvel	13.47*	1.66	2.71
Shear	25.68*	7.78	15.94

Table 7. Multiple regression models for seagrass habitat using predictor variables identified by hierarchical partitioning (see Table 6) as having a significant independent influence on the spatial distribution of the response variables. Abbreviations and transformations used are shown in Table 6. Adjusted R^2-values are shown for models where more than 1 predictor variable has been selected

(a) Time 1

Response variable	Model	F	R^2
Species richness	y = 37.9 - 2.56(Pigm.) +1.6(Bvel) + 2.03 (Shear)	$F_{3,24}$=6.35**	0.37
Total density	y = 6587 + 454(Wrack) + 344(Bvel) + 671(Shear)	$F_{3,24}$=3.02*	0.18
Total biomass	y = 19.4 + 3.04(Chlor.)	$F_{1,26}$=8.17**	0.21

(b) Time 2

Response variable	Model	F	R^2
Species richness	y = 30.6 + 2.04(Seagrass) – 1.48(Org.) – 1.29(Pigm.) + 1.43(Bvel) + 2.48 (Shear)	$F_{5,22}$=5.79***	0.47
Total density	y = 3600 + 632(Seagrass)	$F_{1,26}$=9.38**	0.24
Total biomass	y = 13.6 + 3.20(Fetch)	$F_{1,26}$=7.05*	0.18

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

The spatial patterns of assemblages in time 1 were related (in order of importance) to: distance to estuary entrance ($\lambda = 0.13$), silt/clay content of sediment ($\lambda = 0.10$), bottom velocity ($\lambda = 0.08$), wrack biomass ($\lambda = 0.08$), fetch ($\lambda = 0.06$), water column chlorophyll ($\lambda = 0.06$) (Table 8). The first CCA axis (Fig. 4) represents a gradient of distance to estuary entrance and bottom velocity, with high values for each at the left and right-hand ends, respectively, of the axis. The second CCA axis represents gradients in silt/clay content (high values at the lower end), and wrack biomass, fetch and water column cholorphyll (high values at the upper end). The Fagan's Bay location (sites 1 and 2) was characterized by a large distance from the estuary entrance and low values of bottom velocity. The Wagstaff location (sites 25 and 26) was characterized by a small distance to the estuary entrance and high bottom velocity (Fig. 4). Axes 1 and 2 explained, respectively, 30.0% and 21.7% of the relationship between spatial patterns of assemblages and environmental variables, and this relationship explained 41% of total variation in assemblages (Table 8).

Spatial patterns in assemblages of seagrass in time 2 were related to bottom velocity ($\lambda = 0.13$), distance to estuary entrance ($\lambda = 0.10$), fetch ($\lambda = 0.09$), silt/clay content of sediment ($\lambda = 0.08$), and wrack biomass ($\lambda = 0.07$) (Table 8). The first CCA axis represents a gradient in bottom velocity (high values at the left-hand side) and silt/clay content of sediment (high values at the right-hand end of the axis). The second axis represents a gradient in distance to the estuary entrance (large values at the bottom of the ordination) (Fig. 4). Locations at Fagan's Bay (sites 1 and 2), St. Hubert's Island (sites 17 and 18) and Kincumber Broadwater (sites 21-24) were characterized by increasing amounts of wrack and silt/clay in the sediment (Fig. 4). CCA axes 1 and 2 explained, respectively, 31.7% and 22.2% of the variation in the relationship between spatial patterns of assemblages and environmental variables, and this relationship explained 32% of the total variation in assemblages (Table 8).

Table 8. Summary results of partial canonical correspondence analysis (CCA) for macroinvertebrate species abundance in seagrass at each sampling occasion. Abundance data were square-root transformed prior to analysis. Variables included are those selected by manual forward selection to explain a significant amount (at $\alpha = 0.05$) of variation in the species data and only significant variables are shown. Conditional effect for each selected variable (in brackets) is the proportion of variation in the species data explained by each of the environmental variables selected in addition to the proportion explained by the first variable selected. The significance of conditional effects was determined by Monte Carlo test (999 unrestricted permutations) (* $P<0.05$, ** $P<0.01$).

Time	Variables included	Inter-set correlations		Eigenvalues		% variance explained		Total inertia	Canonical inertia	R^2
		Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2			
1	Distance (0.13**)	-0.80	0.28	0.15	0.11	30.0	21.7	1.23	0.51	0.41
	Silt (0.10**)	-0.25	-0.30							
	Bvel (0.08**)	0.33	-0.47							
	Wrack (0.08**)	0.11	0.12							
	Fetch (0.06**)	0.08	0.21							
	Chl (0.06**)	0.34	0.16							
2	Bvel (0.13**)	-0.83	-0.16	0.15	0.10	31.7	22.2	1.42	0.46	0.32
	Distance (0.10**)	0.41	-0.78							
	Fetch (0.09**)	-0.17	-0.12							
	Silt (0.08*)	0.41	0.19							
	Wrack (0.07*)	0.19	0.29							

Distance: distance to estuary entrance; silt: silt/clay content of sediment; Bvel: bottom velocity; wrack: biomass of seagrass wrack; Chl: water column chlorophyll.

Unvegetated subtidal sediment

General characteristics of the macroinvertebrate fauna of unvegetated subtidal sediment

A total of 67 species (2,891 individuals) were recorded from unvegetated subtidal sediment with an average of 7 species (range=1-16) and 24 individuals (range=1-205) per replicate sample. Macroinvertebrate assemblages of unvegetated subtidal sediment were numerically dominated by polychaetes (53% of total abundance), molluscs (23% of total abundance), crustaceans (19% of total abundance), and ophiuiroids (4% of total abundance). The most abundant species were the polychaetes *Owenia australis* and *Maldene sarsi* (together representing 33% of total abundance), the amphipod *Limnoporeia kingi* (8% of total abundance), the bivalve mollusc *Dosinia sculpta* (4% of total abundance), and a brittlestar (Ophiodermatidae, 4% of total abundance). Biomass was dominated by polychaetes (81% of total biomass) and molluscs (15% of total biomass). Species contributing the most to biomass included the polychaetes *O. fusiformis*, *M. sarsi*, and *S. aequisetis* (together representing 64% of total biomass), the gastropod mollusc *B. lacertinium* (7% of total biomass), and ophiodermatid brittlestars (3% of total biomass).

The greatest numbers of species in unvegetated sediments were recorded at Wagstaff (48 species) and St. Hubert's Island (43 species) (Table 2b). Mean density and biomass of macroinvertebrates were both greatest at Wagstaff: 53.54 ± 16.99 animals per core and 150.36 ± 65.85 mg AFDW per core respectively.

Spatial and temporal variation in macroinvertebrate assemblages of unvegetated subtidal sediments

Six variables showed significant time x site(location) interactions in average values: number of species, total density, total biomass, and density of *Owenia australis*, *Maldene*

sarsi, and *Limnoporeia kingi* (Table 9 and Fig. 5). Number of species declined significantly between sampling times in one site only in each of 2 locations, decreased significantly at both sites in 1 location, increased significantly at 1 site and decreased significantly at the other site in 1 location, and did not change in either site in 1 location (Fig. 5a, Table 9). This time x site(location) interaction contributed the greatest amount to total variation in number of species (σ^2=11.96). Total density significantly declined in only 1 site in each of 3 locations (and was unchanged at the other site) and declined significantly in both sites in 2 locations (Fig. 5b). The magnitude of the variation associated with this significant interaction (σ^2=0.24) was similar to the variation between replicate samples (σ^2=0.27). Total biomass increased significantly over time at 1 site in 1 location, decreased significantly at 1 site in 2 locations, decreased significantly at both sites in 1 location, and did not change at either site in 1 location (Fig. 5c). Variation associated with this significant time x site(location) interaction (σ^2=0.35) was less than the variation that occurred between replicate samples (σ^2=1.34) (Table 9).

Density of the polychaete worm *O. australis* (Owenidae) (Fig. 5d) declined significantly at both sites in 3 locations and did not change significantly at either site in the other 2 locations, producing a significant time x site(location) interaction. Although density declined significantly in both sites in 3 locations, the magnitude of the decline differed between sites, leading to the result that in 2 of these locations sites that were not significantly different in time 1 were significantly different in time 2. The largest variation occurred between locations (σ^2=2.30).Density of the polychaete worm *M. sarsi* (Maldanidae) (Fig. 5e) declined significantly at 1 site in 1 location but was unchanged at the other site in that location, and unchanged at sites in all other locations. The largest variation occurred between replicate samples (σ^2=19.95). Density of the amphipod *L. kingi* (Phoxocephalidae) (Fig. 5f) decreased significantly in density at only 1 site in all locations between sampling times. The significant interaction was reflected in the greatest source of variation occurring in the time x site(location) interaction (σ^2=13.60).

Table 9. Summary of results of 3-factor ANOVA (see Table 1 for design) for species (untransformed, variances heterogeneous), total density (ln(x+1.5) transformed), total biomass (ln(x) transformed), and density of *Owenia australis* (ln(x+0.1) transformed), *Maldene sarsi* (untransformed, variances heterogeneous), *Limnoporeia kingi* (untransformed, variances heterogeneous), *Dosinia sculpta* (ln(x+0.1) transformed), and Ophiodermatidae brittlestars (ln(x+0.01) transformed) from unvegetated sediments.

		Species			Total density		
Source	*df*	MS	*F*	σ^2	MS	*F*	σ^2
Time=T	1	200.21	12.09 *	2.06	19.64	23.28**	0.30
Location=L	4	60.98	3.68 ns [1]	0	7.71	9.14 *[1]	0.25
Site=S(L)	5	20.99	0.28 ns	0	1.26	0.74 ns	0
T x L	4	16.56	0.22 ns	0	0.84	0.5 ns	0
T x S(L)	5	76.33	16.81 ***	11.96	1.70	6.3 ***	0.24
Residual	100	4.54		4.54	0.27		0.27

		Total biomass			*O. australis*		
Source	*df*	MS	*F*	σ^2	MS	*F*	σ^2
Time=T	1	6.05	0.6 ns	0	75.85	5.69 ns	1.04
Location=L	4	10.22	1.01 ns[1]	0	68.44	5.13 ns[1]	2.30
Site=S(L)	5	6.37	1.84 ns	0.24	1.64	0.43 ns	0
T x L	4	10.12	2.92 ns	0.55	13.33	3.49 ns	0.79
T x S(L)	5	3.47	2.59 *	0.35	3.82	2.98 *	0.42
Residual	100	1.34		1.34	1.28		1.28

1 after eliminating S(L) because non-significant at $P > 0.25$ and testing against T x L

ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 9 cont'd. Summary of results of 3-factor ANOVA (see Table 1 for design) for species (untransformed, variances heterogeneous), total density (ln(x+1.5) transformed), total biomass (ln(x) transformed), and density of *Owenia australis* (ln(x+0.1) transformed), *Maldene sarsi* (untransformed, variances heterogeneous), *Limnoporeia kingi* (untransformed, variances heterogeneous), *Dosinia sculpta* (ln(x+0.1) transformed), and Ophiodermatidae brittlestars (ln(x+0.01) transformed) from unvegetated sediments.

		M. sarsi			*L.kingi*		
Source	*df*	MS	*F*	σ^2	MS	*F*	σ^2
Time=T	1	91.88	0.56 ns	0	410.70	83.32 ***	5.47
Location=L	4	241.54	1.47 ns[1]	1.86	4.93	1 ns[1]	0
Site=S(L)	5	144.38	1.29 ns	2.73	82.48	1 ns1	0
T x L	4	164.04	1.47 ns	4.37	4.93	0.06 ns	0
T x S(L)	5	111.58	5.59***	15.27	82.48	91.31 ***	13.60
Residual	100	19.95		19.95	0.90		0.90

		D.sculpta			Ophiodermatidae		
Source	*df*	MS	*F*	σ^2	MS	*F*	σ^2
Time=T	1	38.36	8.87 *	0.57	0.35	0.03 ns	0
Location=L	4	9.11	2.11 ns[1]	0.20	109.81	no test	3.82
Site=S(L)	5	1.91	0.83 ns	0	6.39	2.82 ns	0.32
T x L	4	4.32	1.89 ns	0.17	13.63	6.02 *	0.92
T x S(L)	5	2.29	1.5 ns	0.13	2.26	0.87 ns	0
Residual	100	1.53		1.53	2.60		2.60

1 after eliminating S(L) because non-significant at $P > 0.25$ and testing against T x L

ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

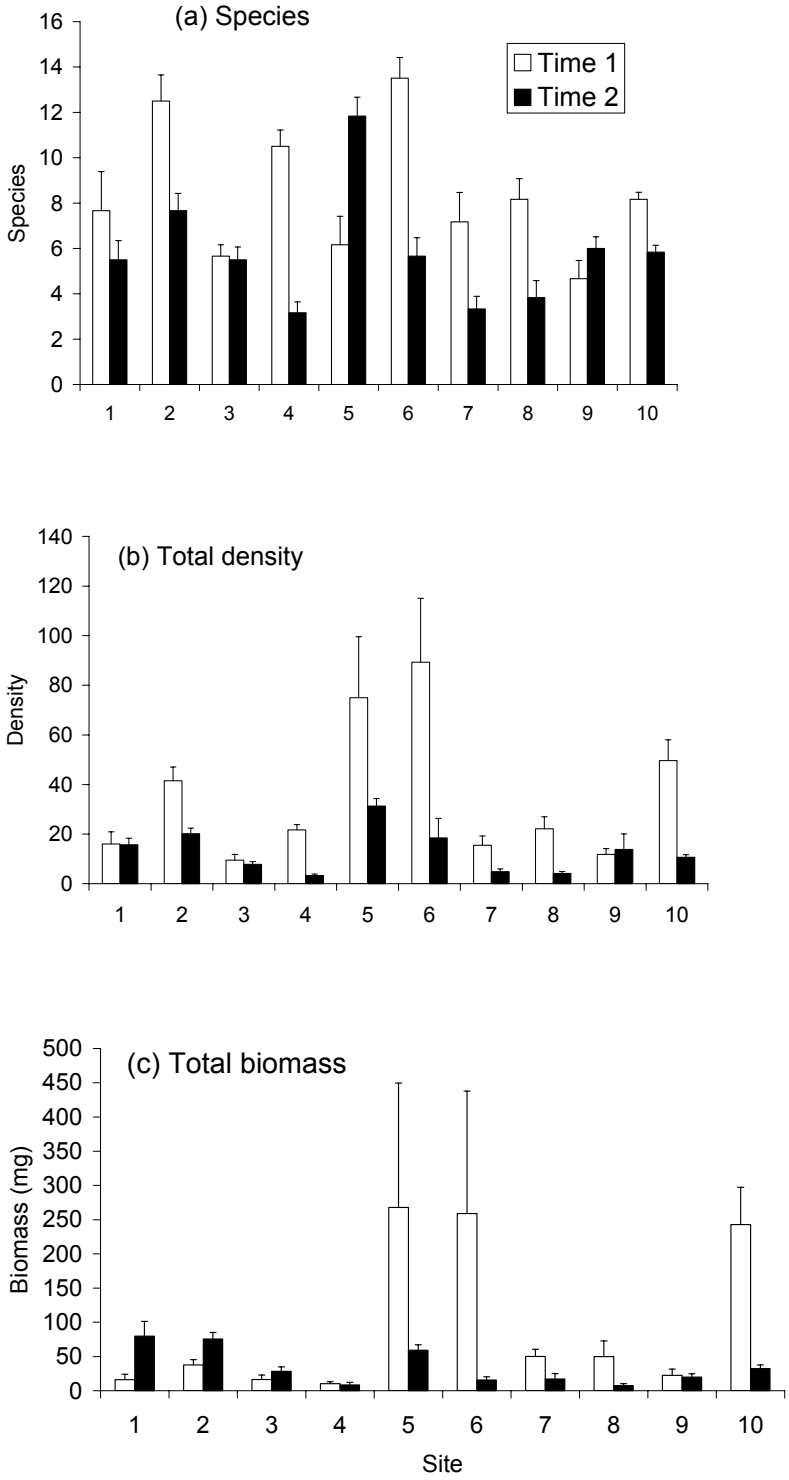

Fig. 5. Mean (± S.E., n = 6) values from unvegetated sediments for each site at each time of sampling.

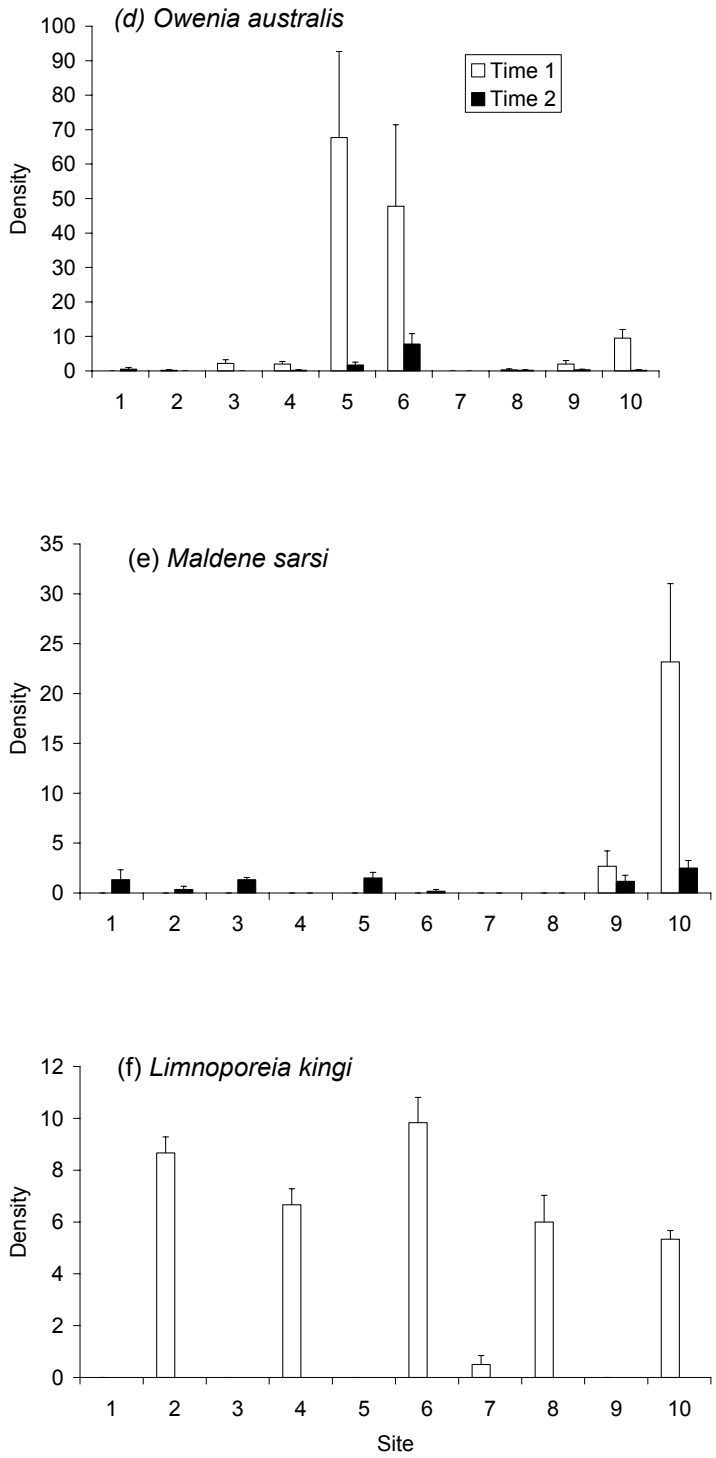

Fig. 5. Mean (± S.E., n = 6) values from unvegetated sediments for each site at each time of sampling.

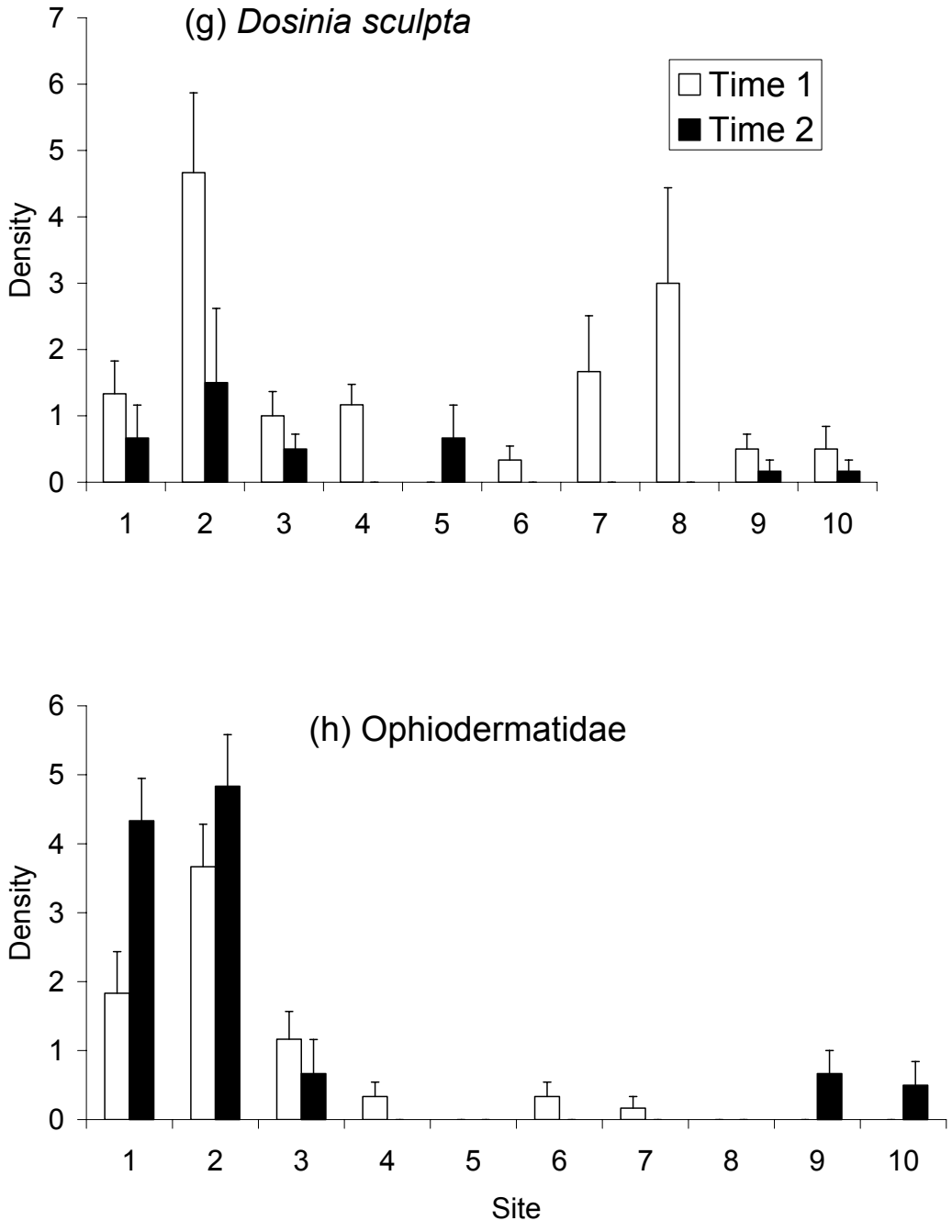

Fig. 5 Mean (± S.E., n = 6) values from unvegetated sediments for each site at each time of sampling.

Brittlestars of the family Ophiodermatidae exhibited a significant time x location interaction (Table 9). Examination of the graph of mean density (Fig. 5h) shows that brittlestars exhibited complex patterns of spatial variation, being present at different locations in each sampling time and changing density in different ways at sites where they were present at both sampling times. The largest variation occurred between locations (σ^2=3.82).

Density of the bivalve mollusc *Dosinia sculpta* (Veneridae) declined significantly between sampling times 1 and 2 across the estuary (Table 9, Fig. 5g). The largest variation occurred between replicate samples (σ^2=1.53).

The spatial pattern of assemblages in unvegetated subtidal sediments in time 1 coincided with the distribution of sites throughout the estuary, and there was little apparent difference in assemblages between sites within locations (Fig. 6). Assemblages at location 1 (sites 1 and 2) (Koolewong) and location 4 (sites 7 and 8) (St Hubert's Is) were separated from the other locations in the top half of the ordination plot, indicating differences in assemblage structure. The differences in assemblage structure between locations 1 and 4 and all other locations were also apparent in time 2, and the differences between all other locations were much less pronounced (Fig. 6).

Results of the PERMANOVA test showed that spatial patterns in the macroinvertebrate assemblages of unvegetated sediments at the scale of sites were not consistent through time, shown as a significant time x site(location) interaction (Table 10). Assemblages significantly differed between sites in each location in time 1 but were significantly different at only one location in time 2. Despite this significant effect, the variation in assemblage structure associated with the interaction between time and site (26.17) was less than the variation that occurred between replicate samples (42.76).

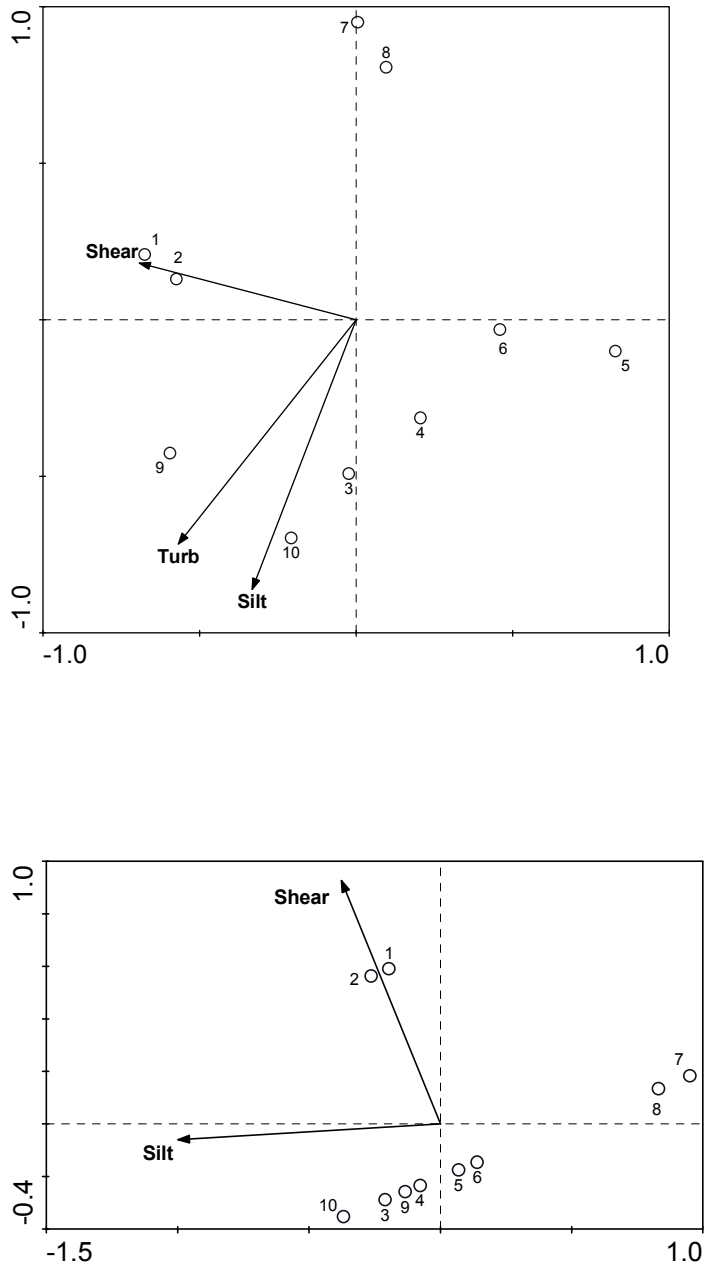

Fig. 6. Partial canonical correspondence analysis (CCA) ordination diagram of macroinvertebrates in unvegetated subtidal sediments based on the total abundance (square-root transformed) of macroinvertebrates in each site in sampling time 1 (upper) and sampling time 2 (lower). Sites are numbered from 1-10 (see Fig. 2). The first (horizontal) and second (vertical) CCA axes are shown. The environmental variables (shown by arrows) that explained a significant proportion of the spatial variation in the assemblages were selected by manual forward selection (Shear: bottom shear velocity; Turb: turbidity; Silt: silt/clay content of sediment).

Table 10. Results of permutational multivariate analysis of variance of macroinvertebrate assemblages in the unvegetated sediment habitat. Analysis was based on the Bray-Curtis dissimilarity measure of square-root transformed data. Variance (σ^2) estimates calculated from the MS values in this table and the same logic as in Table 1. Square-roots of the calculated variances are shown (Anderson et al., 2005)

Source	*df*	MS	*F*	σ^2
Time=T	1	48692.45	5.63***	25.83
Location=L	4	25691.18	2.97[1] ns	26.23
Site=S(L)	5	6470.19	1.09 ns	6.66
T x L	4	8650.63	1.46 ns	15.03
T x S(L)	5	5937.82	3.25 ***	26.17
Residual	100	1828.71		42.76

[1] after eliminating S(L) because non-significant at $P > 0.25$ and testing against T*L

ns $P > 0.05$, ** $P < 0.01$, *** $P < 0.001$

The influence of environmental variation on macroinvertebrate assemblages

Environmental variables in the unvegetated subtidal sediment habitat were significantly correlated (Table 11), although the pairs of variables that were significantly correlated differed between the 2 times. Chlorophyll concentration in surface and bottom water was significantly correlated in both times.

Table 11. Spearman rank correlation coefficients (n=10) between the environmental variables silt/clay content of sediment (% sample weight), turbidity (NFTU), surface water chlorophyll (SC) (μg L^{-1}), bottom water chlorophyll (BC) (μg L^{-1}), distance to estuary entrance (km), fetch (km), and bed shear (Shear) (N m^{-2}). Sediment pigment content was not sampled in this habitat and near-bottom velocity was not included because it did not differ between sites. Unless stated otherwise correlations are not statistically significant at $\alpha = 0.05$ (* $P<0.05$, ** $P<0.01$). Results for each time have not been corrected for multiple comparisons so at $\alpha=0.05$ two of the significant correlations may have occurred by chance.

(a) Time 1

	Silt	Turb.	SC	BC	Dist.	Fetch
Turb.	0.69*					
SC	0.09	0.18				
BC	0.27	0.36	**0.95****			
Dist.	0.27	0.35	**-0.69***	-0.61		
Fetch	0.45	0.48	**0.86****	**0.88****	-0.56	
Shear	0.44	0	0	0.09	-0.35	0.36

(a) Time 2

	Silt	Turb.	SC	BC	Dist.	Fetch
Turb.	-0.22					
SC	0.10	**-0.65***				
BC	0.16	-0.51	**0.82****			
Dist.	0.27	-0.11	-0.02	0.12		
Fetch	0.45	0.32	-0.26	-0.19	-0.56	
Shear	0.44	-0.52	0.61	0.35	-0.35	0.36

Spatial patterns in assemblages in time 1 were related to the silt/clay content of sediment ($\lambda = 0.26$), bottom shear velocity ($\lambda = 0.25$), and turbidity ($\lambda = 0.24$) (Table 12). The first CCA axis is correlated with bottom shear velocity (high values at the left-hand side of the axis) and the second axis is correlated with silt/clay content of sediment and turbidity (high values towards the bottom of the axis) (Fig. 6). Location 1 (sites 1 and 2) (Koolewong) was characterized by high bottom shear velocity. The remaining sites are distributed along a gradient of silt/clay content of sediment and turbidity from high values in sites 9 and 10 (Kincumber Broadwater), 3 and 4 (Woy Woy Bay), medium values in sites 5 and 6 (Wagstaff), and low values in sites 7 and 8 (St. Hubert's Is.). CCA axis 1 describes 37.2% of the variation in the relationship between assemblages and environmental variables and CCA axis 2 explains 36.8% of the variation. The selected variables together explain 54% of the spatial variation in assemblage structure.

Spatial patterns in assemblages in time 2 were related to the silt/clay content of sediment ($\lambda = 0.51$) and bottom shear velocity ($\lambda = 0.25$) (Table 12). The first CCA axis is correlated with silt/clay content of sediment (high values at the left-hand side of the axis) and the second axis is correlated with bottom shear velocity (high values towards the top of the axis) (Fig. 6). As found in sampling time 1 location 1 (sites 1 and 2) (Koolewong) was characterized by high bottom shear velocity. Sites in the lower half of the ordination plot represent a gradient in silt/clay content of sediment from high values at the right-hand side to low values at the left-hand side (sites 7 and 8). CCA axis 1 describes 67.9% of the variation in the relationship between assemblages and environmental variables and CCA axis 2 explains 32.1% of the variation. The selected variables together explain 47% of the spatial variation in assemblage structure.

Table 12. Summary results of partial canonical correspondence analysis (CCA) for macroinvertebrate species abundance in unvegetated sediments at each sampling occasion. Abundance data were square-root transformed prior to analysis. Variables included are those selected by manual forward selection to explain a significant amount (at $\alpha = 0.05$) of variation in the species data and only significant variables are shown. Conditional effect for each selected variable (in brackets) is the proportion of variation in the species data explained by each of the environmental variables selected in addition to the proportion explained by the first variable selected. The significance of conditional effects was determined by Monte Carlo test (999 unrestricted permutations) (* $P < 0.05$, ** $P < 0.01$)

Time	Variables included	Inter-set correlations		Eigenvalues		% variance explained		Total inertia	Canonical inertia	R^2
		Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2			
1	Silt (0.26*)	-0.33	-0.82	0.28	0.27	37.2	36.8	1.40	0.75	0.54
	Shear (0.25*)	-0.68	0.17							
	Turbidity (0.24**)	-0.56	-0.68							
2	Silt (0.51**)	-0.95	-0.05	0.52	0.24	67.9	32.1	1.61	0.76	0.47
	Shear (0.25*)	-0.36	0.89							

Silt: silt/clay content of sediment; Shear: bottom shear velocity.

DISCUSSION

The macroinvertebrates of seagrass and unvegetated sediments changed between sampling occasions and the temporal changes within each habitat were not spatially congruent. Macroinvertebrate biomass in seagrass changed significantly over time in different ways in sites separated by 100 m while total density of macroinvertebrates did not vary significantly between sampling times. Biomass and density of macroinvertebrates of unvegetated sediments varied between times at different ways in different sites. Biomass is regarded as a more stable property of macroinvertebrate assemblages within estuaries than density (Beukema 1974; Edgar 1990; Kaletja and Hockey, 1991; Edgar and Barrett, 2002), reflecting the slower turnover rate of large-bodied organisms. The significant changes in biomass that occurred at many sites between sampling time are therefore surprising.

Of the 5 species tested in seagrass 4 species (*Tellina deltoidalis, Batallaria australis, Simplisetia aequisetis, Owenia australis*) exhibited different patterns of temporal variation between locations 1-2 km apart. Another species (*Barantolla lepete*) exhibited different patterns of temporal variation between sites 100 m apart. Three species in the unvegetated sediments (*Owenia fusiformis, Maldene sarsi, Limnoporeia kingi*) exhibited different patterns of temporal variation at the scale of sites (100 m), 1 group of species (brittlestars of the family Ophiodermatidae) changed differently at the scale of locations (1-2 km) and 1 species (*Dosinia sculpta*) changed consistently between times at the scale of sites and locations. In addition, the entire assemblage of macroinvertebrates in both seagrass and unvegetated sediments showed significant interactions between temporal variation and spatial variation at the scale of sites. Interactions between temporal variation and spatial scale in species and entire assemblages observed in Brisbane Water estuary have also been observed in other estuaries (Ysebaert and Herman, 2002; Noren and Lindegarth, 2005) and can reflect large changes in abundance of smaller species over time scales similar to the time between samples used in this study (Edgar, 1990). Testing for the existence of these interactions is a fundamental requirement for determining the stability, or otherwise, of these systems (Morissey et al., 1992; Turner et al., 1995; Underwood, 1997; Noren and Lindegarth, 2005). This study therefore found that at the temporal scale examined

the macroinvertebrate assemblages of seagrass and unvegetated sediments were highly dynamic and exhibited complex interactions with spatial scale.

Interactions between time and either site (location(area)) or location (area) were the most frequently observed sources of significant variation for individual species and the entire macroinvertebrate assemblage. However, none of the time x site (location(area)) or time x location (area) interactions were spatially congruent between species within the same habitat. This result appears to contradict the general conclusion of Barry and Dayton (1991) that the magnitudes of spatial and temporal changes are correlated. Changes over a time scale of 6 mo in the present study were not widespread but often confined to a single site within 1 or more locations or a single location within 1 or more areas. This suggests that species are responding to different environmental factors that vary in intensity over a period of 6 mo (the time between sampling occasions) and are spatially patchy at the scale of sites (100s m) or locations (kms).

In some circumstances temporal variation may reflect sampling error rather than representing actual temporal variations in density. This could occur, for example, if samples collected on a second time of sampling were collected far enough away from the original collecting positions that they were taken from a different patch within the same habitat (Edgar and Barrett, 2002). Temporal variation would therefore be confounded with spatial variation. Considerable care was exercised in the current study to collect samples on the second sampling occasion as close as possible to the first sampling occasion within the same site without jeopardizing the independence of the samples. An alternative explanation for the observed time and space interaction is that it resulted from a Type 1 error. For example, testing for the source of the significant time x site(location (area)) interactions for total biomass of macroinvertebrates and density of *Barantolla lepete* in seagrass required 28 tests of the difference in sites between times. It is possible that 1.4 significant results may have occurred by chance alone. However, there were 17 and 8 significant differences between the 2 sampling times, respectively, in tests of total biomass and density of *B. lepete*. The significant time x site(location (area)) interactions are therefore unlikely to be a result of a Type 1 error Determining the source of the significant time x location(area) interaction in density of *Tellina deltoidalis, Batillaria australis,*

Simplisetia aequisetis, and *Owenia australis* required 14 tests of the difference in mean density of locations between the 2 sampling times. Significant differences between times occurred in 3, 4, 9 and 7 tests respectively. It is therefore likely that the observed temporal variation was a real difference between sampling occasions rather than being an artifact of the sampling strategy or statistical testing.

The major source of variation for most variables and entire assemblages in both habitats was spatial variation at the scale of individual replicates, representing spatial variation at the scale of 1-2 m in seagrass and 3-5 m in unvegetated sediments. Significant small-scale spatial variability at this and smaller spatial scales occurs in other estuaries (Volckaert et al., 1987; Thrush et al., 1989; Morrisey et al., 1992; Bergström et al., 2002; Ysebaert and Herman, 2002; Noren and Lindegarth, 2005). Considerable variation at this spatial scale is not surprising given the small size of the sampling unit relative to the potential mobility of some taxa (Lawrie and Raffaelli, 1998; Ford et al., 1999; Norderhaug et al., 2002), the random distribution of some macroinvertebrates (Noren and Lindegarth, 2005) and small-sale patchiness in resource availability and intensity of inter-specific interactions (Olafsson et al., 1994).

The results of this study have several important implications for the use of macroinvertebrates in estuarine monitoring programs and the assessment of the impacts of human activities. First, the number of replicate samples used in this study (n=6) was appropriate, as many significant differences were detected. Second, a limited number of places randomly chosen as controls cannot be regarded as sufficiently representative of other unsampled areas for the purposes of testing a significant change at a potentially impacted place. Third, an impact will have to cause a very large change in a variable to be detected as a significant change in the difference between the impacted and controls places in their natural patterns of spatio-temporal variability (Underwood, 1992, 1993). Fourth, variability at several smaller nested temporal scales (e.g. between days, weeks) may be required to ensure that differences between larger temporal scales (months, years) are not confounded by greater differences at smaller temporal scales (Morisey et al., 1992b). Sixth, the existence of significant variability at all of the spatial scales examined indicates that monitoring which targets several species will need to include several nested spatial scales and therefore represent a considerable sampling effort.

Regression models were developed to explain the relationship between biological variables (species richness, total density and total biomass of macroinvertebrates) and the environmental characteristics of the seagrass habitat at the spatial scale of sites (100s m). The environmental variables included in regression models for species richness in both sampling times included variables related to primary productivity (total photosynthetic pigments, biomass of seagrass, sediment organic matter content). Significant relationships between macroinvertebrates and primary productivity have been described for other estuaries (Howard et al., 1989; Heck et al., 1995; Heip et al., 1995). The most consistently selected environmental variables were near-bottom velocity and bed shear, which had a positive effect on species richness in both sampling times and total density in time 1.

Environmental variables selected by CCA to explain spatial patterns in macroinvertebrate assemblages of seagrass differed between sampling occasions but included a consistent set of 3 variables: distance to estuary entrance, fetch, and silt/clay content of sediment. Fetch has also been shown to be important in other estuaries (Edgar and Shaw, 1995). Distance to the estuary entrance is also likely to be a surrogate measure for the degree of estuarine flushing and salinity, both of which have been shown to be significant predictors of estuarine macroinvertebrate density (Ardisson and Bourget, 1997). The total set of selected variables included local-scale characteristics of the seagrass bed (photosynthetic pigment and silt/clay content of sediment, wrack biomass, seagrass biomass, organic matter) and the position of the seagrass within the estuary (measured as distance to estuary entrance and fetch).

A frequently used rationale for describing scales of spatial and temporal variability in estuarine biodiversity and testing for its relationship to environmental variation is to provide guidance to estuary managers about how management can intervene to maintain natural patterns and processes (Noren and Lindegarth, 2005). The results of this study underscore the complexity of this objective, as a result of differences between species in the nature of the interaction between time and spatial scale, differences between habitats in the environmental variables associated with spatial patterns in macroinvertebrate biodiversity, and changes in the identity of these environmental variables over time. Each of the measured environmental variables

explained some of the spatial variation in species and/or assemblages in one or both sampling times. The modest R^2 values indicate that other unmeasured variables are also likely to be important. Although the multiple regression and CCA techniques suggested some environmental variables that may be important in explaining spatial patterns in the species and assemblages of macroinvertebrates this needs to be followed by more detailed studies of individual species and an experimental approach to testing to role of these variables. The change between sampling times in identity of some of the environmental variables significantly associated with spatial variation in macroinvertebrates stresses the importance of continued testing of species-environment relationships and brings into question the generality of species-environment relationships derived from studies conducted at one point in time.

ACKNOWLEDGEMENTS

This study was funded by Gosford City Council. Thanks to Dr Peter Freewater (Gosford City Council) for initiating the study, providing critical input at all stages and for project management. Thanks to the Research Management Committee, University of Newcastle, for supplementary funding that allowed the analysis of environmental variables and partly supported the costs of field work and to Dr Redden for collaborating on the successful grant application. Thanks very much to Vanessa Owen for excellent field work, specimen sorting and counting, data compilation, and assistance at all stages of this project. Thanks to Donna Cohen for her field collection and laboratory analysis of the environmental variables. The collection and laboratory analysis of the environmental samples was supervised by Dr Anna Redden. Thanks very much to Dr Jo Wilson for the benthic grab and pole corer that allowed collection of samples for benthic microalgae. This project involved a considerable amount of species identification and initial species identification was done by Vanessa Owen with the assistance of Anna Murray (Australian Museum) who confirmed species identification and provided general guidance on identification. Further taxonomic advice and input was provided by Dr Pat Hutchings (Australian Museum) and Mohammad Reza Shokri and their assistance is gratefully acknowledged. Additional assistance in the field sampling was provided by Dr Anna Redden, Natalie Donnelly, Mohammad Reza Shokri and Dr Jo Wilson.

REFERENCES

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32-46.

Anderson, M.J., Diebel, C.E., Blom, W.M., Landers, T.J., 2005. Consistency and variation in kelp holdfast assemblages: spatial patterns of biodiversity for the major phyla at different taxonomic resolutions. J. Exp. Mar. Biol. Ecol. 320, 35-56.

Andrew, N.L., Mapstone, B.D., 1987. Sampling and the description of spatial pattern in marine ecology. Oceanogr. Mar. Biol. Ann. Rev. 25, 39-90.

Ardisson, P.-L., Bourget, E., 1997. A study of the relationship between freshwater runoff and benthos abundance: a scale-oriented approach. Estuarine, Coast. Shelf Sci. 45, 535-545.

Barry, J.P., & Dayton, P.K., 1991. Physical heterogeneity and the organization of marine communities. In: Kolasa, J., Pickett, S.T.A. (Eds.), Ecological Heterogeneity. Springer-Verlag, New York, pp. 270-320.

Bergström, U., Englund, G., Bonsdorff, E., 2002. Small-scale spatial structure of Baltic Sea zoobenthos – inferring processes from patterns. J. Exp. Mar. Biol. Ecol. 281, 123-136.

Beukema, J.J., 1974. Seasonal changes in the biomass of the macro-benthos of a tidal flat area in the Dutch Wadden Sea. Neth. J. Sea Res. 8, 94-107.

Cheng, D., 1994. Environmental study of Brisbane Water. University of Technology, Sydney.

Chapman, M.G., 2002. Early colonization of shallow, subtidal boulders in two habitats. J. Exp. Mar. Biol. Ecol. 275, 95-116.

Chevan, A., Sutherland, M., 1991. Hierarchical partitioning. Amer. Stat. 45, 90-96.

Dauvin, J-C., Thiébaut, E., Gesteira, J.L.G., Ghertsos, K., Gentil, F., Ropert, M., Sylvand, B., 2004. Spatial structure of a subtidal macrobenthic community in the Bay of Veys (western Bay of Seine, English Channel). J. Exp. Mar. Biol. Ecol. 307, 217-235.

Edgar, G.J., 1990. The use of the size of benthic macrofaunal communities to estimate faunal biomass and secondary production. J. Exp. Mar. Biol. Ecol. 137, 195-214.

Edgar, G.J., Barrett, N.S., 2002. Benthic macrofauna in Tasmanian estuaries: scales of distribution and relationships with environmental variables. J. Exp. Mar. Biol. Ecol. 270, 1-24.

Edgar, G.J., Shaw, C., 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia III. General relationships between sediments, seagrasses, invertebrates and fishes. J. Exp. Mar. Biol. Ecol. 194, 107-131.

Fletcher, D.J., Underwood, A.J., 2002. How to cope with negative estimates of components of variance in ecological field studies. J. Exp. Mar. Biol. Ecol. 273, 89-95.

Ford, R.B., Thrush, S.F., Probert, P.K., 1999. Macrobenthic colonisation of disturbances on an intertidal sandflat: the influence of season and buried algae. Mar. Ecol. Prog. Ser. 191, 163-174.

Gaston, K.J., 1994. Rarity. Chapman and Hall, London, 205 pp.

Graham, M.H., Edwards, M.S., 2001. Statistical significance versus fit: estimating the importance of individual factors in ecological analysis of variance. Oikos 93, 505-513.

Heck, K.L., Able, K.W., Roman, C.T., Fahay, M.P., 1995. Composition, abundance, biomass, and production of macrofauna in a New England estuary: comparisons among eelgrass meadows and other nursery habitats. Estuaries 18, 379-389.

Heip, C.H.R., Goosen, N.K., Herman, P.M.J., Kromkamp, J., Middelburg, J.J., Soetaert, K., 1995. Production and consumption of biological particles in temperate tidal estuaries. Oceanogr. Mar. Biol. 33, 1-149.

Howard, R.K., Edgar, G.J., Hutchings, P.A., 1989. Faunal assemblages of seagrass beds. In: Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (Eds.), Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region. Elsevier, Amsterdam, pp. 536-564.

Kalejta, B., Hockey, P.A.R., 1991. Distribution, abundance and productivity of benthic invertebrates at the Berg River estuary, South Africa. Est. Coast. Shelf Sci. 33, 175-191.

Kendall, M.A., Widdicombe, S., 1999. Small scale patterns in the structure of macrofaunal assemblages of shallow soft sediments. J. Exp. Mar. Biol. Ecol. 237, 127-140.

Lawrie, S.M., Raffaelli, D.G., 1998. In situ swimming behaviour of the amphipod *Corophium volutator* (Pallas). J. Exp. Mar. Biol. Ecol. 224, 237-251.

Legendre, P., Thrush, S.F., Cummings, V.J., Dayton, P.K., Grant, J., Hewitt, J.E., Hines, A.H., McArdle, B.H., Pridmore, R.D., Schneider, D.C., Turner, S.J., Whitlach, R.B., Wilkinson, M.R., Spatial structure of bivalves in a sandflat: scale and generating processes. J. Exp. Mar. Biol. Ecol. 216, 99-128.

MacNally, R., 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – 'predictive' and 'explanatory' models. Biodivers. Conserv. 9, 655-671.

MacNally, R., 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. Biodivers. Conserv. 11, 1397-1401.

Mannino, A., Montagna, P.A., 1997. Small-scale spatial variation of macrobenthic community structure. Estuaries 20, 159-173.

Manté, C., Claudet, J., Rebzani-Zahaf, C., 2003. Fairly processing rare and common species in multivariate analysis of ecological series. Acta Biotheoret. 51, 277-294.

Morrisey, D.J., Howitt, L., Underwood, A.J., Stark, J.S., 1992a. Spatial variation in soft-sediment benthos. Mar. Ecol. Prog. Ser. 81, 197-204.

Morrisey, D.J., Underwood, A.J., Howitt, L., Stark, J.S., 1992b. Temporal variation in soft-sediment benthos. J. Exp. Mar. Biol. Ecol. 164, 233-245.

Norderhaug, K.M., Christie, H., Rinde, E., 2002. Colonisation of kelp imitations by epiphyte and holdfast fauna; a study of mobility patterns. Mar. Biol. 141, 965-973.

Noren, K., Lindegarth, M., 2005. Spatial, temporal and interactive variability of infauna in Swedish coastal sediments. J. Exp. Mar. Biol. Ecol. 317, 53-68.

Olafsson, E.B., Peterson, C.H., Amborse, W.G., 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. Oceanogr. Mar. Biol. Ann. Rev. 32, 65-109.

Pusceddu, A., Dell'Anno, A., Fabiano, M., Danovaro, R., 2004. Quantity and biochemical composition of organic matter in marine sediments. Biol. Mar. Medit. 11 (Suppl 1), 39-53.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, 537 pp.

SMEC/Umwelt (Australia). 2002. Brisbane Water Data Compilation Study. Report to Gosford City Council.

Thrush, S.F., 1991. Spatial patterns in soft-bottom communities. Trends. Ecol. Evol. 6, 75-79.

Thrush, S.F., Hewitt, J.E., Pridmore, R.D., 1989. Patterns in the spatial arrangement of polychaetes and bivalves in intertidal sandflats. Mar. Biol. 102, 529-535.

Turner, S.J., Thrush, S.F., Pridmore, R.D., Hewitt, J.E., Cummings, V.J., Maskery, M., 1995. Are soft-sediment communities stable? An example from a windy harbour. Mar. Ecol. Prog. Ser. 120, 219-230.

Underwood, A.J., 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Ann. Rev. 19, 513-605.

Underwood, A.J., 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable world. J. Exp. Mar. Biol. Ecol. 161, 145-178.

Underwood, A.J., 1993. The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. Aust. J. Ecol. 18, 99-116.

Underwood, A.J., 1997. Ecological Experiments: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge, 504 pp.

Underwood, A.J., Chapman, M.G., Connell, S.D., 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. J. Exp. Mar. Biol. Ecol. 250, 97-115.

Volckaert, F., 1987. Spatial patterns of soft bottom polychaeta of Nova Scotia, Canada. Mar. Biol. 93, 627-639.

Walsh, C.J., MacNally, R., 2004. The hier/part package Version 0.5-2. Hierachical partitioning (http://cran.r-project.org/).

Walsh, C.J., Papas, P.J., Crowther, D., Sim, P.T., Yoo, J., 2004. Stormwater drainage pipes as a threat to a stream-dwelling amphipod of conservation significance, *Austrogammarus australis*, in southeastern Australia. Biodivers. Conserv. 13, 781-793.

Wetzel, R.G., Likens, G.E., 2000. Limnological Analyses, 3rd Edition. Springer-Verlag, New York, 429 pp.

Ysebaert, T., Herman, P.M.J., 2002. Spatial and temporal variation in benthic macrofauna and relationships with environmental variables in an estuarine, intertidal soft-sediment environment. Mar. Ecol. Prog. Ser. 244, 105-124.

APPENDIX 1
Species recorded in seagrass habitat at locations in Brisbane Water. Positions of each location are shown in Figure 2. X present, - not collected.

Phylum	**Class**	**Family**	**Species**	**1.1**	**1.2**	**2.1**	**2.2**	**3.1**	**3.2**	**4.1**	**4.2**	**5.1**	**5.2**	**6.1**	**6.2**	**7.1**	**7.2**
Platyhelminthes	Turbellaria		Turbellaria sp.		X	X	X	X	X	X	X	X	X	X	X	X	X
Nemertea			Nemertea sp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Annelida	Oligochaeta		Oligochaeta sp.	X	X	X	X	X	-	X	X	X	X	-	-	X	X
	Polychaeta	Polynoidae	*Paralepidonotus ampuliferus*	-	X	X	X	X	X	-	X	X	X	-	-	-	-
			Lepidonotus sp.	-	X	-	X	-	-	-	-	X	-	-	-	-	-
		Nereididae	*Simplisetia aequisetis*	X	X	X	X	X	X	X	X	X	X	X	X	X	X
			Ceratonereis australis	X	-	-	X	X	X	X	X	-	X	X	X	X	X
			Ceratonereis pseudoerythraensis	-	-	-	-	X	-	-	-	X	-	-	-	X	-
			Australanereis ehlersi	-	-	-	-	X	-	X	X	-	X	X	X	X	X
		Nephtyidae	*Nephtys australiensis*	X	X	X	X	X	X	X	-	X	X	-	X	X	X
			Nephtys longipes	-	X	X	-	-	-	-	-	-	-	-	-	-	X
			Nephtys inornata	-	X	-	X	-	X	X	X	X	X	-	X	-	X
		Glyceridae	*Glycera* sp.	-	-	X	X	X	-	-	X	X	-	X	-	-	X
			Hemipodia c.f. yenourensis or *simplex*	X	X	-	X	X	X	X	X	-	X	X	X	X	X
		Syllidae	*Paraehlersia* sp.	X	X	-	X	X	X	-	-	X	X	X	X	X	X
			Odontosyllis trilinea (n.sp)	X	-	-	-	X	X	X	-	-	X	X	-	X	X
			Syllis (Typosysyllis) sp.1	-	-	-	X	X	X	X	X	-	X	-	-	X	X
			Syllis (Typosysyllis) sp.2	-	X	-	-	-	-	X	-	-	-	-	-	-	X

Appendix 1 cont'd

Phylum	Class	Family	Species	1.1	1.2	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2
Annelida	Polychaeta	Phyllodocidae	*Phyllodoce novaehollandiae*	-	X	-	X	X	-	-	-	-	-	X	-	-	X
			Phyllodoce sp.	-	X	-	-	X	X	X	-	-	-	X	-	-	-
		Pilargidae	*Sigambra parva*	X	X	-	-	-	-	X	X	X	-	-	-	-	X
		Eunicidae	*Marphysa* sp.2	-	-	-	-	-	-	-	-	-	X	-	-	X	-
			Nematonereis unicornis	-	-	-	-	-	-	-	-	-	-	X	-	-	-
		Lumbrineridae	*Lumbrineris* sp. *(c.f. gulielmi* or *setosa)*	X	-	X	X	-	X	X	X	X	X	X	X	X	X
		Orbiniidae	*Leitoscoloplos normalis*	-	X	-	-	-	-	X	-	-	-	-	-	-	-
			Phylo felix	-	-	-	-	-	-	-	-	X	X	-	-	-	X
			Leodamas johnstonei	-	-	-	-	-	-	-	-	-	-	-	X	-	X
		Spionidae	*Prionospio multicristata*	X	X	X	X	X	X	X	X	X	X	X	X	X	X
		Polynoidae	*Harmothoe charlottae*	X	-	-	-	X	X	X	X	-	-	-	-	X	-
		Cirratulidae	*Chaetozone setosa*	-	-	-	-	X	-	-	-	-	-	-	-	-	-
			Aphelochaeta sp.	-	-	-	-	-	X	-	-	-	X	X	X	X	-
			Cirriformia c.f. capensis	-	-	-	-	-	-	X	X	-	-	-	X	X	X
		Capitellidae	*Barantolla lepte*	X	X	X	X	X	X	X	X	X	X	X	X	X	X
			Notomastus sp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X
			Capitella sp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X
		Terebellidae	*Lysilla or Amaena* sp.	X	X	X	X	X	X	X	X	X	X	-	X	X	X
			Streblosoma acymatum	-	-	X	X	-	X	X	X	X	X	X	X	X	X
		Pectrinariidae	*Pectinaria antipoda*	X	-	X	X	X	X	X	X	X	-	X	-	-	X

Appendix 1 cont'd.

Phylum	Class	Family	Species	1.1	1.2	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2
Annelida	Polychaeta	Opheliidae	*Armandia intermedia*	X	X	X	X	X	X	X	X	X	X	X	X	X	X
		Paronoidae	*Aricidea* sp.	-	X	X	-	X	X	X	X	X	X	X	-	X	X
			Paraonidae sp.1	-	X	-	-	X	-	X	X	-	-	X	X	X	X
			Paraonidae sp.2	-	-	-	-	-	-	X	X	-	-	X	X	-	X
			Paraonidae sp.3	X	-	-	-	X	-	X	X	X	-	-	X	X	-
		Owenidae	*Owenia australis*	X	X	X	X	X	X	X	X	X	X	X	X	X	X
		Magelonidae	*Magelona dakini*	-	X	X	X	-	X	X	X	X	X	-	-	X	-
			Magelona sp.	-	-	-	-	-	-	-	X	-	-	-	X	-	-
		Spirorbidae	*Spirorbidae* sp.	X	X	X	X	X	X	X	X	-	X	X	-	X	-
Arthropoda	Crustacea	Tanaidae	Tanaidae sp.	-	-	X	X	X	X	X	X	X	X	X	X	X	X
		Sphaeromatidae	Sphaeromatidae sp. 1	X	X	-	X	X	X	-	X	-	X	-	-	-	-
			Sphaeromatidae sp.2	-	X	-	-	X	-	X	X	-	X	-	-	-	-
			Paracerceis sculpta	-	-	-	X	-	-	-	-	-	-	-	-	-	-
		Armadillidae	*Cubaris* sp.	-	-	-	-	-	-	-	-	X	-	-	-	-	-
		Ampithoidae	*Cymadusa filosa*	X	X	-	-	X	X	X	X	X	X	X	X	X	X
			Cymadusa sp.1	X	-	X	X	X	-	X	-	-	X	X	-	X	X
		Melitidae	*Melita plumulosa*	X	X	X	X	X	X	X	X	X	X	X	X	X	X
			Melita sp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X
		Anothidae	Anothidae sp.	X	-	X	-	-	-	-	-	-	-	-	-	-	-
		Phoxocephalidae	*Limnoporeia kingi*	X	X	X	X	X	X	X	X	X	X	X	X	X	X
		Penaeidae	*Metapenaeus* sp.	X	X	X	-	X	X	X	X	X	X	X	X	X	X
		Goneplacidae	Goneplacidae sp.	-	X	X	X	X	X	X	X	X	-	X	X	X	X

Appendix 1 cont'd.

Phylum	Class	Family	Species	1.1	1.2	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2
Arthropoda	Crustacea	Ocypodidae	*Macropthalmus* sp.	-	-	-	-	X	-	-	-	-	-	-	-	X	X
		Xanthidae	Xanthidae sp.	-	X	-	X	-	X	-	-	-	-	-	-	-	-
		Hymenosomatidae	Hymenosomatidae sp.	X	-	X	X	X	-	X	X	X	X	X	-	-	X
		Paguridae	Paguridae sp.	-	-	-	-	X	-	-	-	-	-	-	-	X	X
		Nebaliidae	*Nebalia* sp.	-	-	-	X	-	X	-	-	-	-	-	-	-	-
Mollusca	Gastropoda	Lottidae	Lottidae sp.	X	X	-	X	X	X	X	X	-	X	-	-	-	-
		Neritidae	*Smaragdia souverbiana*	-	-	-	-	-	-	-	-	-	X	-	-	-	-
		Trochidae	*Prothalotia comtessei*	-	-	-	X	X	X	X	X	X	X	X	X	X	X
			Calthalotia fragum	X	X	-	X	X	X	X	X	X	X	-	-	X	X
			Leiopyrga lineolaris	X	X	-	X	X	X	X	X	-	X	X	-	X	-
		Litiopidae	*Alaba opiniosa*	-	-	-	-	-	X	-	-	-	X	-	-	-	-
			Alaba monile	-	-	-	-	-	-	X	X	-	-	-	-	X	X
			Alaba translucida	X	X	X	-	X	X	X	X	X	X	-	-	X	X
		Cerithiidae	*Cacozeliana granarium*	-	-	X	X	X	X	X	X	X	X	-	-	-	-
		Batillariidae	*Batillaria australis*	X	X	X	X	X	X	X	X	X	X	X	X	X	X
		Turritellidae	*Gazameda gunnii*	-	-	-	-	-	-	X	-	-	-	-	-	-	-
		Littorinidae	*Bembicium auratum*	X	X	-	X	X	X	-	-	X	X	-	X	X	X
			Littorina scabra	-	-	-	X	X	X	X	-	-	X	-	X	X	-
		Stenothyridae	*Stenothyra* sp.	X	X	X	X	-	-	-	X	X	-	X	-	-	-
		Assimineidae	*Assiminea tasmanica*	X	X	X	-	-	X	X	X	X	X	X	X	X	X
		Hydrobiidae	*Bittium lacertinum*	-	-	-	-	-	X	X	-	X	X	-	-	X	X
			Tatea huonensis	X	-	-	-	-	X	-	-	-	-	-	-	-	-

Appendix 1 cont'd.

Phylum	Class	Family	Species	1.1	1.2	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2
Mollusca	Gastropoda	Vitrinellidae	*Pseudoliotia micrans*	X	X	X	X	X	X	X	X	X	X	X	X	X	X
			Pseudoliotia speciosa	-	X	X	X	X	X	X	X	X	X	-	X	-	-
		Cypraeidae	*Cypraea* sp.	-	-	-	-	-	-	-	-	X	X	-	-	-	-
		Cerithiopsidae	*Ataxocerithium serotinum*	-	-	-	-	X	-	-	-	-	-	-	-	-	-
		Janthinidae	Janthinidae sp.	-	-	-	-	-	X	-	-	-	X	-	-	-	-
		Epitoniidae	*Epitonium parspeciosum*	-	-	X	-	-	-	X	-	X	-	-	-	-	-
		Muricidae	*Bedeva hanleyi*	X	X	X	X	X	X	-	X	X	-	X	X	X	-
		Buccinidae	*Engina australis*	-	-	-	X	-	-	-	-	X	X	-	-	-	-
		Nassariidae	*Nassarius burchardi*	X	X	X	X	X	X	X	X	X	X	X	X	X	X
			Nassarius jonasii	-	-	-	-	-	X	-	-	-	-	X	-	X	-
		Marginellidae	Marginellidae sp.	-	-	-	-	-	-	-	-	X	X	-	-	-	-
		Mitridae	Mitridae sp.	-	-	-	-	-	X	-	-	-	X	-	-	X	-
		Cancellariidae	*Trigonostoma bicolor*	-	-	-	-	-	-	-	-	-	-	-	-	X	-
		Turridae	*Austrodrilla beraudiana*	X	X	X	X	X	X	X	X	X	X	X	X	X	-
		Architectonicidae	*Psilaxis* sp.	-	-	-	-	-	X	-	-	X	X	-	-	X	-
		Pyramidellidae	*Linopyrga* sp.	X	-	-	-	-	X	-	-	-	-	-	-	-	X
		Pyramidellidae	*Agatha simplex*	-	-	-	-	-	X	-	-	-	-	-	-	-	-
		Pyramidellidae	*Paregila henni*	-	-	-	-	X	X	-	-	-	-	-	-	X	-
		Philinidae	Philinidae sp.	-	-	-	-	X	-	-	-	-	-	-	-	X	-
		Amphibolidae	*Salinator solida*	X	-	X	X	-	-	-	-	-	-	-	-	-	-

Appendix 1 cont'd.

Phylum	Class	Family	Species	1.1	1.2	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2
Mollusca	Bivalvia	Arcidae	*Anadara trapezia*	X	X	X	X	X	X	X	X	X	X	X	-	-	X
		Mytilidae	*Xenostrobus securis*	-	X	X	X	X	X	X	X	X	X	X	-	X	X
		Montacutidae	*Arthritica helmsi*	X	-	-	-	-	-	-	-	-	-	-	-	-	-
		Cardiidae	*Hemidonax pictus*	-	-	-	-	-	-	-	-	X	-	-	-	-	-
		Mactridae	*Mactra jacksonensis*	-	-	-	-	-	X	-	X	-	X	-	-	-	-
			Spisula trigonella	-	X	-	-	X		X	X	-	X	-	-	-	-
		Solenidae	*Solen correctus*	-	-	-	-	-	-	-	-	-	X	-	-	-	-
		Tellinidae	*Tellina deltoidalis*	X	X	X	X	X	X	X	X	X	X	X	X	X	X
		Semelidae	*Theora fragilis*	-	X	X	-	X	-	X	X	-	-	X	X	X	X
		Veneridae	*Eumarcia fumigata*	-	-	X	-	-	X	-	-	X	-	-	-	X	-
			Katelysia rhytiphora	-	-	-	-	X	-	X	X	-	X	-	-	-	-
			Dosinia sculpta	-	X	X	X	X	X	X	X	X	X	-	X	X	X
			Tapes watlingi	-	-	-	X	-	X	-	-	-	-	-	-	-	X
			Paphia undulata	-	-	-	-	X	X	-	X	X	-	-	-	-	X
		Lucinidae	*Wallucina assimilis*	-	-	-	-	-	X	X	-	X	-	-	-	X	-
		Pholadidae	*Pholas* sp.	-	X	-	-	X	-	X	-	X	X	-	-	X	-
		Laternulidae	*Laturnula creccina*	X	-	X	X	-	-	X	X	X	-	-	X	-	X
		Laternulidae	*Laturnula tasmanica*	X	-	-	X	-	X	X	-	-	X	X	X	X	-
Echinodermata	Ophiuroidea	Ophiodermatidae	Ophiodermatidae sp.	-	X	-	X	X	-	-	-	X	-	-	-	X	X

APPENDIX 2

Species recorded in unvegetated sediment habitat at Koolewong (Ko), Woy Woy Bay (WW), Wagstaff (W), St. Hubert's Island (SH), and Kincumber Broadwater (Ki). Positions of each location are shown in Figure 2. X present, - not collected.

Phylum	**Class**	**Family**	**Species**	**Ko**	**WW**	**W**	**SH**	**Ki**
Nemertea			Nemertea sp.	X	-	X	X	X
Annelida	Polychaeta	Nereididae	*Simplisetia aequisetis*	X	X	X	X	X
			Ceratonereis australis	X	X	X	-	X
		Nephtyidae	*Nephtys longipes*	-	X	X	X	X
		Glyceridae	*Glycera* sp.	-	X	-	-	-
		Syllidae	*Syllis (Typosysyllis)* sp.1	-	-	X	X	X
		Phyllodocidae	*Phyllodoce* sp.	X	X	X	-	X
		Lumbrineridae	*Lumbrineris* sp. *(c.f. gulielmi* or *setosa)*	-	X	X	X	X
		Spionidae	*Prionospio multicristata*	-	-	X	X	X
		Capitellidae	*Barantolla lepte*	-	-	-	-	X
			Capitella sp.	X	-	X	-	X
		Maldanidae	*Maldane sarsi*	X	X	X	-	X
		Terebellidae	*Lysilla or Amaena* sp.	X	X	X	X	X
			Streblosoma acymatum	X	X	X	X	X
		Paronoidae	*Aricidea* sp.	-	-	X	X	-
		Owenidae	*Owenia australis*	X	X	X	X	X
		Sabellidae	*Branchiomma* sp.	X	-	X	-	X
Arthropoda	Crustacea	Diastylidae	Diastylidae sp.	X	X	X	X	X
		Tanaidae	Tanaidae sp.	X	X	X	X	X
		Unknown	Mysidacea sp.	X	X	X	X	-

Appendix 2 cont'd.

Phylum	Class	Family	Species	Ko	WW	W	SH	Ki
Arthropoda	Crustacea	Platyischnopiidae	*Platyischnopus mirabilis*	X	X	X	X	X
		Cirolanidae	*Natatolana* sp.	X	X	X	X	X
		Ampithoidae	*Cymadusa* sp.1	X	-	X	-	-
			Cymadusa sp.2	X	X	X	X	X
		Melitidae	*Melita plumulosa*	X	-	X	-	-
		Phoxocephalidae	*Limnoporeia kingi*	X	X	X	X	X
		Paguridae	Paguridae sp.	-	-	-	X	-
Mollusca	Gastropoda	Trochidae	*Prothalotia comtessei*	-	-	-	X	-
			Talopena gloriola	-	-	-	X	-
		Litiopidae	Litiopidae sp.	-	-	-	X	-
			Alaba monile	-	-	-	X	-
			Alaba translucida	-	-	X	X	-
		Batillariidae	*Batillaria australis*	-	X	X	X	-
		Turritellidae	*Gazameda gunnii*	-	-	-	X	-
		Assimineidae	*Assiminea tasmanica*	X	X	X	X	-
		Cerithiidae	*Bittium* sp.	-	-	X	X	-
		Hydrobiidae	*Tatea huonensis*	-	-	-	-	-
		Vitrinellidae	*Pseudoliotia micrans*	X	-	X	X	-
			Pseudoliotia speciosa	-	-	X	-	-
		Caecidae	*Caecum amputatum*	X	X	X	-	X
		Ranellidae	*Cymatium extratum*	-	X	X	X	-

Appendix 2 cont'd.

Phylum	Class	Family	Species	Ko	WW	W	SH	Ki
Mollusca	Gastropoda	Janthinidae	Janthinidae sp.	-	-	X	-	-
		Epitoniidae	*Epitonium parspeciosum*	-	-	X	-	-
		Muricidae	*Bedeva hanleyi*	-	-	-	X	-
		Nassariidae	*Nassarius burchardi*	-	-	-	X	-
			Nassarius pauperus	-	-	-	X	-
		Mitridae	Mitridae sp.	-	-	X	-	-
		Turridae	*Austrodrilla beraudiana*	-	X	X	X	X
		Architectonicidae	*Psilaxis* sp.	-	-	-	X	-
		Pyramidellidae	*Linopyrga* sp.	-	-	-	X	-
		Philinidae	Philinidae sp.	X	X	X	-	-
Mollusca	Bivalvia	Mytilidae	*Musculus varicosus*	-	X	-	-	-
		Mactridae	*Mactra jacksonensis*	X	X	X	X	-
			Spisula trigonella	X	-	X	X	X
		Solenidae	*Solen correctus*	-	-	X	X	-
		Tellinidae	*Tellina deltoidalis*	X	X	X	X	X
		Psammobiidae	*Heteroglypta contraria*	-	X	-	-	-
		Semelidae	*Theora fragilis*	X	X	X	-	X
		Veneridae	*Eumarcia fumigata*	X	X	X	X	X
			Katelysia rhytiphora	-	-	X	X	-
			Dosinia sculpta	X	X	X	X	X
			Tapes watlingi	X	-	-	-	-

Appendix 2 cont'd.

Phylum	Class	Family	Species	Ko	WW	W	SH	Ki
Mollusca	Bivalvia	Veneridae	*Paphia undulata*	-	-	X	-	-
		Laternulidae	*Laturnula creccina*	X	-	-	-	-
	Scaphopoda	Dentaliidae	*Compressidens platyceras*	X	X	X	X	X
Echinodermata	Ophiuroidea	Ophiodermatidae	Ophiodermatidae sp.	X	X	X	X	X
	Echinoidea	Clypeasteridea	Clypeasteridea sp.	X	-	-	-	-