

Differences in composition of small, motile invertebrate assemblages from seagrass and unvegetated habitats in a southern Australian estuary

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Abstract

Assemblages of small, motile invertebrates (epifauna) from eelgrass (*Zostera muelleri*) and unvegetated habitats in a shallow, marine-dominated estuary were compared at five sampling periods over one year. Assemblages based on abundance and biomass of 21 taxa from the two habitats grouped separately in multivariate analyses (MDS ordination), and these groupings were shown to be significant using an analysis of similarities (ANOSIM) randomisation routine. Secondly to habitat differences, weak influences of water temperature and distance to open water, but not of salinity, were detected at some periods. Abundance and biomass of key taxa and all species combined were higher in eelgrass than in unvegetated habitat. Cumaceans were exceptional in being collected predominantly from unvegetated habitat. Total epifaunal production and crustacean production estimated using two variables, (1) the biomass of individuals of each size class, and (2) water temperature, were also higher in eelgrass than in unvegetated habitat. The higher abundance in eelgrass of taxa such as amphipods, harpacticoid copepods and polychaetes that are major components of the diets of small fish is consistent with a model explaining higher fish numbers in eelgrass in terms of prey availability.

Introduction

The abundance of small, motile invertebrates associated with seagrass is often greater than that associated with adjacent unvegetated patches (Orth et al., 1984). This difference is more obvious for epifaunal (associated with the surface of either the seabed or vegetation) than for infaunal invertebrates (buried in the sediment) (Howard et al., 1989; Edgar et al., 1994). Artificial seagrass placed in unvegetated areas near natural seagrass beds attracts a fauna similar to that in the natural beds (Howard et al., 1989; Edgar, 1990b). Howard et al. (1989) suggest that the type of seagrass may be less important than the presence of seagrass. Larger epifaunal invertebrates (macrofauna, defined as animals retained on 0.5 mm mesh) are, however, capable of selecting amongst different densities of seagrass (Leber, 1985). Bell & Westoby (1986) manipulated

seagrass densities in field experiments and used predator exclusion cages to show that decapods were more common in denser seagrass regardless of the presence or absence of predators. They showed convincingly that low decapod numbers in patches with less dense seagrass cover were not due to increased predation, and concluded that decapods select habitat. Stoner (1980) demonstrated that amphipods can also detect and respond to differences in canopy density. The high mobility of epifaunal invertebrates, even in their adult stages, enhances their ability to exercise behavioural selection for seagrass of differing densities. Although less experimental work has been done on meiofauna (Howard et al., 1989), defined as animals passing through 0.5 mm mesh but retained on 0.1 mm mesh, harpacticoid copepods are known to colonise artificial seagrass placed near natural seagrass beds (Bell & Hicks, 1991).

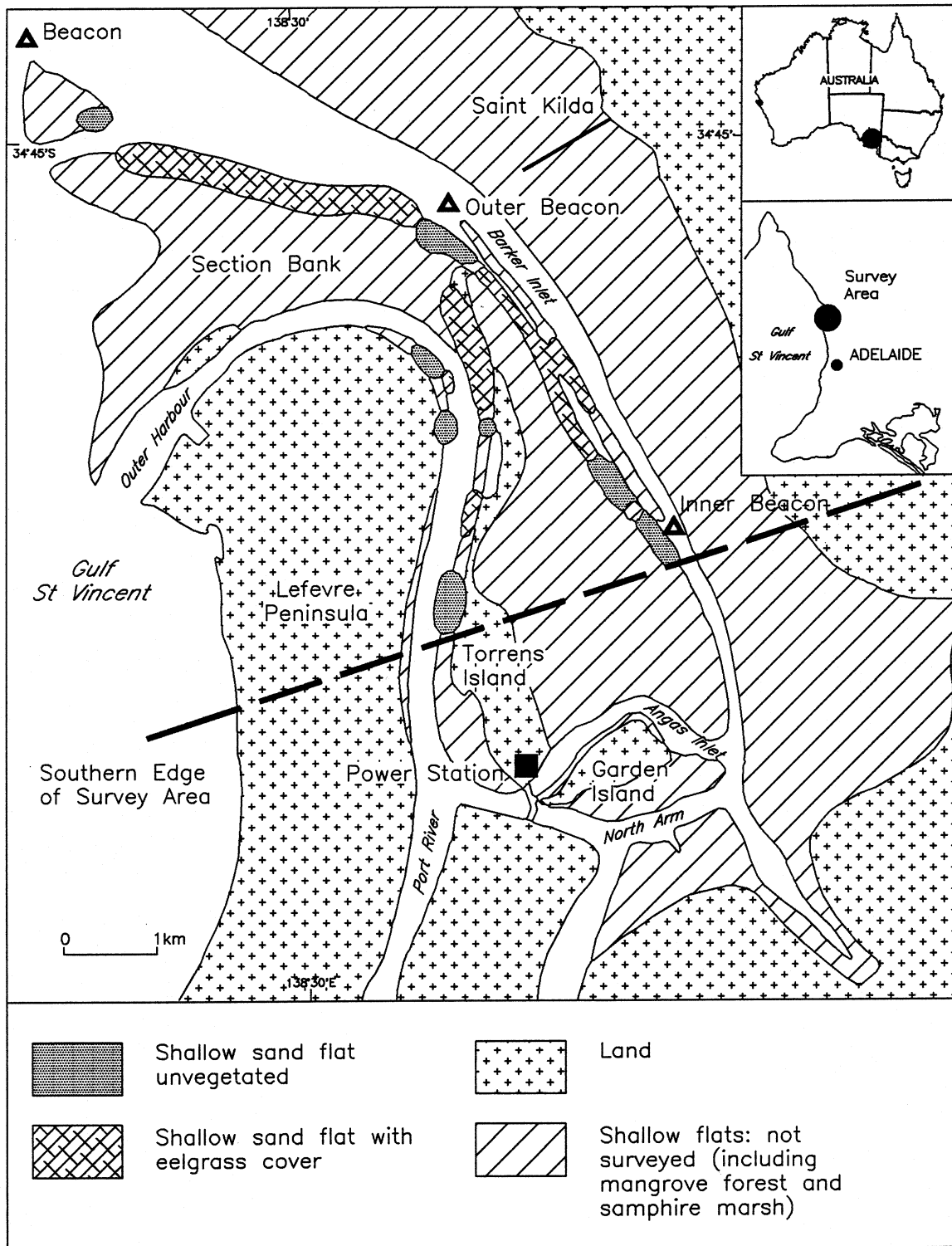


Figure 1. Survey region and habitat locations.

Table 1. List of taxa into which animals were grouped. Abbreviations shown are those used in Table 3.

Crustacean		Non-crustacean	
	Brachyura	Pol	Polychaeta
	Caridea		Gastropoda
	Mysidacea		Bivalvia
Amp	Amphipoda- Gammaroidea	Oph	Ophiuroidea
	Amphipoda - Caprellidea		Actinaria
Tan	Tanaidacea		Echinodermata, larvae
Iso	Isopoda		Chironomidae, larvae
	Cumacea		Nematoda
Har	Copepoda - Harpacticoida		
	Copepoda- Cyclopoida		
	Copepoda- Calanoida		
	Copepoda - nauplii (unidentified)		
	Ostracoda		

The aim of the current work was to determine whether the abundance, biomass or production of epifaunal taxa differed between seagrass and unvegetated habitats in the Barker Inlet – Port River estuary in South Australia. The work is part of a body of work using surveys (Connolly, 1994a) and manipulative experiments (Connolly, 1994b, c; 1995a) to examine the role of seagrass in structuring invertebrate and fish communities in this estuary. Previous studies in seagrass meadows in Australia and elsewhere have shown that the majority of fish inhabiting these meadows and adjacent unvegetated flats predominantly eat epifaunal rather than infaunal invertebrates (Klumpp et al., 1989). The epifaunal taxa of most importance in the diet of fish include crustaceans, polychaetes and molluscs (Klumpp et al., 1989). The main prey of *Sillaginodes punctata* Cuvier & Valenciennes (King George whiting), the most economically important fish species in South Australia, are epifaunal crustaceans and polychaetes (Connolly 1995b).

Materials and methods

Epifaunal invertebrates were sampled from eelgrass (*Zostera muelleri* Irmisch ex Aschers.) and unvegetated habitat in conjunction with a survey of fish in the Barker Inlet – Port River estuary (138° 30' E, 34° 45' S). Excluding the southern part of the estuary, which is grossly affected by warm water effluent from a power station, there were seven eelgrass and eight unvegetated areas (Figure 1). At each of five sampling periods

between January 1990 and February 1991, between 15 and 20 sites were selected for sampling, with about half in each habitat type (see sample sizes in Table 8). Although the spatial distribution of areas of the two habitats was predetermined by the state of the estuary, there was some interspersed of habitats. The situation of having all or most of one type of habitat at one end of the estuary was thereby avoided. Sites for epifauna collections were the same as for fish collections, and a fuller description of the estuary and the sampling design is contained in Connolly (1994a).

The above-ground biomass was measured at each eelgrass site in January 1990 only. At each site, three quadrats of 625 cm² were harvested and dried at 60 °C for two days. The mean above-ground biomass for all eelgrass sites was 146 g dry weight/m² (s.e. = 20.7, *n* = 9 sites).

A sample of epifauna was taken in water between 30 and 50 cm deep. A 95 µm mesh net with a 25 × 25 cm opening was used, following the method of Sergeev et al. (1988) in which the net was placed rapidly over the canopy onto the sediment. Whilst the net was held in place, shears were slipped under the net, and seagrass, where present, was cut level with the sediment surface. In habitats without seagrass, the same action was taken, ensuring that the sediment surface was ruffled as it was where seagrass was present. The net was then slipped off its frame and closed along the sediment surface. Animals were later separated into sieve size classes of 2 mm, 1 mm, 500 µm, 250 µm, 125 µm and 75 µm before being identified to major taxa and counted. Numbers of very abundant taxa were counted from

Table 2. Mean ash free dry weights (mg) of different forms of epifaunal invertebrates in each sieve size-class. Values were calculated using Edgar's (1990a) equation: $\log B = a + b \log S$ (where $B = \text{AFDW (mg)}$, $S = \text{sieve mesh size (mm)}$ and a and b vary depending on taxonomic category). Sieve size (S) is a geometric mean, as explained in text. Taxa not fitting within any of the named categories shown were treated as general forms. Crustacea includes all crustaceans except caprellid amphipods, which have a form different enough to warrant a separate category. No value is shown where category was not found in that sieve size.

Sieve size (mm)	General	Crustacea	Caprellidea	Polychaeta	Mollusca
1.0	0.2448	0.2302	0.1181	0.2440	0.2484
0.5	0.0392	0.0361	0.0316	0.0433	0.0367
0.25	0.0063	0.0057		0.0077	0.0054
0.125	0.0010	0.0009		0.0014	0.0008
0.075	0.0002	0.0002		0.0003	

random subsamples with the aim of counting between 50 and 200 individuals of each taxon per sieve size in any sample. Twenty-one taxa were used, 13 crustaceans and 8 others (Table 1). Nematodes were counted but, as they are typically not a component of fish diets (Klumpp et al., 1989, but see exceptions in Gee, 1989), were treated separately in analyses. Nematode numbers are presented here but have been excluded from estimates of total epifaunal abundance.

Animals from the largest sieve were ashed and ash-free dry weights (AFDW) were calculated. Ash-free dry weights for other sieve sizes were calculated by converting abundances for each taxon for each sieve size using Edgar's (1990a) equation, $\log B = a + b \log S$ (where $B = \text{AFDW (mg)}$, $S = \text{sieve mesh size (mm)}$, and a and b vary depending on broad taxonomic category). Since each sieve size retains animals ranging from that sieve size to the next, S is expressed as a geometric mean calculated using the equation, $\log S = (\log S_i + \log S_{i+1})/2$, in which $S_i = \text{mesh size of the } i^{\text{th}} \text{ sieve}$ and $S_{i+1} = \text{mesh size of the next size up}$ (Edgar, 1990a). Mean ash-free dry weights for each taxonomic group for each sieve size are shown in Table 2. The slopes of lines based on Edgar's (1990a) equations are less than would be expected if body weight increases with the cube of body dimensions. One possible reason for this is that the volume of larger individuals may include proportionately more inorganic material, such as shell or exoskeleton (Edgar, 1990a). Edgar warns that the relationship between sieve mesh size and AFDW for polychaetes depends on their form. As in Edgar's (1990a) study, the majority of polychaetes caught during my surveys were epifaunal, and string-

shaped forms such as capitellids were rarely collected; Edgar's equation is therefore appropriate.

Epifaunal production is a more useful measure than abundance, but field measurements of production are extremely difficult. A useful index of community production has been developed by Edgar (1990a) using the relationship between epifaunal biomass and production. Smaller individuals have a relatively higher production rate than larger individuals, and the abundance of different sized animals can be used to estimate production (Edgar, 1990a; Edgar et al., 1994). Edgar (1990a) used production rates for small, benthic invertebrates from several published sources to determine the relationship between biomass and daily production. Biomass alone explained much of the variability in production, and when water temperature was also taken into account, the two factors explained very nearly all of the variability in production (Edgar, 1990a). As an approximate indication, at least, of epifaunal production in eelgrass and unvegetated habitats, I have used Edgar's (1990a) equation, $P = 0.0049 B^{0.80} T^{0.89}$, relating production (P , $\mu\text{g d}^{-1}$) to sample AFDW (B , μg) and water temperature (T , $^{\circ}\text{C}$). Since temperature did not differ significantly between eelgrass and unvegetated sites at any sampling period (Table 9), the temperature for all sites was taken as the mean value of all sites at that sampling period, as follows: 1990 – January 22.7 $^{\circ}\text{C}$, April 22.3, August 14.9, October 18.8, 1991 – February 27.6. Production, as calculated using Edgar's equation, can be considered as a general index of community processes such as respiration and consumption as well as of community production (Edgar, 1993), although for the purpose of comparing availability of food to fish in different habitats it is used here as

an index of production. Production values are useful in that they permit comparisons between habitats using data from a wide range of size-classes without being dominated by a particular size class (Edgar, 1994).

Water temperature was measured at each site at the time of netting, at 30 cm depth in water 60 cm deep. Water samples for salinity analysis were taken at the same time and place. The Practical Salinity Scale has been used in this paper.

Data analysis

Epifaunal assemblages (described both by abundance and biomass (AFDW)) from eelgrass and unvegetated habitats were compared using an analysis of similarities (ANOSIM), which is a non-parametric analogue to a multivariate analysis of variance (MANOVA) without the assumption of multivariate normality. ANOSIM has an additional advantage over MANOVA in being able to detect differences between groups without any need for assumptions of constant spread within each group (Clarke, 1993). ANOSIM compares ranked similarities between and within groups selected a priori (here eelgrass and unvegetated habitats) using a randomisation test for significance. At each sampling period, assemblages from the two waterways, Barker Inlet and Port River, were also compared using a two-way crossed ANOSIM with habitat (eelgrass or unvegetated) as the second factor. This analysis determines whether assemblages from the two waterways differ after accounting for habitat differences. All ANOSIM tests involved 5000 simulations using the Primer package from Plymouth Marine Laboratory, England.

Non-metric multidimensional scaling (MDS) is an ordination technique that uses the same matrix of ranked similarities as ANOSIM; it displays samples in low (usually two) dimensional space while retaining as nearly as possible the similarity rankings between samples. The degree to which rankings are not preserved in the two-dimensional plot is indicated by a stress value. Analysis of the similarity matrix used in MDS and ANOSIM has also been used to highlight the species making the largest contribution to between-group differences (Clarke, 1993).

For comparisons of epifaunal assemblages between unvegetated and eelgrass sites, raw counts were transformed using $x^{0.25}$ to emphasise the distribution of less common species in the analysis. The Bray-Curtis similarity coefficient was used throughout, as a meaningful and robust measure (Clarke, 1993).

The association of environmental variables with patterns in biotic data can be measured by correlating the ranked similarity matrices of the environmental and biotic data (Clarke & Ainsworth, 1993). At each sampling period, the association between epifaunal assemblages and the environmental variables (1) water temperature, (2) salinity, and (3) distance to open water were measured using the weighted Spearman's coefficient recommended by Clarke & Ainsworth (1993). Distance to open water was measured as the shortest distance by sea from sites to gulfwaters unprotected by islands or shoals. Distances ranged from 1.0 to 9.1 km.

Comparisons were done for each of the five periods separately, but an MDS ordination was also performed on data from all periods combined, and a two-way crossed ANOSIM was used to test differences amongst periods after taking into account differences between habitats.

The abundance and biomass of epifauna (all taxa combined and key taxa separately) and total epifaunal and crustacean production from the two habitats were compared using one-way ANOVA. Analyses were done on log-transformed data, except where zeros occurred, in which case the transformation $\log_{10}(x + 1)$ was used. Significance levels are 0.05 throughout the paper, except where stated otherwise. No adjustment has been made for testing each taxon separately (Table 5); results for each taxon should be seen as pieces of evidence from one experiment.

Results

Two-dimensional ordination plots of epifaunal assemblages show a very similar pattern for both abundances (Figure 2) and biomasses (Figure 3). At every period, there is separation of seagrass and unvegetated sites. Assemblages were significantly different using both variables, at each sampling period, as tested with ANOSIM (Table 3). After accounting for differences due to habitat, assemblages from the two waterways, Barker Inlet and Port River, differed in some periods but not at others (Table 3).

The correlations between epifaunal assemblages and environmental variables differed depending on the sampling period, but were weak at all periods and were secondary to the main difference between eelgrass and unvegetated sites. Salinity was not correlated with assemblages at any period, and no environmental variable was correlated with assemblages in October 1990 and February 1991. In January 1990, distance

Table 3. Results of ANOSIM comparisons of epifaunal assemblages between habitats and between the two waterways, Barker Inlet and Port River. Results are probabilities (ns = not significant). Results for the factor habitat were all $p < 0.001$ both for one-way and two-way ANOSIM. Contributing taxa are those making a consistently large contribution to differences between samples from the two habitats, listed in order of decreasing importance. Probabilities for factor waterway relate to the question of whether assemblages differ between waterways after accounting for differences due to habitat, using two-way ANOSIM.

Sampling period	Variable	ANOSIM result, factor Habitat	Main contributing taxa to Habitat differences	ANOSIM result, factor Waterway
January 1990	Abundance	< 0.001	Iso, Har, Pol, Tan, Amp	0.001
	Biomass	< 0.001	Iso, Amp, Har	0.011
April 1990	Abundance	< 0.001	Har, Tan, Amp, Pol	0.285 ns
	Biomass	< 0.001	Har, Tan, Amp, Pol	0.309 ns
August 1990	Abundance	< 0.001	Iso, Har, Pol, Oph, Amp	0.356 ns
	Biomass	< 0.001	Iso, Har, Oph, Amp, Pol	0.844 ns
October 1990	Abundance	< 0.001	Iso, Amp, Har, Tan	0.005
	Biomass	< 0.001	Iso, Har, Tan, Amp	0.002
February 1991	Abundance	< 0.001	Har, Iso, Tan, Pol	0.241 ns
	Biomass	< 0.001	Tan, Har, Iso, Amp	0.125 ns

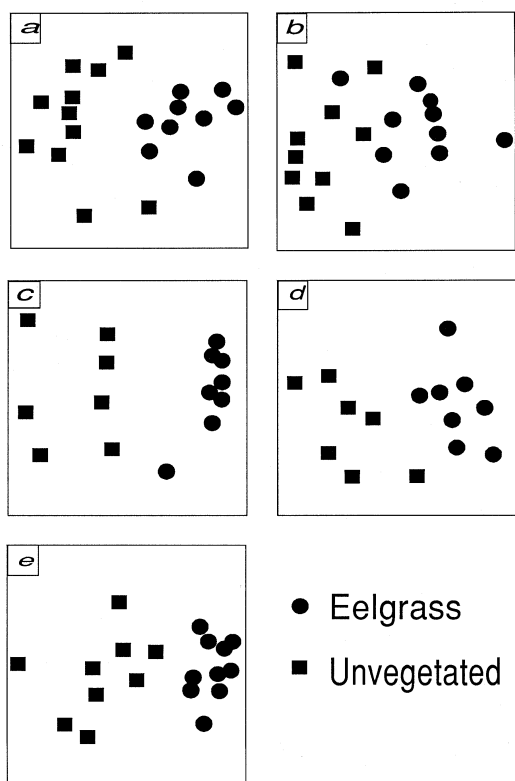


Figure 2. Two-dimensional MDS ordination plots of epifaunal assemblages based on abundance: (a) January 1990 (stress value (Kruskal's formula (1))=0.127), (b) April 1990 (0.141), (c) August 1990 (0.076), (d) October 1990 (0.088), (e) February 1991 (0.109).

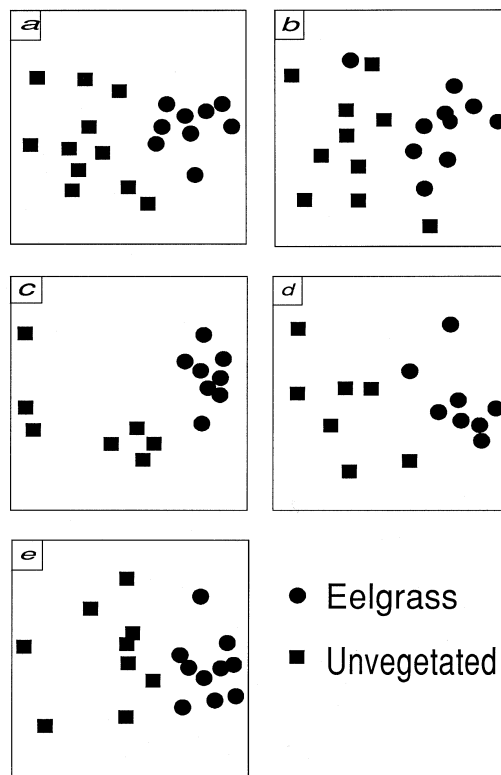


Figure 3. Two-dimensional MDS ordination plots of epifaunal assemblages based on biomass: (a) January 1990 (stress value=0.135), (b) April 1990 (0.153), (c) August 1990 (0.061), (d) October 1990 (0.099), (e) February 1991 (0.118).

to open water was the most closely correlated variable (abundance: $\rho_w = 0.194$; biomass: 0.265); although no formal test of this correlation is available, these values are low (Clarke & Ainsworth, 1993), and demonstrate only a weak association between distance and epifauna. Despite thorough interspersions of eelgrass and unvegetated sites (as shown in Figure 1), a test comparing mean distance to open water of eelgrass (mean distance = 4.2 km) and unvegetated (6.6 km) sites detected a significant difference (t -test, after check for homoscedasticity: $t = 2.858$, $p = 0.011$). This suggests that, in January 1990, the difference between eelgrass and unvegetated sites could have been confounded with the association of epifauna with distance to open water. Given the weakness of the association with distance, however, it is not possible that the marked distinction between assemblages of eelgrass and unvegetated habitat is solely the result of the greater average distance to open water of unvegetated sites. It is possible, though, that the weak association with distance is a result of the marked differences between assemblages of the two habitats. In April 1990, water temperature was the variable most closely correlated with assemblages (abundance: $\rho_w = 0.264$; biomass: 0.188). Again, these values are low, and demonstrate only a weak association between temperature and epifauna. The mean temperatures at eelgrass and unvegetated sites were not significantly different (Table 8). In August 1990, distance to open water was the variable most closely correlated with assemblages (abundance: $\rho_w = 0.390$; biomass: 0.453), and the values, whilst not showing a strong correlation (Clarke & Ainsworth, 1993), do imply a moderately close association. A simple overlay of distance to open water onto MDS plots of epifaunal assemblages for abundance (Figure 4a) and biomass (Figure 4b) shows no obvious pattern for eelgrass sites, but for unvegetated sites suggests that distance is associated with three separate groups. Both for abundance and biomass, one site high and far to the left of the plot has a small distance, two sites lower on the far left have large distances, and four sites near the centre of the plot have intermediate distances. Each of the two groups with more than one site includes sites from both waterways, Barker Inlet and Port River, and they are not grouped by temperature or salinity, so differences amongst the groups can best be explained by distance to open water.

When all periods are combined, the distinction between eelgrass and unvegetated sites remains the overwhelming difference based on both abundance (Figure 5) and biomass (pattern very similar to Fig-

Table 4. Results of two-way ANOSIM comparisons of epifaunal assemblages between habitats and amongst sampling periods on data from all periods together. Results are probabilities. Pairwise tests are for differences between pairs of periods: Jan = January 1990, Apr = April 1990, Aug = August 1990, Oct = October 1990, Feb = February 1991. Significance level for each pairwise comparison is 0.005 so that overall significance level for ten comparisons is 0.05 (ns = not significant). Pairwise tests for habitat are unnecessary because there are only two habitats.

Variable	Global ANOSIM result	Pairwise comparison	ANOSIM result
Abundance	Habitat < 0.001	Jan, Apr	< 0.001
		Jan, Aug	< 0.001
	Period < 0.001	Jan, Oct	< 0.001
		Jan, Feb	0.020 ns
		Apr, Aug	< 0.001
		Apr, Oct	< 0.001
		Apr, Feb	< 0.001
		Aug, Oct	0.002
		Aug, Feb	0.001
		Oct, Feb	< 0.001
Biomass	Habitat < 0.001	Jan, Apr	< 0.001
		Jan, Aug	< 0.001
	Period < 0.001	Jan, Oct	< 0.001
		Jan, Feb	0.062 ns
		Apr, Aug	< 0.001
		Apr, Oct	< 0.001
		Apr, Feb	< 0.001
		Aug, Oct	0.020 ns
		Aug, Feb	0.083 ns
		Oct, Feb	< 0.002

ure 5, and not shown). After accounting for differences between habitats, sampling periods are, however, also different (Table 4). Pairwise comparisons on abundances show that all periods differ except January 1990 and February 1991. Given that sampling actually occurred at the end of January 1990 and the beginning of February 1991, these two periods are almost identical seasonally, and the similarity of assemblages at these two sampling periods may reflect a seasonal pattern. Pairwise comparisons on biomass data showed a similar pattern except that assemblages from August 1990 were also found to be not significantly different from February 1991 and October 1990.

Mean abundances and biomasses of all taxa combined (excluding nematodes) were significantly greater in eelgrass than in unvegetated habitat at all sampling periods (Table 5). Abundances and biomasses of all taxa important in distinguishing between assemblages of the two habitats (Table 3) were also significantly

Table 5. Comparisons of abundances and biomasses of total epifauna and key taxa from eelgrass and unvegetated habitats. Abundances are means (individuals/net). Precision estimates are not shown as all means have been tested for significance using ANOVA. ANOVA results are probabilities.

Taxon	Abundances			Biomasses		
	Eelgrass	Unveg.	ANOVA result	Eelgrass	Unveg.	ANOVA result
a) January 1990						
All taxa combined	2583	551	< 0.001	66.3	6.6	< 0.001
Amphipods	70	5	0.008	6.9	0.3	0.001
Tanaids	22	6	0.001	2.0	0.3	0.009
Isopods	47	1	< 0.001	26.9	0.3	< 0.001
Harpacticoids	2076	412	< 0.001	7.4	1.8	< 0.001
Polychaetes	128	40	0.001	7.0	1.3	0.003
Nematodes	832	148	< 0.001	4.9	0.8	< 0.001
b) April 1990						
All taxa combined	1462	302	< 0.001	24.5	8.2	< 0.001
Amphipods	90	15	< 0.001	9.2	2.1	0.002
Tanaids	23	1	< 0.001	3.2	0.1	< 0.001
Harpacticoids	1242	261	< 0.001	4.2	0.9	< 0.001
Polychaetes	15	7	0.060	1.3	0.6	0.020
Nematodes	854	163	< 0.001	3.0	0.5	< 0.001
c) August 1990						
All taxa combined	1174	151	< 0.001	29.3	2.6	< 0.001
Amphipods	69	3	< 0.001	14.4	0.3	< 0.001
Isopods	7	0	< 0.001	5.1	0.0	< 0.001
Harpacticoids	1014	102	< 0.001	3.2	0.3	< 0.001
Polychaetes	33	3	< 0.001	0.9	0.3	0.005
Ophiuroids	3	0	0.001	0.7	0.0	0.006
Nematodes	792	185	0.007	2.8	0.5	0.001
d) October 1990						
All taxa combined	2660	439	< 0.001	53.1	5.2	< 0.001
Amphipods	139	6	< 0.001	11.7	0.8	< 0.001
Tanaids	73	1	< 0.001	3.6	0.1	0.010
Isopods	6	0	< 0.001	2.8	0.0	< 0.001
Harpacticoids	1789	181	< 0.001	8.4	0.7	< 0.001
Nematodes	1321	110	< 0.001	6.2	0.4	< 0.001
e) February 1991						
All taxa combined	1443	196	< 0.001	28.6	4.3	< 0.001
Amphipods	34	8	0.001	4.2	0.6	0.001
Tanaids	26	0	< 0.001	1.4	0.0	0.001
Isopods	17	1	< 0.001	9.5	0.3	< 0.001
Harpacticoids	1195	152	< 0.001	4.1	0.5	< 0.001
Polychaetes	40	12	0.011	2.8	0.5	0.012
Nematodes	809	203	0.002	3.5	0.7	< 0.001

Table 6. Comparisons of abundances and biomasses of cumaceans from eelgrass and unvegetated habitats. Abundances are means (individuals/net) with medians shown in parentheses. Precision estimates are not shown as medians have been tested for significance using Mann-Whitney U-tests. Mann-Whitney U-test results are probabilities; all are not significant at $\alpha = 0.05$. Tests were not done for periods when no cumaceans were collected from eelgrass habitat (January 1990 and April 1990).

Sampling period	Abundances			Biomasses		
	Eelgrass	Unveg.	M-W result	Eelgrass	Unveg.	M-W result
January 1990	0 (0)	0.727 (0)		0 (0)	0.097 (0)	
April 1990	0 (0)	0.100 (0)		0 (0)	0.023 (0)	
August 1990	0.125 (0)	1.000 (1)	0.062	0.005 (0)	0.175 (0.036)	0.053
October 1990	0.750 (0)	3.857 (2)	0.111	0.051(0)	0.233 (0.072)	0.200
February 1991	0.400 (0)	2.778 (0)	0.208	0.014 (0)	0.402 (0)	0.170

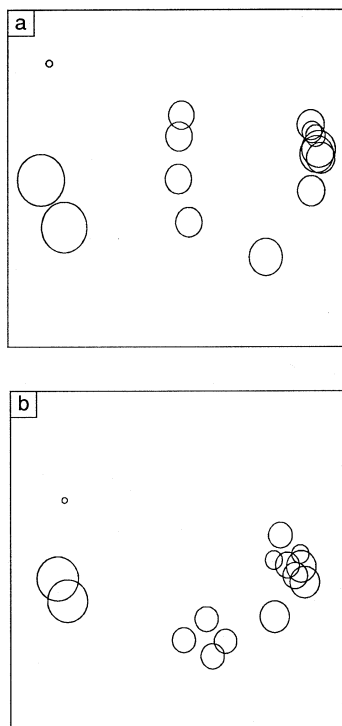


Figure 4. Overlay of distance from site to open water onto MDS ordination plots for August 1990 using (a) abundance (see Figure 2c) and (b) biomass (see Figure 3c). Diameter of circle is proportional to distance. Smallest circle in any plot = 1.0 km, largest = 9.1 km.

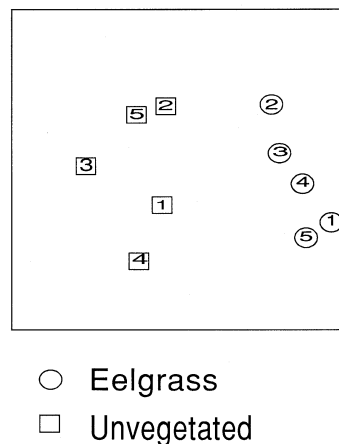


Figure 5. Two-dimensional MDS ordination plot of epifaunal assemblages over all periods combined. Stress = 0.166. Sites of a given habitat (eelgrass or unvegetated) at a given period have been combined and plotted at their centroid. Periods are indicated by numbers: 1 = January 1990, 2 = April 1990, 3 = August 1990, 4 = October 1990, 5 = February 1991.

greater in eelgrass than in unvegetated habitat at all

periods (Table 5). Taxa important in distinguishing between assemblages from the two habitats were similar at all periods, with amphipods and harpacticoid copepods important at all periods and tanaids, isopods and polychaetes important at all but one period. Nematodes were analysed separately but showed the same consistent pattern of greater abundance and biomass in eelgrass than in unvegetated habitat at all periods. When nematodes were included in multivariate analy-

Table 7. Total epifaunal production and total crustacean production ($\mu\text{g}/\text{day}/0.0625 \text{ m}^2$) in eelgrass and unvegetated habitats at each sampling period. Numbers are means. Precision estimates are not shown as all means have been tested for significance using ANOVA. ANOVA results for total epifaunal production are the same as those for total biomass in Table 5. ANOVA results for total crustacean production are $p < 0.001$ at all sampling periods.

Sampling period	Total epifaunal production		Total crustacean production	
	Eelgrass	Unveg.	Eelgrass	Unveg.
January 1990	539	86	407	53
April 1990	249	94	212	46
August 1990	199	27	171	12
October 1990	391	59	241	37
February 1991	339	73	265	39

Table 8. Water temperature and salinity at eelgrass and unvegetated sites at each sampling period (after Connolly, 1994a). Habitats: e = eelgrass, u = unvegetated. Temperature measured in degrees Celsius. Numbers are means with standard errors in parentheses. No significant differences in temperature or salinity were found between habitats at any period using Mann-Whitney U-tests.

Sampling period	Habitat	Number of sites	Temperature	Salinity
Jan 90	e	9	22.7 (0.46)	38.5 (0.22)
	u	11	22.8 (0.44)	38.3 (0.37)
Apr 90	e	10	21.9 (0.39)	38.1 (0.15)
	u	10	22.8 (0.40)	38.3 (0.18)
Aug 90	e	8	15.2 (0.61)	35.3 (0.18)
	u	7	14.6 (0.86)	35.3 (0.14)
Oct 90	e	8	19.1 (0.80)	36.1 (0.31)
	u	7	18.5 (0.63)	36.5 (0.19)
Feb 91	e	10	27.7 (0.40)	37.8 (0.16)
	u	9	27.4 (0.23)	38.0 (0.17)

ses of assemblages, they were important at several periods in distinguishing between the two habitats. The inclusion of nematodes did not alter the order of importance of other taxa and altered ANOSIM results very little.

Cumaceans were found in small numbers from a few sites at each sampling period. Although they provided only a minor contribution to differences between assemblages from the two habitats, there is some evi-

dence that cumaceans occur more frequently in unvegetated than in eelgrass habitat. Mean cumacean abundances and biomasses were lower in eelgrass than in unvegetated habitat at all periods (Table 6). Cumaceans were absent from many sites in both habitats, and transforming data using $\log_{10}(x+1)$ failed to render data normal. A non-parametric Mann-Whitney U-test with a correction for tied ranks was therefore used to test whether median cumacean abundance and biomass differed between the two habitats. In January and April 1990 no cumaceans were collected in eelgrass, and no test was done for these periods. Despite mean abundances and biomasses being greater in unvegetated habitat at all periods, no significant differences between medians at any one period were found (Table 6). The sign test was used to test the significance of the mean abundance and biomass being higher in unvegetated habitat at all periods ($n = 5, p = 0.031$). The evidence from all periods taken together, therefore, is that cumaceans are more often found over unvegetated habitats.

Total epifaunal production and crustacean production for the two habitats are shown for each sampling period in Table 7. Results of statistical comparisons between habitats were the same for total production and crustacean production; at all sampling periods production was significantly higher in eelgrass than in unvegetated habitat (ANOVA results; total epifaunal and total crustacean production: All periods, $p < 0.001$).

Although water temperature and salinity fluctuated between sampling periods (Table 8), within any period no differences were detected between eelgrass and unvegetated sites using Mann-Whitney U-tests.

Discussion

Epifauna associated with eelgrass differed from that associated with unvegetated habitat. Total abundance, biomass and production were greater in eelgrass. Epifaunal assemblages from eelgrass and unvegetated areas were different at all sampling periods. This habitat difference was clearly evident over and above changes in epifauna with time (possibly with a seasonal component), associations of epifauna with water temperature and distance to open water, and differences at some periods between the two waterways.

At the taxonomic level used here, differences between assemblages from eelgrass and unvegetated habitats lay mainly in abundances and biomasses of taxa rather than presence or absence of taxa.

Cumaceans were an exception, being absent (or at least not collected) at eelgrass sites in January and April 1990. Taxa having much greater abundances in eelgrass habitat included both macrofaunal groups (such as amphipods and isopods) and meiofaunal groups (such as harpacticoid copepods).

Collections reported in this paper were made only during the day, but in an experiment into the effects of altering eelgrass canopy height, epifauna were collected during both the night and day (Connolly & Butler, 1996). Abundances and biomasses of key taxa were higher at night than during the day, and this reflects a pattern typical of seagrass systems (e.g. Howard, 1987). It is important to sample epifauna at night but in the shallow tidal waters of Barker Inlet transport between sites several kilometres apart is treacherous; alternatives exist but these would require more resources.

Several of the taxa found in greater numbers in eelgrass, most notably harpacticoid copepods, amphipods and polychaetes, form a major part of the diet of most fish species associated with shallow inshore areas (Klumpp et al., 1989) and of *Sillaginodes punctata* in particular (Connolly, 1995b). Although in pollution studies multivariate analyses at higher taxonomic levels (family, or even phylum) reproduce very closely the results obtained at species level (Warwick, 1988), in the present survey differences between the two habitats at lower taxonomic levels would be of interest. Depending on feeding preferences of fish, these lower level differences may be important in determining the suitability of epifauna as fish food. The significant differences detected between epifaunal assemblages of the two habitats demonstrates that the level of taxonomic resolution used in this survey was adequate for answering the general question posed, but more detailed taxonomic work may be useful in refining statements about availability of prey items to particular fish species.

The much greater production in eelgrass areas of epifauna generally and of crustacean taxa in particular is consistent with a model explaining the importance of seagrass to fish in which small fish are more abundant in seagrass because of greater food availability there. This simple feeding model has fish swimming (with or without pattern) until they find food, stopping to eat it, then swimming again until finding more food. Under this scenario, fish will spend more time where there is more food. Experiments showing that the habitat selection model, in which fish preferentially select vegetated over unvegetated habitat, does not fully explain fish abundances (Connolly, 1994c) have

given results pointing towards the simple feeding model. The present survey results are also consistent with, but do not alone prove, the simple feeding model.

Explanations for the greater abundance of epifauna in seagrass include the possibilities mentioned above for fish, viz. preferential selection of vegetated habitat, or aggregation in places of higher food availability. Food for epifaunal invertebrates includes any or all of the following: detritus, bacteria, microscopic algae, and even smaller invertebrates themselves. Other possible explanations for the greater abundance of epifauna in seagrass are listed by Lewis (1984) as: the presence of physical structure usable as living space, dampened hydrodynamic forces, increased number of microhabitats, and greater stabilisation and deposition of sediment. Manipulative experiments are necessary to distinguish between these explanations. Experimental removal of eelgrass canopy from 30 m² patches within the Barker Inlet Port River estuary reduced epifaunal abundance slightly but did not reduce it to match the very low abundance of unvegetated patches (Connolly, 1995a). This result discounts those explanations mentioned above in which presence of canopy is of central importance. Nevertheless, until there is a more comprehensive understanding of the importance of seagrass to invertebrates, the much greater invertebrate production in eelgrass than in adjacent unvegetated areas demonstrated during the present study should be borne in mind when discussing conservation of seagrass meadows in shallow, sheltered embayments.

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