Do the assemblages of benthic macroinvertebrates in nearshore waters of Western Australia vary among habitat types, zones and seasons?

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Benthic macroinvertebrates were sampled seasonally in the subtidal and upper and lower swash zones at two sites in each of six nearshore habitat types on the lower west coast of Australia. The habitat types, which differed mainly in the extent of their exposure to wave activity and whether sea grass and/or nearshore reefs were present, had been distinguished quantitatively using values for a suite of seven statistically-selected enduring environmental characteristics (Valesini et al., 2003). The core samples yielded 121 species representing eight phyla, among which the Polychaeta, Malacostraca and Bivalvia were the most speciose classes, contributing $\sim$38, 23 and 10%, respectively, to the total number of individuals. The total number of species and mean density of macroinvertebrates at the most protected habitat type (1), i.e. 70 and 209.2 individuals $0.1\,\mathrm{m}^{-2}$, respectively, were far greater than in any other habitat type. Habitat type influenced species composition to a greater extent than either zone or season. Furthermore, the extents of the differences among the species compositions of the six habitat types statistically matched the extents of the differences among the values for the suite of enduring environmental characteristics that distinguished each of those habitat types. Overall, the species composition at habitat type 1 was the most distinct, containing five abundant species of polychaetes that were adapted to deposit-feeding in calm waters with high levels of organic material and which were rare in all other habitat types. In contrast, the fauna at the most exposed habitat type was characterized by four crustacean species and a species of bivalve and polychaete, whose mobility and tough external surface facilitated their survival and feeding in turbulent waters. The zonal differences in faunal compositions among habitat types were greatest in the case of the subtidal zone. The faunal compositions differed among zones and seasons only at the most protected habitat type.

INTRODUCTION

Numerous workers have explored the ways in which certain characteristics of benthic macroinvertebrate assemblages in sandy, nearshore marine environments are related to single physical variables (e.g. Dexter, 1984; Edgar, 1990; Jaramillo & McLachlan, 1993; Hutchings & Jacoby, 1994). These workers have shown, for example, that the number of species and densities of benthic macro-invertebrates are typically inversely correlated with sediment grain-size and exposure to wave action and positively correlated with sedimentary organic content and the amount of detached and attached macrophytes. However, the distributions of these faunas among habitats will also reflect differences in the suite of environmental variables that characterize those habitats (Roff & Taylor, 2000; Skilleter & Loneragan, 2003). Furthermore, many environmental variables, which are traditionally used in attempts to determine the basis for the patterns of spatial distribution of benthic faunas, undergo pronounced temporal changes, i.e. are non-enduring (Valesini et al., 2003). Thus, when attempting to explore the ways in which the characteristics of benthic fauna vary amongst habitat types during the course of a year, it is advantageous to use a suite of enduring environmental variables,

i.e. those which undergo little or no temporal change, (Roff & Taylor, 2000; Valesini et al., 2003). In other words, the use of enduring environmental variables allows any association between faunal composition and habitat type to be determined using the same suite of environmental criteria for all times of the year, thereby dispelling the need to undertake regular sampling of variables, which would be the case with those that change temporally (Valesini et al., 2004).

A thorough exploration of the ways in which the characteristics of faunas vary among habitat types relies on the habitat types having been identified in a rigorous manner. Furthermore, the rigorous statistical analyses of faunal habitat relationships depend firstly on the habitat types having been distinguished on the basis of sound quantitative data and then on the ability to match statistically those data with quantitative data on species composition. The use of the BVSTEP routine in PRIMER v 5.2 (Clarke & Gorley, 2001) statistically selected seven of a large suite of enduring environmental variables (27) as providing the best basis for quantitatively distinguishing the six habitat types identified in nearshore waters along the lower west coast of Australia. These differences mainly reflected variations in the extent to which the habitat types were exposed to wave activity and contained sea grass and

nearshore reefs. Subsequently, differences among the composition of fish faunas in the different habitat types in these waters were shown to be statistically correlated with the extent of differences in the values for the seven enduring environmental variables that were selected as characterizing those habitat types (Valesini et al., 2004). The approaches developed in the latter study now enable the composition of the ichthyofauna at any nearshore site on the lower west coast of Australia to be predicted, once that site has been designated statistically to its appropriate habitat type.

The number of species and density of benthic macro-invertebrates typically increase from swash regions to shallow subtidal regions, where the environment is more stable due to it being covered by water for the whole tidal cycle (Borzone et al., 1996; McLachlan et al., 1996). Although the species composition of the benthic macro-invertebrate fauna of subtidal and upper and lower swash zones in a habitat vary significantly, few attempts have been made to compare such faunal compositions in the corresponding zones of different habitat types (e.g. Jaramillo et al., 1993).

Since environmental variables, such as water temperature, sediment characteristics and food availability, change throughout the year in nearshore marine areas, it follows that such variables are likely to influence the recruitment, growth and survival of the benthic macro-invertebrate species that occupy those waters (Braziero, 2001). Yet, the numbers of species, density and composition of benthic faunal assemblages in sandy beach habitats have not been found to vary markedly throughout the year (e.g. Poore & Rainer, 1979; Dexter, 1984; Haynes & Quinn, 1995).

Most of the few studies, which have focused on determining spatial and/or temporal characteristics of the benthic macroinvertebrate assemblages in sandy near-shore environments in Australia, have been undertaken on its east coast, where the beaches are exposed to moderate to high levels of wave activity (e.g. Dexter, 1984; James & Fairweather, 1996; Barros et al., 2002). The few studies undertaken on the benthic macroinver-tebrate assemblages of the low to moderate energy beaches on the lower west coast of Australia have focused either on determining overall densities or the densities of selected taxa (McLachlan & Hesp, 1984; Edgar & Shaw, 1995), or on making comparisons between assemblages at various sites that were selected on the basis of differences in a single environmental variable (McLachlan, 1985).

During the present study, the densities of each benthic macroinvertebrate taxon in the sandy subtidal and lower and upper swash zones at two sites representing each of six nearshore habitat types on the lower west coast of Australia were recorded seasonally for a year. The resul-tant data for the six habitat types, which had been distinguished on the basis of differences in a suite of statistically-selected enduring environmental characteris-tics (Valesini et al., 2003), were used to test the following hypotheses. (1) The number of species and density of benthic macroinvertebrates will be greatest in the habitat type that is least exposed to wave activity and contains areas of dense sea grass beds and, within each habitat type, they will be greatest in the subtidal zone. (2) The overall species composition of the benthic macroinverte-brate faunas at the six habitat types will be significantly different. (3) The extent of differences in the benthic macrofaunal composition among habitat types will be significantly correlated with the extent of differences among the enduring environmental characteristics that define those habitat types. (4) The characteristics of the benthic macroinvertebrate assemblages in each habitat type will differ among zones and possibly, to a certain extent, also among seasons. The question is also addressed as to whether single non-enduring environmental vari-ables, such as volume of detached macrophytes, depth of redox discontinuity layer, sediment grain-size composition and organic content, differ among habitat types desig-nated on the basis of enduring characteristics (Valesini et al., 2003) and, if so, whether they can help explain any differences in the characteristics of the benthic macro-invertebrate fauna in those habitat types.

MATERIALS AND METHODS

Study area

The microtidal (range $<0.5\,\mathrm{m}$) beaches of the lower Western Australian coast are relatively protected from moderate oceanic swell by the presence of two offshore chains of limestone reefs and shallow sandy banks (Pattiaratchi et al., 1997). However, gaps in these reefs and banks, the presence of offshore islands and headlands and variations in local bathymetry, coastline orientation and strength and direction of winds, result in the extent of swell and locally-generated seas varying markedly among beaches and seasons (Hegge et al., 1996; Pattiar-atchi et al., 1997). The nearshore waters of this region are nutrient-poor due to prevention of oceanic upwelling by the warm Leeuwin Current, which flows southward along the adjacent continental shelf (Johannes et al., 1994; Caputi et al., 1996).

Our study focused on the six habitat types identified in nearshore waters on the lower Western Australian coast and which were distinguished by differences in the values for seven enduring variables (Valesini et al., 2003). The seven variables were direct fetch, north-westerly fetch, minimum distance from the shoreline to the $2\,\mathrm{m}$ depth contour, distance from the shore to the first offshore reef chain along a south-westerly transect and the areas of nearshore substrate comprising bare sand, subtidal reef and sea grass (Valesini et al., 2003). Each habitat type was represented by two sampling sites (see figure 1 in Valesini et al. (2003) for site locations).

Habitat type 1 was highly sheltered from wave activity and contained areas of dense sea grass within $50\,\mathrm{m}$ of the shoreline, while habitat type 2 was moderately sheltered from wave activity, with areas of sparse sea grass present both within $50\,\mathrm{m}$ of the shoreline and further offshore. Although habitat types 3 and 4 were both moderately exposed to wave activity, no sea grass beds were present in the vicinity of the former, whereas there were sea grass beds $>50\,\mathrm{m}$ offshore from the latter. Habitat type 5 was moderately exposed to wave activity and contained reefs within $50\,\mathrm{m}$ of the shoreline and habitat type 6 was rela-tively exposed to wave activity and not located near sea grass.

Three zones were sampled at each site. Zone A (upper swash) was the region between the high tide mark (i.e. drift line on upper shore) and the effluent line (i.e. point of groundwater outflow). Zone B (lower swash) was the region between the effluent line and the lower swash line (i.e. point at which the swash curls before breaking on to the beach). Zone C (subtidal) was located in waters where the average depth was ∼1 m.

Sampling regime

Sampling was undertaken during daylight in each season between the summer and spring of 2000. Each site was sampled twice at a two to three week interval in the middle of each season to reduce the chances of the resultant data being unduly affected by an atypical sample (Morrisey et al., 1992).

Five randomly-located sediment cores were collected in each season from each of the three zones at both sites in each of the six habitat types. The cylindrical corer was 11 cm in diameter, covered a surface area of 96 cm² and sampled to a depth of 15 cm. The samples were preserved in 5% formalin buffered in seawater and wet-sieved through 500-μm mesh. Invertebrates retained on the mesh were removed from any remaining sediment using a dissecting microscope, identified to the lowest possible taxon and stored in 70% ethanol. The number of individuals of each macroinvertebrate taxon in each replicate sample was converted to a density, i.e. number of individuals $0.1\,\mathrm{m}^{-2}$.

The non-enduring environmental characteristics measured at each site in each season were water temperature, volume of any detached macrophytes on the beachface, sediment grain-size, contribution of particulate organic matter (POM) to that sediment and the depth of the redox discontinuity layer (i.e. the point at which the interstitial spaces in the sediment become depleted of oxygen).

At each site on each sampling occasion, three replicate water temperatures (°C) were recorded in the middle of the water column (i.e. in Zone C) and the volume of detached macrophytes, accumulated between the sand dunes and seaward limit of the swash zone, was measured along a 50 m transect running parallel to the shoreline.

Sediment grain-size and the contribution of POM to the sediment in three randomly-located cores of sediment (3 cm diameter×15 cm high) collected in each of the three zones at each site on each sampling occasion were determined. The depth of the redox discontinuity layer in each core was then recorded to the nearest 1 mm. The contents of each core were wet-sieved through nested meshes of 2000, 1000, 500, 250, 125 and 63 μm, with any sediment grains <63 μm being collected in a base pan. The fraction of sediment retained on each mesh was dried at 80°C for 24 h and weighed, thereby enabling the percentage contributions of each grain-size fraction to each core sample to be calculated. Each sieve-fraction was then ashed at 550°C for 2 h and reweighed to the nearest 1 mg. The sum of the ashed sediment weights was subtracted from the sum of the dried sediment weights in each core sample to determine the percentage contribution of POM in that sample (Heiri et al., 2000).

Statistical analyses

Univariate analyses

Prior to undertaking analysis of variance (ANOVA), the relationships between the means and associated standard deviations for the number of species and densities of benthic macroinvertebrates, water temperature, percentage contribution of POM, depth of the redox discontinuity layer and volume of detached macrophyte accumulations were examined to ascertain which type of transformation, if any, was required to satisfy the assumptions of normality and constant variance (Clarke & Warwick, 2001). The relationships showed that the first two and last variable required a $\log_{10}$ (n+1) transformation, the third variable did not require transformation, while the fourth and fifth variables necessitated fourth-root and square-root transformations, respectively. The replicate values for each of the above variables were then subjected to either two- or three-way ANOVA to ascertain whether they differed significantly among habitat types, seasons and, except for water temperature and volume of detached macrophytes, also zones.

The null hypothesis that the values for a dependent variable did not differ significantly among any independent variable was rejected when the significance level (P) was <0.05. When ANOVA showed that values for a dependent variable not involved in a significant interaction were significant, Scheffé's a posteriori test was used to determine where those differences occurred.

Multivariate analyses

Multivariate analyses were carried out using the PRIMER 5.2 statistical package (Clarke & Gorley, 2001). The Bray–Curtis similarity coefficient was employed to construct a similarity matrix from the $\log_{10}$ (n+1) transformed mean densities of the various macroinvertebrate species in each zone at both sites in each habitat type in each season. This matrix was then subjected to two- or three-dimensional non-metric multidimensional scaling (nMDS) ordination, depending on the stress level. One-way and two-way crossed analysis of similarity tests (ANOSIM; Clarke & Warwick, 2001)

Table 1. *Mean squares and their significance levels for ANOVA of the number of species and density of benthic macroinvertebrates in Zones A, B and C at habitat types 1–6 during the summer, autumn, winter and spring in 2000. Df, degrees of freedom.* ***P<0.001.

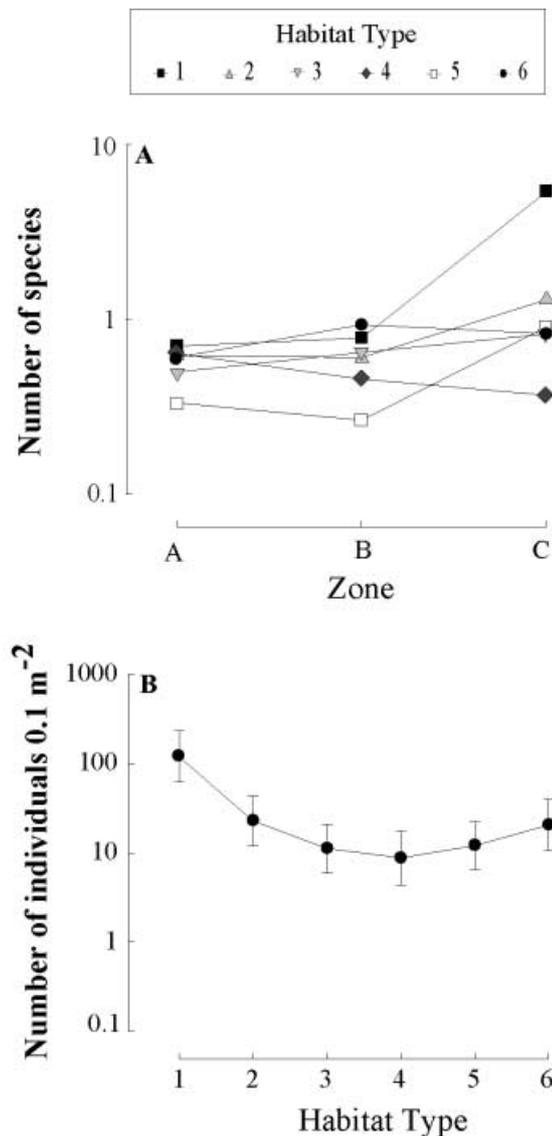|	Df	No. of species	Density
Main effects			
Habitat	5	0.212***	3.272***
Zone	2	0.361***	0.642
Season	3	0.082	0.961
Two-way interactions			
Habitat×zone	10	0.133***	0.380
Habitat×season	15	0.032	0.380
Zone×season	6	0.034	0.221
Three-way interactions			
Habitat×zone×season	30	0.011	0.172
Residual	72	0.033	0.394

Figure 1. Mean (95% confidence interval) (A) number of species in Zones A, B and C at habitat types 1–6 and (B) densities of benthic macroinvertebrates at habitat types 1–6, derived from samples collected in all seasons during 2000. For clarity, the overall mean ±95% confidence interval is provided for (A).

Figure 2. Three-dimensional MDS ordination of the densities of benthic macroinvertebrate species in samples collected at habitat types 1–6 during the summer, autumn, winter and spring of 2000 in (A) Zones A, B and C, (B) Zone B and (C) Zone C. Each sample is coded for habitat type.

were carried out to ascertain whether the compositions of the benthic macroinvertebrate assemblages differed significantly among habitat types, zones and/or seasons. The rationale for selecting the particular combinations of factors employed in each of these tests is provided in the Results. In each ANOSIM test, the null hypothesis that there were no significant differences among groups was rejected if the significance level (P) was <5%. The R-statistic value was used to ascertain the extent of any significant differences, i.e. values close to unity demonstrate that the compositions of samples in a group are more similar to each other than to those of samples from another group, while those close to zero demonstrate that the average similarity within and between groups are similar (Clarke & Warwick, 2001). R-statistic values <0.1 were regarded as negligible. When ANOSIM detected a significant difference among a priori groups
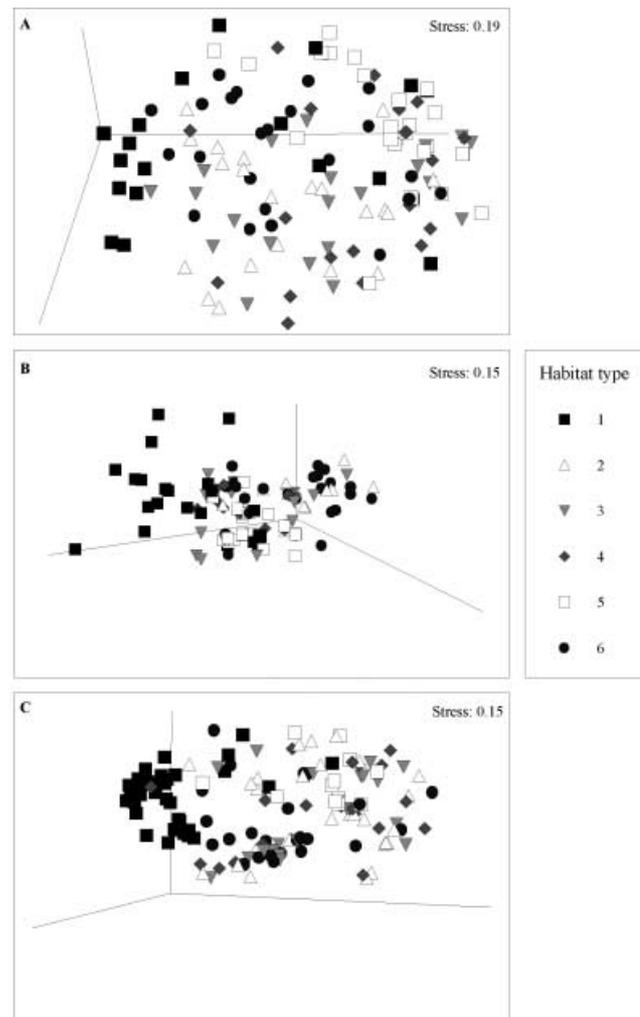
and the R-statistic was >0.1, similarity percentages (SIMPER; Clarke & Warwick, 2001) was used to identify which species typified each group and which contributed most to those differences.

The square-root transformed mean percentage contributions of each sediment grain-size fraction, derived from the three replicate samples collected at each site on each sampling occasion, were subjected to the same multivariate procedures and tests as described above for the densities of benthic macroinvertebrates.

The RELATE procedure was employed to determine, for each zone, whether the arrangement of the rank orders of similarity in the Bray–Curtis matrix constructed from the mean densities of the benthic macroinvertebrate species at the various sites representing habitat types 1 to 6 was significantly correlated with those in the following complementary matrices: (1) the Euclidean distance matrix calculated from the values for seven environmental variables that distinguished between those habitat types (see Valesini et al., 2003); and (2) the Bray–Curtis

Table 2. *Species identified by SIMPER as those which typified the fauna at habitat types 1–6 (e.g. 1 vs 1, 2 vs 2 etc.) and distinguished between the faunas at each pair of those habitat types (e.g. 1 vs 2, 1 vs 3 etc.). Samples collected in the different zones and seasons have been pooled in this analysis. The habitat type at which distinguishing taxa were most abundant is provided in each case (see superscripts). Grey shading represents those pairs of habitat types that did not contain significantly different faunal compositions.*

	1	2	3	4	5	6
1	*Capitella* sp. 1 *Capitella* sp. 2 Eusyllinae spp. Exogoninae spp. *Aricidea* sp.					
2	*Donacilla* sp. 1[2] *Capitella* sp. 2[1] Eusyllinae spp.[1]	*Donacilla* sp. 1 *Donax columbella* *Scolelepis carunculata* Phoxocephalopsid sp. 1 *Exoediceroides* sp. 3				
3	*Capitella* sp. 2[1] Eusyllinae spp.[1] *Donax columbella*[3] *Leptocuma* sp.[3] *Capitella* sp. 1[1]	*(grey shading)*	*Scolelepis carunculata* *Isocladus* sp. *Leptocuma* sp. *Donacilla* sp. 1			
4	*Capitella* sp. 2[1] Eusyllinae spp.[1] *Capitella* sp. 1[1]	*Donacilla* sp. 1[2] *Scolelepis carunculata*[4] *Donax columbella*[2] Phoxocephalopsid sp. 1[2] *Scolelepis lamellicincta*[4]	*(grey shading)*	*Scolelepis lamellicincta* *Scolelepis carunculata* *Hippa australis* *Donacilla* sp. 1 *Atheta* sp.		
5	*Capitella* sp. 2[1] *Scolelepis lamellicincta*[5] Eusyllinae spp.[1] *Capitella* sp. 1[1]	*Donacilla* sp. 1[2] *Scolelepis lamellicincta*[5] *Scolelepis carunculata*[2] *Donax columbella*[2]	*Scolelepis lamellicincta*[5] *Donax columbella*[3] *Leptocuma* sp.[3] Oniscid sp. 1[5] *Isocladus* sp.[3]	*(grey shading)*	*Scolelepis lamellicincta* *Pisionidens* sp. Oniscid sp. 1 *Isocladus* sp.	
6	*Capitella* sp. 2[1] *Donax columbella*[6] Phoxocephalopsid sp. 1[6] Eusyllinae spp.[1]	*Donax columbella*[6] *Donacilla* sp. 1[2] Phoxocephalopsid sp. 1[6] *Leptocuma* sp.[2] *Scolelepis carunculata*[2] Oniscid sp. 1[6]	*Donax columbella*[6] Phoxocephalopsid sp. 1[6] *Leptocuma* sp.[3] Oniscid sp. 1[6]	Phoxocephalopsid sp. 1[6] *Donax columbella*[6] Oniscid sp. 1[6] *Leptocuma* sp.[4] *Scolelepis carunculata*[4] *Scolelepis lamellicincta*[4]	*Scolelepis lamellicincta*[5] *Donax columbella*[6] Oniscid sp. 1[5] Phoxocephalopsid sp. 1[6] *Pisionidens* sp.[6]	Phoxocephalopsid sp. 1 *Donax columbella* Oniscid sp. 1 *Hippa australis* *Leptocuma* sp. 1 *Pisionidens* sp.

similarity matrix calculated from the mean contributions of the different grain-size fractions to the sediments.

RESULTS

Benthic macroinvertebrate fauna

Samples from the three zones in the two sites at each of the six habitat types in the four seasons in 2000 yielded 4181 benthic macroinvertebrates, which corresponds to 43,992 individuals, when each sample is adjusted to $0.1 \, m^{-2}$ and summed (Appendix 1). These samples contained 121 species representing eight phyla, namely Annelida, Crustacea, Mollusca, Sipuncula, Uniramia, Nematoda, Turbellaria and Porifera. The Polychaeta, Malacostraca and Bivalvia, which were the most speciose classes, were represented by 41, 35 and 21 species, respectively, and contributed 37.7, 22.6 and 10.1%, respectively, to the total number of individuals.

The number of species and individuals recorded at habitat type 1 were approximately five and two times greater, respectively, than those at each of the other five habitat types (Appendix 1). Six annelid species contributed about 60% to the number of individuals collected from habitat type 1, while the bivalve *Donacilla* sp. 1 comprised approximately 30% of the invertebrates at habitat type 2 (Appendix 1). The cumacean *Leptocuma* sp. ranked first in terms of abundance at habitat types 3 and 4, comprising approximately 30 and 18% of the individuals at those two habitat types, respectively. The insect Coelopid sp. comprised about 45% of the individuals in habitat type 5, while the amphipod Phoxocephalopsid sp. 1 and bivalve *Donax columbella* collectively represented ∼50% of the individuals at the exposed habitat type 6.

Number of species and densities of benthic macroinvertebrates

Three-way ANOVA showed that the mean number of species differed significantly among habitat types and zones, but not among seasons, and that there was a significant two-way interaction between habitat type and zone (Table 1). Although the mean number of species was greatest in Zone C at habitat types 2, 3, 5 and especially 1, it showed no overall tendency to be consistently greater or less in Zone B than Zone A (Figure 1A). For Zone C, the mean number of species was far greater in habitat type 1 than in any of the other five habitat types and, in Zones A and B, it was least in habitat type 5 (Figure 1A).

The mean density of benthic macroinvertebrates was significantly influenced by habitat type, but did not differ significantly among either zones or seasons (Table 1). The

Table 3. *Species identified by SIMPER as those which typified the fauna in Zone B at habitat types 1–6 (e.g. 1 vs 1, 2 vs 2 etc.) and distinguished between the faunas at each pair of those habitat types (e.g. 1 vs 2, 1 vs 3 etc.). Samples collected in the different seasons have been pooled in this analysis. The habitat type at which distinguishing taxa were most abundant is also provided in each case (see superscripts). Data from two habitat types have been pooled in those cases in which the compositions of their benthic macroinvertebrate faunas did not differ significantly from each other and also differed significantly from those at other habitat types in the same manner.*

	1	2 & 3	4	5	6
1	*Capitella* sp. 2 Eusyllinae spp. Exogoninae spp.				
2 & 3	*Donax columbella*[2&3] *Capitella* sp. 2[1] *Donacilla* sp. 1[2&3] Eusyllinae spp.[1] *Scolelepis carunculata*[2&3] Exogoninae spp.[1]	*Donax columbella* *Scolelepis lamellicincta* *Donacilla* sp. 1			
4	*Capitella* sp. 2[1] Eusyllinae spp.[1] *Scolelepis carunculata*[4] Exogoninae spp.[1] *Capitella* sp. 1[1]	*Donax columbella*[2&3] *Scolelepis carunculata*[4] *Donacilla* sp. 1[2&3] *Scolelepis lamellicincta*[2&3] *Exoediceroides* sp. 3[4] *Atheta* sp.[2&3] Phoxocephalopsid sp.1[2&3]	*Scolelepis carunculata* *Exoediceroides* sp. 3		
5	*Scolelepis lamellicincta*[5] *Capitella* sp. 2[1] Eusyllinae spp.[1] *Pisionidens* sp.[5] Exogoninae spp.[1]	*Scolelepis lamellicincta*[5] *Donax columbella*[2&3] *Scolelepis carunculata*[2&3] *Donacilla* sp. 1[2&3] *Pisionidens* sp.[5] *Atheta* sp.[2&3] Phoxocephalopsid sp.1[2&3]	*Scolelepis lamellicincta*[5] *Pisionidens* sp.[5] *Scolelepis carunculata*[4] *Exoediceroides* sp. 3[4] *Atheta* sp.[5]	*Scolelepis lamellicincta*	
6	*Donax columbella*[6] Phoxocephalopsid sp.1[6] *Pisionidens* sp.[6] *Capitella* sp. 2[1] Eusyllinae spp.[1]	*Donax columbella*[6] Phoxocephalopsid sp.1[6] *Pisionidens* sp.[6] *Donacilla* sp. 1[2&3] *Hippa australis*[6] Phoxocephalopsid sp. 2[6] *Scolelepis carunculata*[2&3]	*Donax columbella*[6] Phoxocephalopsid sp.1[6] *Pisionidens* sp.[6] *Hippa australis*[6] *Donacilla* sp. 2[6] *Scolelepis carunculata*[4] Phoxocephalopsid sp. 2[6]	*Scolelepis lamellicincta*[5] *Donax columbella*[6] *Pisionidens* sp.[6] Phoxocephalopsid sp.1[6] *Hippa australis*[6] *Donacilla* sp. 2[6]	*Donax columbella* Phoxocephalopsid sp. 1 Phoxocephalopsid sp. 2 *Pisionidens* sp.

mean density of benthic macroinvertebrates was significantly greater in habitat type 1 than in each of the other five habitat types, which did not differ significantly from each other. The mean density of benthic macroinvertebrates at habitat type 1 was ∼ten times greater than at habitat types 3, 4 and 5 and ∼six times greater than at habitat types 2 and 6 (Figure 1B).

Comparisons between assemblages in different habitat types

One-way ANOSIMs, derived using the mean densities of each benthic macroinvertebrate taxon in each zone in each site in each habitat in each season, showed that overall the species compositions of the benthic macroinvertebrate fauna differed significantly among habitat types, zones and seasons. The Global R-statistic was greater for habitat type (0.222) than zone (0.126), while that for season was negligible (<0.1).

When the same data were subjected to MDS ordination, the majority of the samples from habitat type 1 formed a relatively discrete group on the extreme left of the plot, whereas the vast majority of those from habitat type 5 lay in the right of the plot. Samples from habitat types 2, 3, 4 and 6 were relatively dispersed throughout the middle of the plot and formed overlapping groups (Figure 2A). Pairwise ANOSIM comparisons showed that the species compositions in each habitat type was significantly different from that in each other habitat type, except for habitat types 2 vs 3, 3 vs 4 and 4 vs 5. The R-statistics values for each pairwise comparison involving habitat type 1 ranged from 0.316 to 0.393 ($P=0.1\%$) and were greater than any of those involving habitat types 2 to 6, which never exceeded 0.279 ($P=0.1\%$).

The benthic macroinvertebrate species composition in habitat 1 was typified by five polychaete taxa, of which, *Capitella* sp. 2 and Eusyllinae spp. distinguished habitat type 1 from all other habitat types (Table 2). *Donacilla* sp. 1 and *Scolelepis carunculata* were among the typifying species of the assemblages at habitat types 2, 3, and 4. The assemblages in habitat types 4 and 5 were each typified mainly by *Scolelepis lamellicincta*, while that at habitat type 6 was characterized primarily by Phoxocephalopsid sp. 1 and *Donax columbella* (Table 2).

Comparisons between assemblages in different habitat types for each zone and/or season

Attention was next focused on examining the extent of the differences among habitat types, after any confounding influences due either to differences among zones and/or seasons had been removed. Thus, since one-way ANOSIM demonstrated that, after habitat type, the

Table 4. *Species identified by SIMPER as those which typified the fauna in Zone C at habitat types 1–6 (e.g. 1 vs 1, 2 vs 2 etc.) and distinguished between the faunas at each pair of those habitat types (e.g. 1 vs 2, 1 vs 3 etc.). Samples collected in the different seasons have been pooled in this analysis. The habitat type at which distinguishing taxa were most abundant is also provided in each case (see superscripts). Data from two habitat types have been pooled in those cases in which the compositions of their benthic macroinvertebrate faunas did not differ significantly from each other and also differed significantly from those at other habitat types in the same manner.*

	1	2 & 4	3	5	6
1	*Capitella* sp. 2 *Capitella* sp. 1 Eusyllinae *Aricidea* sp. *Marphysa* sp.				
2 & 4	*Capitella* sp. 2[1] *Capitella* sp. 1[1] Eusyllinae[1] *Leptocuma* sp.[2&4]	*Scolelepis carunculata* *Leptocuma* sp.			
3	*Capitella* sp. 2[1] *Capitella* sp. 1[1] Eusyllinae[1] *Leptocuma* sp.[3]	*Leptocuma* sp.[3] *Scolelepis carunculata*[2&4] *Scolelepis lamellicincta*[2&4]	*Leptocuma* sp.1		
5	*Capitella* sp. 2[1] *Capitella* sp. 1[1] Eusyllinae[1] *Scolelepis lamellicincta*[5]	*Scolelepis lamellicincta*[5] *Scolelepis carunculata*[2&4] Phoxocephalopsid sp. 2[5] *Scoloplos* sp.[2&4] *Leptocuma* sp.[2&4]	*Scolelepis lamellicincta*[5] *Leptocuma* sp.[3]	*Scolelepis lamellicincta* Phoxocephalopsid sp. 2	
6	*Capitella* sp. 2[1] *Capitella* sp. 1[1] Eusyllinae[1] *Leptocuma* sp.[6]	*Leptocuma* sp.[2&4] Phoxocephalopsid sp. 1[2&4] *Scolelepis carunculata*[2&4] *Donax columbella*[6]	*Leptocuma* sp.[6] Phoxocephalopsid sp. 1[6] *Donax columbella*[6]	*Scolelepis lamellicincta*[5] *Leptocuma* sp.[6] Phoxocephalopsid sp. 1[6] Phoxocephalopsid sp. 2[5] *Donax columbella*[6]	*Leptocuma* sp.1 Phoxocephalopsid sp. 1

species compositions of the samples differed more among zones than seasons, two-way crossed habitat×season ANOSIM tests were performed separately for Zones A, B and C, but focusing on the results for habitat. These tests demonstrated that, in Zones B and C, the species composition differed significantly overall among habitat types 1–6 ($P=0.1\%$, Global $R=0.116$ and 0.327, respectively), whereas no such significant difference was detected for Zone A. Overall, Zone A was characterized by Oniscid sp. 1, *Isocladus* sp., Coelopid sp., *Atheta* sp., and Enchytraid spp.

Following separate ordinations of the densities of benthic macroinvertebrates in Zones B (Figure 2B) and C (Figure 2C), the majority of the samples from habitat type 1 formed a discrete group, which, in the case of Zone C, was particularly tightly clustered.

For Zone B, pairwise comparisons demonstrated that, unlike the situation for habitat types 2, 3, 4 and 6, the composition in habitat types 1 and 5 were each always significantly different from those in all other habitat types and for each comparison the R-statistic value lay between 0.1 and 0.2. The highest R-statistic values only exeeded 0.2 for habitat types 6 vs 4 and 5, for which the values were 0.221 and 0.225, respectively. The species that both typified and distinguished among the faunal compositions of the different habitat types are shown in Table 3.

In Zone C, the composition of the benthic macroinvertebrate assemblage in each habitat type differed significantly from that in each other habitat type, except for those in habitat types 2 vs 4. The differences in faunal composition were greatest for those at habitat type 1 vs each of the other habitat types ($R=0.642$ to 0.831) and these were far greater than any of those in Zone B (all <0.221). For Zone C, the highest R-statistic values for each possible pairwise comparison between the fauna in habitat types 2 to 6 were only 0.174 and 0.178, i.e. for habitat types 5 vs both 2 and 3, respectively. The species composition at habitat type 1 was characterized by Eusyllinae spp., *Capitella* sp. 1 and 2, *Aricidea* sp. and *Marphysa* sp., with the first three species distinguishing the fauna in this habitat type from that at each other habitat type (Table 4). *Scolelepis lamellicincta* typified the subtidal fauna at habitat type 5 and distinguished the fauna at this habitat type from those at all others (Table 4).

Comparisons between assemblages in different zones and seasons for each habitat type

Zone×season ANOSIM tests, derived using the densities of the various benthic macroinvertebrate taxa in each habitat type, showed that the species composition differed significantly among both zones and seasons. In habitat type 1, the Global R-statistic was substantial for zone (0.424) but low for season (0.113) and <0.1 for both of these variables at habitat types 2 to 6.

On the three-dimensional MDS ordination plot, derived using the densities of the benthic macroinvertebrate taxa in habitat type 1, the majority of the samples for Zone C formed a group on the right of the plot that was largely discrete from those for Zones A and B (Figure 3A). When the same data were coded for season,
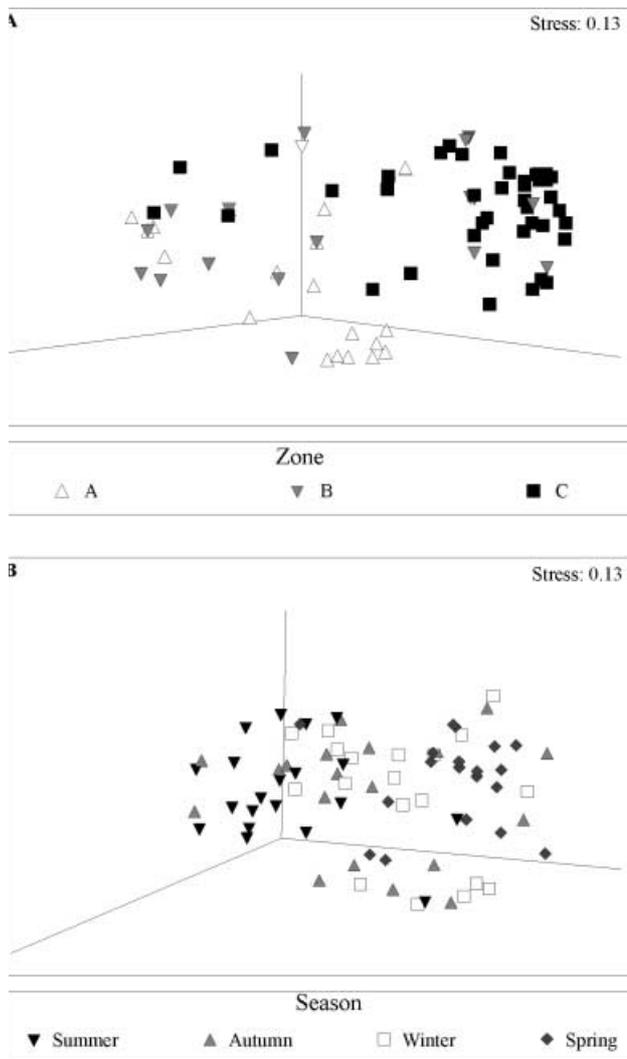
Figure 3. Three-dimensional MDS ordination of the densities of benthic macroinvertebrate species in samples collected at habitat type 1, coded for (A) zone and (B) season.

the groups of samples for summer and spring were well separated on the plot, while those for autumn and winter were located more centrally (Figure 3B).

Pairwise comparisons among the samples for the three zones in habitat type 1 showed that the species composition in Zone C differed significantly from that in both Zones A and B ($P=0.1\%$), for which the R-statistic values were 0.719 and 0.502, respectively. The species assemblage in Zone A was typified by Enchytraid spp. 3 and 4, Coelopid sp. and Staphilinid sp., whereas those in Zones B and C were typified by *Capitella* spp. 1 and 2 and Eusyllinae spp. (Table 5A). Relatively high densities of the latter three species also distinguished the fauna in Zone C from that in Zone B.

Pairwise comparisons among the samples for the various seasons in habitat type 1 showed that the species compositions differed significantly between summer and winter and between spring and each of the other three seasons. The greatest differences were between spring

and both summer and winter, with R-statistic values of 0.232 and 0.180, respectively. In habitat type 1, the composition of the samples in spring was distinguished from that in all other seasons by greater densities of *Capitella* sp. 2 and *Mysella* sp. 1, while that in summer was distinguished from that in winter by greater densities of Exogoninae spp. and lower densities of *Capitella* spp. 1 and 2 (Table 5B).

Relationships between faunal composition and habitat characteristics

The RELATE procedure showed that, in each zone, the arrangement of the rank order of similarities in the matrix derived from the faunal compositions at sites representing habitat types 1–6 were significantly correlated with that derived from the values for the enduring environmental characteristics that distinguished those habitat types ($P=0.1$ to 1.9%, Rho=0.389 to 0.676). However, the former matrix was not significantly matched with that derived using sediment grain-size composition data for each habitat type ($P>0.05$).

Non-enduring environmental variables

Two-way ANOVA showed that water temperature differed significantly among habitat types and particularly among seasons and that there was a significant interaction between these main effects (Table 6). The mean water temperature was greatest in summer and least in winter in each habitat type and was similar in autumn and spring in all habitat types except 4 (Figure 4A). The volume of detached macrophytes differed significantly among habitat types and seasons, with the mean square being considerably greater for the first of these main effects (Table 6). The mean volume of detached macrophytes was significantly greater at habitat types 2, 3, 4 and 5 than at habitat type 6 and was significantly greater in autumn than in summer and spring (Figure 4B,C, respectively).

Three-way ANOVA showed that the depth of the redox discontinuity layer differed significantly among habitat types and zones and that there was a significant interaction between these main effects (Table 6). The mean square was slightly greater for zone than habitat type, both of which were far greater than that for the interaction. Although the mean redox depth in each habitat type was least (shallowest) in Zone C at habitat types 2, 3 and 4 and particularly 1, it varied little among zones at the relatively exposed habitat types 5 and 6 (Figure 4D). Moreover, the lowest mean redox depth for each zone was recorded at habitat type 1, while, in Zone C, those recorded at habitat types 2 and 3 were appreciably less than those recorded at habitat types 4, 5 and 6 (Figure 4D). The contribution of POM to the sediment differed significantly among habitat types, but not among zones or seasons (Table 6). The mean POM was greater at habitat type 1 than habitat types 2, 4, 5 and 6 and was greater at habitat type 3 than habitat type 5 (Figure 4E).

Multivariate comparisons of sediment grain-size compositions

Although the grain-size compositions of the sediment samples were shown by one-way ANOSIMs to differ
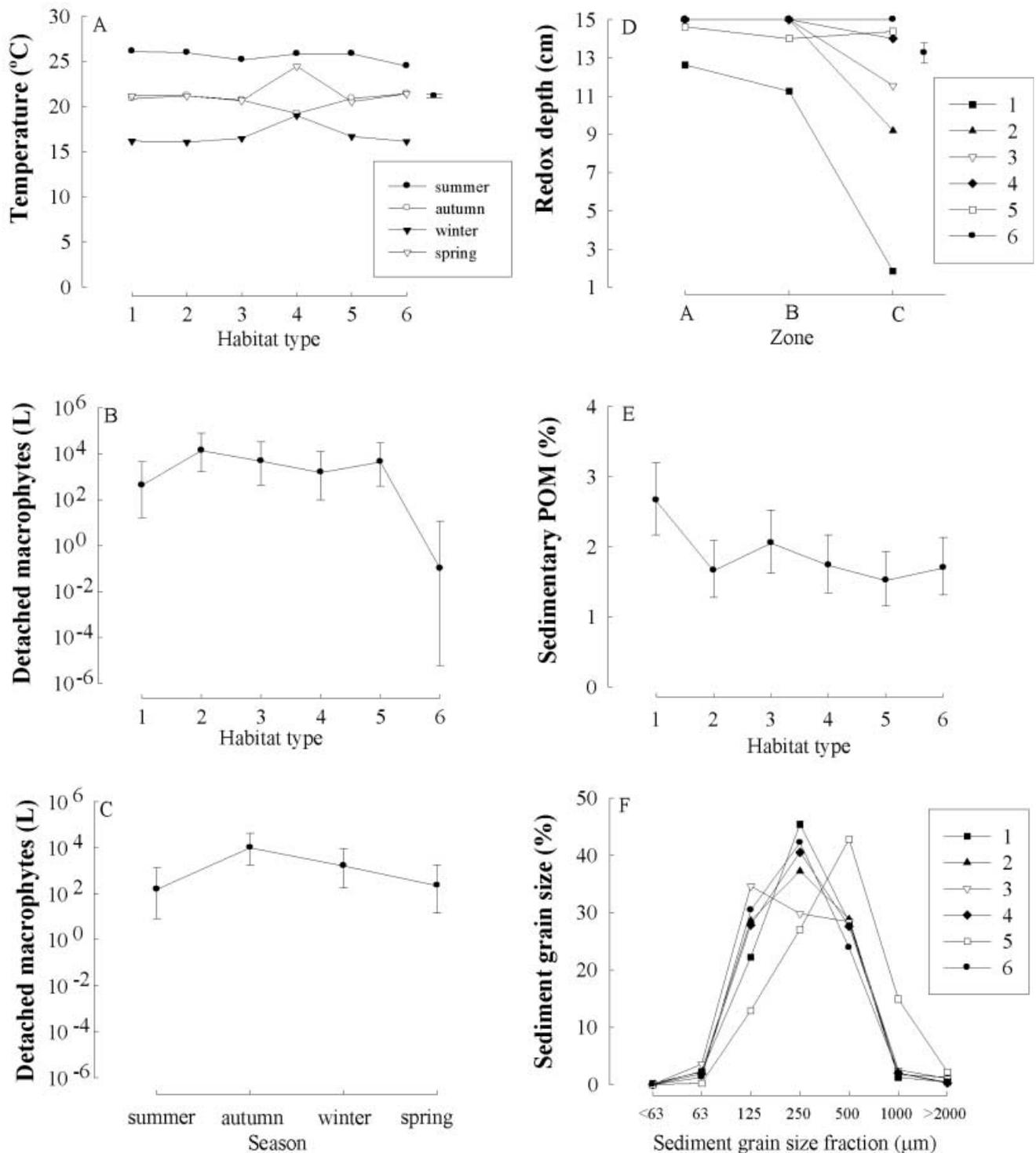
Figure 4. Mean (95% confidence interval) (A) water temperature at habitat types 1–6 in each season, volume of detached macrophytes in (B) habitat types 1–6 and (C) each season, (D) depth of the redox discontinuity layer in each zone. At habitat types 1–6, (E) percentage contribution of sedimentary particulate organic material and (F) percentage contributions of different sediment grain-size fractions at habitat types 1–6, using data derived from samples collected in 2000.

significantly among habitat types and zones ($P=0.1\%$), the Global R-statistic values of 0.181 and 0.138, respectively, were low. Pairwise comparisons demonstrated that the difference among habitat types was largely attributable to differences between habitat type 5 and all other habitat types, with the R-statistic values ranging from 0.442 to 0.541. The fauna at habitat type 5 was distinguished from

that at the other habitat types by larger contributions of grain-size fractions $\geqslant 500\,\mu$m (see Figure 4F for the overall contributions of the various grain-size fractions to the sediments at each habitat type). When the differences among habitat types were analysed separately for each zone (i.e. since the extent of the overall differences in grain-size composition were next greatest for the latter

Table 5. *Species detected by SIMPER as typifying (e.g. A vs A, S vs S etc.) and distinguishing (e.g. A vs B, S vs A) the fauna in (A) Zones A, B and C and (B) summer (S), autumn (AU), winter (W) and spring (SP) at habitat type 1. The zone or season in which distinguishing taxa were most abundant is provided in each case (see superscripts). Grey shading represents those pairs of zones or seasons that did not contain significantly different compositions.*

(A) Zone

	A	**B**	**C**
A	Enchytraid sp. 3 Enchytraid sp. 2 Coelopid sp. Staphilinid sp.		
B		*Capitella* sp. 2 Exogoninae spp. Enchytraid sp. 3 Eusyllinae spp. Enchytraid sp. 2	
C	*Capitella* sp. 2[C] *Capitella* sp. 1[C] Eusyllinae spp.[C]	*Capitella* sp. 2[C] *Capitella* sp. 1[C] Eusyllinae spp.[C]	*Capitella* sp. 2 *Capitella* sp. 1 Eusyllinae spp.

(B) Season

	S	**AU**	**W**	**SP**
S	*Capitella* sp. 1 Exogoninae spp. *Capitella* sp. 2 *Pseudopolydora* sp. *Aricidea* sp.			
AU		Eusyllinae spp. *Capitella* sp. 2 *Capitella* sp. 1		
W	*Capitella* sp. 1[W] *Capitella* sp. 2[W] Exogoninae spp.[S]		*Capitella* sp. 2 *Capitella* sp. 1 Eusyllinae spp.	
SP	*Capitella* sp. 2[SP] Eusyllinae spp.[SP] Exogoninae spp.[S] *Capitella* sp. 1[S] *Mysella* sp. 1[SP]	*Capitella* sp. 2[SP] Eusyllinae spp.[SP] *Mysella* sp. 1[SP]	*Capitella* sp. 2[SP] Eusyllinae spp.[SP] *Mysella* sp. 1[SP] *Capitella* sp. 1[W] Enchytraid sp. 3[W]	*Capitella* sp. 2 *Mysella* sp. 1 Eusyllinae spp.

Table 6. *Mean squares and their significance levels for two-way ANOVA of water temperature and volume of detached macrophytes and three-way ANOVA of the depth of the redox discontinuity layer and contribution of particulate organic matter (POM) to the sediment at habitat types 1–6 during summer, autumn, winter and spring 2000 and also in Zones A, B and C for the latter two dependent variables. Df, degrees of freedom. $**P<0.01$, $***P<0.001$.*

	Df	Temperature	Df	Detached macrophytes	Df	Redox	% POM
Main effects							
Habitat	5	5.71***	5	6.55***	5	134.61***	1.52***
Season	3	450.73***	3	3.78**	3	16.38	0.21
Zone	—		—		2	178.47***	0.26
Two-way interactions							
Habitat×season	15	100.71***	15	1.34	15	7.01	0.79
Habitat×zone	—	—	—	—	10	42.22***	0.80
Zone×season	—	—	—	—	6	9.92	0.77
Three-way interactions							
Habitat×season×zone	—	—	—	—	30	4.81	0.21
Residual	118	1.36	72	0.98	70	10.25	0.17

factor), ANOSIM and SIMPER tests produced similar results (data not shown).

Two-way crossed ANOSIM tests showed that sediment grain-size differed significantly among zones only in habitat type 5 ($P=2.6\%$, Global R=0.347), which was largely attributable to differences between Zones A and B ($P=3.7\%$, R=0.688) and it was not influenced significantly by season in any habitat type. In habitat type 5, the sediment in Zone A contained significantly greater proportions of the 125 to 499-μm grain sizes and significantly lower proportions of grain-sizes >1000 μm than that in Zone B.

DISCUSSION

The number of benthic macroinvertebrate species found in the six habitat types identified in nearshore waters on the lower west coast of Australia ranged from 30 to 70, which is slightly greater than the 12 to 48 species recorded by Dexter (1984) during seasonal sampling of four different nearshore habitats at a similar latitude on the east coast of Australia. This suggests that the diversity of benthic macroinvertebrates in nearshore coastal waters is greater on the lower west than lower east coast of Australia. In contrast, our overall mean density of benthic macroinvertebrates (61.1 individuals 0.1 m^{-2}) was far less than the 94.1 individuals 0.1 m^{-2} calculated from the data provided by Dexter (1984) for nearshore sites on the east coast of Australia. The relatively low densities of benthic macroinvertebrates in nearshore waters on the lower west coast presumably reflect the influence of the low concentrations of nutrients in these waters (Caputi et al., 1996) on the production of the phytoplankton and microphytobenthos that contribute to the diet of many benthic macroinvertebrates (Fauchald & Jumars, 1979; Whitlatch, 1981).

The overall number of species recorded during the present study in nearshore coastal waters (121) is far greater than the 37 to 53 species found during extensive sampling of sites in the Swan and Peel-Harvey estuaries (Rose, 1994), which are located along the same stretch of Western Australian coastline. In contrast, our overall mean density of benthic macroinvertebrates (61.1 individuals 0.1 m^{-2}) is far less than both the ~1150 individuals 0.1 m^{-2} recorded in the middle regions of the Swan Estuary and the ~3000 individuals 0.1 m^{-2} recorded in the Peel-Harvey Estuary during the 1980s when that system was highly eutrophic (Rose, 1994). These comparisons emphasize the marked extent to which, in southwestern Australia, the benthic macroinvertebrate assemblages in nearshore coastal waters are far more speciose, but contain far fewer individuals than do estuaries.

Characteristics of benthic macroinvertebrate assemblages among different habitat types

This study demonstrated that the composition of benthic macroinvertebrates in nearshore waters along the lower west coast of Australia was influenced more by habitat type than by either zone or time of year. Since habitat type 1 contained the greatest number of species, density and the most distinct fauna, it is highly relevant that this habitat type was the most sheltered from wave

activity and contained dense sea grass. The low water turbulence and the ability of sea grass to stabilize sediments and dampen current and wave action would facilitate successful larval settlement and the retention of juveniles and adults in habitat type 1. Although no samples were taken within sea grass beds at any habitat, some of the detritus derived from the dense beds of sea grass present within the most protected habitat (1) would be deposited on neighbouring areas of bare sand (Klumpp et al., 1989). Indeed, the sedimentary organic material, to which sea grass detritus is a contributor, was found to be greatest in this habitat type. Sea grass detritus provides a substrate for epiphytic algae and bacteria, which each provide a food source for benthic macroinvertebrates (Klumpp et al., 1989; Vizzini & Mazzola, 2003). The number of species and densities of benthic macroinvertebrates also tend to be greatest in protected habitats in coastal regions elsewhere, particularly if they contain sea grass (e.g. Dexter, 1984; Edgar, 1990; Edgar & Shaw, 1995).

The benthic macroinvertebrate assemblage in habitat type 1 was characterized by five polychaete taxa that were among the ten most abundant taxa in this habitat type and which were rare in the other five habitat types, i.e. *Capitella* spp. 1 and 2 (Capitellidae), Eusyllinae spp. and Exogoninae spp. (Syllidae) and *Aricidea* (Paraonidae). These polychaetes are sub-surface deposit-feeders (Fauchauld & Jumars, 1979) and thus belong to a trophic group that typically attain high densities in environments in which turbulence is low and substantial amounts of organic material are able to settle and become incorporated into the subsurface sediment layer (Dexter, 1984; McLachlan & Turner, 1994). The presence of substantial amounts of a sedimentary organic food source allows different species of deposit-feeding polychaetes to coexist and attain elevated densities (e.g. Fauchauld & Jumars, 1979). Furthermore, the absence of marked turbulence allows these deposit-feeders to remain within their burrows without risk of becoming dislodged (Whitlatch, 1981; McLachlan et al., 1993).

The faunal composition at habitat type 6, which was the most exposed to wave action, was characterized by four species of crustaceans, i.e. Phoxocephalopsid sp. 1 (Amphipoda), Oniscid sp. (Isopoda), *Hippa australis* (Decapoda) and *Leptocuma* sp. (Cumacea), and by the bivalve mollusc *Donax collumbella* (Donacide) and the polychaete *Pisionidens* sp. (Pisionidae). These species possess either a hard exoskeleton, shell or cuticle and are mobile, which enable them to overcome the problems of living in the relatively turbulent conditions found in this type of habitat (McLachlan & Hesp, 1984; Barnes, 1987). Furthermore, turbulence suspends organic material in the water column and thereby provides a food source for the above six macroinvertebrate taxa that are capable of filtering food from the water column (Defeo et al., 1992; McLachlan et al., 1993). Moreover, the frequent flushing of the interstitial spaces in the substrate of exposed habitats keeps the sediments in those habitat types clean and thereby provides conditions crucial for the maintenance of the fine feeding structures of filter-feeders (McLusky & Elliot, 1981).

Although the composition of the benthic macroinvertebrate assemblage at the most sheltered habitat type (1)

was the most distinct of all habitat types and clearly very different from that at the most exposed habitat type (6), the compositions in some sequential pairs of habitat types, i.e. 2 vs 3, 3 vs 4 and 4 vs 5, were not significantly different from each other. This implies that the fauna changes gradually and progressively with changes in the characteristics of the habitat and therefore accounts for the bivalve *Donacilla* sp. 1 and the polychaetes *Scolelepis carunculata* and *Scolelepis lamellicincta* being among the suite of species that typified habitat types 2, 3, 4 and 5. These filter-feeding and burrowing species thus apparently have an affinity for habitats where the moderate wave activity will lead to a sufficient suspension of organic material as a food source, and yet turbulence is not sufficiently strong to dislodge them from the sediment. Soft-bodied species of *Scolelepis* in similar environments in Tahiti rapidly retract into the sediment at the approach of a wave and protrude their palps into a shallow film of water as the wave recedes and thus collect organic material from the retreating water (Frouin et al., 1998). Although *Donacilla* sp. 1, *S. carunculata* and *S. lamellicincta* each belonged to the suite of typifying species for habitat types 2 to 5, the densities of the first two species decreased from habitat types 2 to 5, whereas the density of the third species exhibited the opposite trend. Those changes thus contributed to the gradual change that occurred in the compositions of the benthic macroinvertebrate faunas between habitats types 2 and 5.

The faunal differences among habitat types were far more marked in Zone C than in Zone B and no such differences were found in Zone A. It is thus relevant that the substrate in the subtidal zone (C) remains permanently covered by water, whereas that in both Zone B and more particularly Zone A receive variable amounts of swash. Since the environment in Zone C is far more stable than that in the other two zones, its fauna will presumably show less variation and thereby be more likely to differ between habitat types. The above findings essentially parallel those recorded for some other benthic macroinvertebrate communities (e.g. Jaramillo et al., 1993).

Characteristics of the assemblages in different zones and seasons in each habitat type

The compositions of the benthic macroinvertebrate fauna differed markedly among zones only in the most sheltered habitat type (1), with the composition in the subtidal zone (C) differing markedly from that in both Zones A and B, which receive variable amounts of swash. The relative lack of turbulence in Zone C leads to deposition of substantial amounts of particulate organic material, which provide a food source for the deposit-feeding polychaetes that were particularly speciose and abundant in this zone. Although present in lower densities, the same deposit-feeding species also typify Zone B in habitat type 1, presumably reflecting the fact that turbulence in the swash zone in this habitat type is relatively low.

In Zone A, in which the sediment is never saturated and where detached macrophytes are present, the fauna was characterized by a number of air-breathing and detritivorous oligochaetes and insects, as is often the case with macrofaunal assemblages in this type of zone

elsewhere (e.g. Giere & Pfannkuche, 1992; James & Fairweather, 1996). The ability of the oligochaetes to burrow into damp sediment on the upper beach level and feed on decaying macrophytes makes these organisms ideally adapted to living in this type of environment. In the case of insects, their exoskeleton protects them from desiccation during periods of low swash (Barnes, 1987).

The compositions of the benthic macroinvertebrate assemblages along the lower west coast of Australia also changed seasonally in habitat type 1. The composition was most distinct in spring, due to the presence of particularly large densities of *Capitella* sp. 2, a Eusyllinae species and *Mysella* sp. 1. These increases in density presumably reflect marked increases in reproductive activity in response to the increases in water temperature and light intensity that occur in this season (Barnes, 1987).

The lack of a significant difference in the composition of the benthic macroinvertebrate fauna among different zones and seasons at habitat types 2 to 6 parallels the situation recorded for habitats elsewhere in which there is at least moderate water turbulence (Dexter, 1984; Defeo et al., 1992; James & Fairweather, 1996). The lack of such differences has been attributed to greater small-scale spatial and temporal variations in the fauna of more exposed habitats, where environmental conditions are less stable. In our study, such small-scale variation can be attributed to faunal transportation between zones through the action of the moderate to relatively high wave activity found in habitat types 2–6.

Relationships between faunal composition and habitat characteristics

The RELATE procedure showed that, for each zone, faunal differences among habitat types were significantly correlated with differences in the values for the suite of enduring environmental characteristics that were used to distinguish between those habitat types. This relationship thus helps explain the ways in which benthic macroinvertebrate species are distributed along the lower west coast of Australia. Furthermore, it allows the composition of the benthic macroinvertebrate fauna at any site along that coast to be predicted once that site has been assigned to a habitat type on the basis of its enduring characteristics. This predictive capacity will enable managers to set in place plans that will facilitate the conservation of habitat types for a selected purpose. Such selection may be based on the need to maintain biodiversity or to conserve those habitats that are important in providing a source of prey for fish species that prefer a particular type of food (Schafer et al., 2001; Hourston et al., 2004). In conclusion, it is emphasized that the relationship that has been established between the compositions of the benthic macroinvertebrate fauna and habitat type in nearshore waters along the lower west coast of Australia provides further support for the designation by Valesini et al. (2003) of each of those habitat types as distinct.

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Appendix 1. *Mean density (M), standard deviation (±1 SD), percentage contributions to the total number of individuals (%) and the rank by density (Rk) of the benthic macroinvertebrate taxa in samples collected at habitat types 1–6 in all zones and seasons during 2000. Each taxon has been assigned to its respective phyla (Ph) (A, Annelida; C, Crustacea; M, Mollusca; S, Sipuncula; Un, Uniramia; N, Nematoda; T, Turbellaria; Po, Porifera) and predominant feeding mode (F) (Dp, deposit feeder; Dt, detritus feeder; S, suspension feeder; P, predator; U, Unknown). The number of taxa, number of samples collected and the total number of individuals (after the number of individuals in each sample had been adjusted to that in 0.1 m^{-2}) are also provided for each habitat type.*

Habitat types			1				2				3				4				5				6			
	Ph	F	M	SD	%	Rk	M	SD	%	Rk	M	SD	%	Rk	M	SD	%	Rk	M	SD	%	Rk	M	SD	%	Rk
Enchytraid sp. 3	A	Dt	29.2	94.2	14.0	1													0.6	3.0	1.5	7				
Capitella sp. 1	A	Dp	25.7	53.6	12.3	2									0.4	1.7	1.9	8								
Capitella sp. 2	A	Dp	24.5	40.3	11.8	3																	0.2	0.6	0.5	16
Enchytraid sp. 1	A	Dt	17.4	52.5	8.3	4													1.8	8.1	4.5	4	0.2	0.9	0.5	16
Eusyllinae spp.	A	Dt	15.9	33.4	7.6	5	0.6	2.6	1.9	11	0.2	0.9	0.6	17												
Enchytraid sp. 2	A	Dt	15.4	38.3	7.4	6																				
Aricidea sp.	A	Dp	7.3	28.8	3.5	7																				
Pseudopolydora sp.	A	Dp	6.3	22.2	3.0	8																	1.2	5.1	3.3	6
Phylo sp. 1	A	Dp	6.0	28.9	2.9	9	0.2	0.9	0.5	20													0.2	0.9	0.5	16
Exogoninae spp.	A	Dp/C	5.6	12.7	2.7	10																				
Notomastus sp.	A	Dp	5.6	20.4	2.7	10					0.1	0.4	0.3	23									0.3	1.3	0.7	12
Donacilla sp. 2	M	S	5.4	18.0	2.6	12									0.2	0.9	1.0	17					0.7	1.7	1.9	9
Kalliapseudid sp.	C	S/Dp	4.5	15.6	2.2	13																				
Muscid sp.	Un	Dt	4.0	19.6	1.9	14																				
Sipunculan sp. 2	S	Dp	3.8	12.1	1.8	15									0.1	0.4	0.5	24								
Coelopid sp.	Un	Dt	3.7	9.9	1.8	15									0.1	0.4	0.5	24	18.2	84.5	45.5	1	0.1	0.4	0.2	19
Mysella sp. 1	M	S	3.6	10.3	1.7	17					0.1	0.4	0.3	23												
Spio sp.	A	Dp	3.3	13.0	1.6	18	0.1	0.4	0.3	25	0.2	0.9	0.6	17	0.2	0.9	1.0	17								
Leptocuma sp.	C	Dp/S	2.8	8.8	1.3	19	3.9	16.6	12.3	2	8.3	34.0	29.1	1	3.2	15.7	17.7	1					2.3	8.5	6.2	5
Pontodrilus litoralis	A	Dt	1.7	4.9	0.8	20	0.3	0.9	0.8	14									0.5	2.2	1.3	9				
Staphilinid sp.	Un	Dt	1.7	5.3	0.8	20													0.2	0.9	0.4	15				
Polydora sp.	A	Dp	1.5	4.1	0.7	22	0.1	0.4	0.3	25													0.1	0.4	0.2	19
Tanais sp.	C	Dp	1.5	5.4	0.7	22																				
Polydorella sp.	A	Dp	0.9	2.8	0.4	24																				
Capitellid sp. 4	A	Dp	0.9	3.0	0.4	24																				
Oniscid sp. 1	C	Dt	0.8	2.1	0.4	24					0.1	0.4	0.3	23	0.2	0.6	1.0	17	6.0	21.7	14.9	3	3.0	8.3	8.3	4
Marphysa sp.	A	P	0.8	1.9	0.4	24																				
Exoediceroides sp. 1	C	U	0.6	1.6	0.3	28	0.7	2.6	2.2	9									0.1	0.4	0.2	20	0.3	0.9	0.7	12
Exoediceroides sp. 2	C	U	0.6	3.0	0.3	28					0.4	1.3	1.2	13	0.1	0.4	0.5	24					0.1	0.4	0.2	19
Phoxocephalopsid sp. 1	C	U	0.5	2.6	0.3	30	2.9	8.5	9.0	4	1.8	6.0	6.4	6	2.3	11.1	12.9	3	0.2	0.6	0.4	15	10.4	19.2	28.6	1
Prionospio sp.	A	Dp	0.5	2.6	0.3	30	0.3	1.3	0.8	14																
Capitellid sp. 1	A	Dp	0.5	1.4	0.3	30																				
Nephtys gravereii	A	P	0.4	1.5	0.2	33																				
Soletolina biradiata	M	Dp	0.4	1.2	0.2	33																				
Phoxocephalopsid sp. 2	C	U	0.4	1.7	0.2	33	1.4	3.1	4.4	7					0.7	2.6	3.8	6	0.4	1.4	1.1	10	5.3	23.8	14.5	3
Sipunculan sp. 1	S	Dp	0.4	1.7	0.2	33	0.2	0.6	0.5	20					0.2	0.9	1.0	17								
Linga crassilirata	M	S	0.4	1.7	0.2	33	0.1	0.4	0.3	25																
Lysidice sp.	A	P	0.4	1.3	0.2	33																				
Corophium minor	C	Dt/S	0.3	1.3	0.1	39																	0.1	0.4	0.2	19
Scoloplos sp.	A	Dt	0.3	0.9	0.1	39	1.9	6.5	6.0	5					0.3	1.3	1.4	10								
Diopatra sp.	A	P	0.3	0.9	0.1	39																				
Oniscid sp. 2	C	Dt	0.2	0.9	0.1	42													0.3	0.9	0.6	11				
Septifer sp.	M	S	0.2	0.9	0.1	42					0.1	0.4	0.3	23												
Mysella sp. 2	M	S	0.2	0.6	0.1	42																				
Psammobiid sp.	M	Dp	0.2	0.6	0.1	42																				
Cyamid sp.	M	S	0.2	0.9	0.1	42																				
Pisionidens sp.	A	Dp	0.1	0.4	<0.1	47									0.3	1.3	1.4	10	0.7	0.4	1.7	6	1.2	2.9	3.3	6
Transorchestia sp.	C	Dt	0.1	0.4	<0.1	47													0.1	0.4	0.2	20	0.1	0.4	0.2	19
Gomphina sp.	M	S	0.1	0.4	<0.1	47																	0.1	0.4	0.2	19
Mandalotus sp.	Un	Dt	0.1	0.4	<0.1	47									0.2	0.6	1.0	17	0.2	0.9	0.4	15				
Haplostylus sp.	C	S	0.1	0.4	<0.1	47	0.5	1.5	1.6	12	0.4	1.0	1.2	13	0.2	0.9	1.0	17								
Poriferan sp.	Po	S	0.1	0.4	<0.1	47													0.2	0.9	0.4	15				
Microspio sp.	A	Dp	0.1	0.4	<0.1	47	0.3	0.9	0.8	14	1.8	7.3	6.4	6					0.1	0.4	0.2	20				
Sipunculid sp.	S	Dp	0.1	0.4	<0.1	47	0.1	0.4	0.3	25	0.2	0.9	0.6	17												
Ceratonereis aquisetis	A	Dt/Dp	0.1	0.4	<0.1	47	0.1	0.4	0.3	25	0.1	0.4	0.3	23												
Phylo sp. 2	A	Dt	0.1	0.4	<0.1	47																				
Capitellid sp. 2	A	Dp	0.1	0.4	<0.1	47																				
Capitellid sp. 3	A	Dp	0.1	0.4	<0.1	47																				
Decamastus sp.	A	Dp	0.1	0.4	<0.1	47																				
Caullierella sp.	A	Dp	0.1	0.4	<0.1	47																				
Dodecaceria sp.	A	Dp	0.1	0.4	<0.1	47																				
Waitangi sp.	C	S	0.1	0.4	<0.1	47																				
Orthorrhapha sp.	Un	Dt	0.1	0.4	<0.1	47																				
Trachyselis sp.	Un	Dt	0.1	0.4	<0.1	47																				
Ochthebius sp.	Un	Dt	0.1	0.4	<0.1	47																				
Colon sp.	Un	Dt	0.1	0.4	<0.1	47																				
Lucinid sp.	M	S	0.1	0.4	<0.1	47																				
Tellina sp. 2	M	S/Dp	0.1	0.4	<0.1	47																				
Tellina sp. 1	M	S/Dp	0.1	0.4	<0.1	47																				

(continued)

Appendix 1. *(Continued).*

	Ph	F	1 M	SD	%	Rk	2 M	SD	%	Rk	3 M	SD	%	Rk	4 M	SD	%	Rk	5 M	SD	%	Rk	6 M	SD	%	Rk
Nucula sp.	M	S	0.1	0.4	<0.1	47																				
Donacilla sp. 1	M	S					9.3	17.8	29.2	1	0.7	2.2	2.5	8	0.4	0.8	1.9	8					0.1	0.4	0.2	19
Donax columbella	M	S					3.0	5.0	9.3	3	2.8	6.9	9.8	3									7.7	18.2	21.2	2
Scolelepis carunculata	A	S					1.8	3.7	5.7	6	0.6	1.2	2.1	10	3.0	7.3	16.3	2	0.2	0.6	0.4	15	0.3	1.3	0.7	12
Exoediceroides sp. 3	C	U					1.3	3.9	4.1	8	2.0	7.2	7.1	5	1.0	4.3	5.3	5	0.1	0.4	0.2	20				
Uldanamia pillare	C	U					0.7	2.4	2.2	9	0.2	0.6	0.6	17												
Atheta sp.	Un	Dt					0.4	0.8	1.1	13	3.5	14.1	12.3	2	0.5	1.5	2.9	7	0.3	0.7	0.6	11	0.1	0.4	0.2	19
Hippa australis	C	S/Dt					0.3	1.3	0.8	14	0.1	0.4	0.3	23	0.3	0.9	1.4	10	0.1	0.4	0.2	20	0.5	0.9	1.4	10
Haploscoloplos sp.	A	Dt					0.3	0.9	0.8	14					0.3	0.7	1.4	10								
Gynodiastylid sp. 2	C	U					0.3	0.7	0.8	14																
Amphipod sp. 1	C	U					0.2	0.6	0.5	20									0.6	2.6	1.5	7				
Leptonereis sp.	A	Dt/Dp					0.2	0.9	0.5	20																
Nereis diversicolor	A	Dt/Dp					0.2	0.6	0.5	20																
Rhyncospio sp.	A	Dp					0.1	0.4	0.3	25																
Capitomastus sp.	A	Dp					0.1	0.4	0.3	25																
Heteromastus sp.	A	Dp					0.1	0.4	0.3	25																
Ophelid sp.	A	Dp					0.1	0.4	0.3	25																
Cypridinodes sp.	C	S					0.1	0.4	0.3	25																
Gynodiastylid sp. 1	C	U					0.1	0.4	0.3	25																
Gynodiastylid sp. 3	C	U					0.1	0.4	0.3	25																
Scolelepis lamellicincta	A	S									2.1	6.5	7.4	4	2.3	5.4	12.9	3	6.6	14.0	16.5	2				
Isocladus sp.	C	Dt									0.7	1.7	2.5	8	0.1	0.4	0.5	24	0.3	0.7	0.6	11				
Golgingid sp.	S	Dp									0.5	2.2	1.8	11					0.1	0.4	0.2	20				
Nematode sp.	N	U									0.4	1.7	1.5	12												
Gastrosaccus sorrentoensis	C	S									0.3	1.3	0.9	15									1.0	3.1	2.6	8
Donax deltoides	M	S									0.3	0.9	0.9	15	0.1	0.4	0.5	24								
Turbellarian sp.	T	U									0.2	0.6	0.6	17	0.3	0.7	1.4	10								
Ogyridid sp.	C	Dt									0.2	0.9	0.6	17												
Magelona sp.	A	Dp									0.1	0.4	0.3	23									0.3	0.9	0.7	12
Amphipod sp. 3	C	U									0.1	0.4	0.3	23	0.3	1.3	1.4	10	1.7	6.0	4.3	5				
Dirimus sp.	C	U									0.1	0.4	0.3	23	0.1	0.4	0.5	24								
Glycera sp.	A	Dp									0.1	0.4	0.3	23												
Amphipod sp. 2	C	U													0.3	0.4	1.4	10	0.1	0.4	0.2	20				
Orbinia sp.	A	Dt													0.2	0.9	1.0	17								
Portunis pelagicus	C	P/Dt													0.1	0.4	0.5	24	0.3	1.3	0.6	11				
Talitrid sp. 1	C	Dt													0.1	1.3	0.5	24	0.1	0.4	0.2	20				
Abraeinae sp.	Un	Dt													0.1	0.4	0.5	24	0.1	0.4	0.2	20				
Mactrid sp.	M	S													0.1	0.4	0.5	24					0.1	0.4	0.2	19
Eunice sp.	A	P													0.1	0.4	0.5	24								
Mycopod sp.	C	S													0.1	0.4	0.5	24								
Birubius sp.	C	U													0.1	0.4	0.5	24								
Exoediceroides sp. 4	C	U													0.1	0.4	0.5	24								
Decapod sp.	C	U													0.1	0.4	0.5	24								
Exosphaeroma sp.	C	Dt													0.1	0.4	0.5	24								
Talitrid sp. 2	C	Dt																	0.1	0.4	0.2	20				
Sphaeromatid sp.	C	Dt																	0.1	0.4	0.2	20				
Haustorioidea sp.	C	U																					0.4	0.8	1.0	11
Conchostracan sp.	M	S																					0.1	0.4	0.2	19
Epicodakei tatei	M	S																					0.1	0.4	0.2	19
Glycymeris radians	M	U																					0.1	0.4	0.2	19
Glycymeris sp.	M	U																					0.1	0.4	0.2	19
Musculista sp.	M	S																					0.1	0.4	0.2	19

	1	2	3	4	5	6
Number of taxa	70	36	32	39	30	32
Overall mean density	209.2	32.4	28.8	18.9	40.4	36.9
Number of samples	120	120	120	120	120	120
Total no. individuals	25 104	3 888	3 456	2 268	4 848	4 428