Sublittoral sand dollar (*Echinodiscus bisperforatus*) communities in two bays on the South African south coast

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Macrofaunal community assemblages associated with *Echinodiscus bisperforatus* beds were investigated at three relatively sheltered, sandy subtidal areas in Plettenberg Bay and St. Francis Bay on the South African south coast. Macrofauna, meiofauna and sediment parameters together with sand dollar abundance and distribution were recorded along transects with stations at 2 m depth intervals from 4 m to 12 m. A wave-induced, depth-related turbulence gradient was evident with both mean particle size and sediment sorting decreasing with depth, whereas macrofauna diversity and biomass increased. Macrofaunal species assemblages corresponded to those of subtidal transition zones of more exposed beaches along the southern Cape coast. No single abiotic variable could be identified as the dominant influence on community structure. Distribution of sand dollars within these sites was found to be extremely patchy with densities ranging from 1–10 m^{-2} over a depth range of 4–10 m.

Makrofauna-gemeenskappe verwant aan *Echinodiscus bisperforatus* populasies is by drie relatief beskutte, sanderige subgetygebiede in Plettenbergbaai en St. Francisbaai aan die Suid-Afrikaanse suidkus ondersoek. Makrofauna, meiofauna en sediment parameters is gemonitor by stasies wat elke 2 m langs 'n transek van 4 m tot 12 m diepte gespasieer is saam met gesiggieskulp-verspreiding en digtheid. Makrofauna, meiofauna en sedimentparameters het 'n gradient getoon onderhewig aan diepteverwante-golfturbulensie. Gemiddelde sandkorrelgrootte en sedimentsortering het 'n duidelike afname getoon met 'n toename in diepte, terwyl verskeidenheid en biomassa van makrofauna toegeneem het. Spesieversamelings van makrofauna het ooreengestem met dié van subgetyoorgangsones van blootgestelde strande langs die suidelike Kaapse kus. Geen enkele omgewingsparameter kon as die dominante invloed op gemeenskapstruktuur geïdentifiseer word nie. Verspreiding van gesiggieskulpe in dié gebiede was baie onreëlmatig, met digthede van 1 tot 10 m^{-2} oor dieptes van 4 tot 10 m.

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Burrowing urchins are common members of shallow sublittoral sand communities and a number of morphologically similar species inhabit a variety of relatively sheltered habitats. *Echinodiscus bisperforatus* (Leske 1778), an Indo-Pacific species, is a member of the family Astriclypeidae, one of four families of true sand dollars constituting the echinoid suborder Scutellina. Southern African *E. bisperforatus* populations are confined to sheltered bays and estuaries, where they inhabit sandy intertidal and subtidal areas to a depth of about 20 m (Clark & Courtman-Stock 1976).

Since the pioneering work of Peterson (1918) and Thorson (1957), most studies in the field of benthic marine ecology have focused on factors influencing macrobenthic community assemblages (Whitlatch 1977). The agents responsible for controlling these assemblages are often complex combinations of the prevailing biological and physical parameters of the particular environment. Morin, Kastendick, Harrington & Davis (1985) showed that distinct depth zones occur off sandy beaches, with zonation persisting in spite of the shifting and unstable sandy substratum and the general motility of its members. Notwithstanding regular mention of *E. bisperforatus* in classifications of both the echinoderms in general (Durham 1966; Clark & Courtman-Stock 1976) and the clypeasteroids in particular (Ghiold & Hoffman 1986; Ghiold 1989; Mooi 1989), little published information is available on the ecology or biology of this species or the community structure associated with sand dollar populations.

In South Africa *E. bisperforatus* has been classed as an endangered species and is protected by the Sea Fisheries Act of 1973: No. 82. Localized populations have recently come under threat from human interference in the form of marinas (Wooldridge 1988) and illegal removal of live individuals for sale in curio shops. As little information is available on the distribution, biology or ecology of this species in South African waters, this study aims to describe the macrobenthic community assemblages in two areas having relatively high sand dollar densities and to identify factors affecting community structure in general and the abundance and distribution of sand dollars in particular.

Study areas

Plettenberg Bay and St. Francis Bay are two of a number of log-spiral bays typical of the south coast of South Africa (Figure 1). S and SW swells predominate and sea surface temperatures, influenced by the warm Agulhas counter-current, range from 15–17°C in winter and 21–25°C in summer. Tides are semidiurnal, subequal and the maximum range between high and low spring tides is about 2 m. Winds blow parallel to the coastline with SE and SW winds being predominant in summer and winter respectively. Average wind speeds along this stretch of coast are considerably higher than for other South African coastal regions. These east-facing log-spiral bays are protected from the dominant SW winds and the accompanying W to SW swells.

Preliminary investigation revealed a single *E. bisperforatus* population along the Santareme Bay coastline in St. Francis Bay and two populations in Plettenberg Bay, one in the shelter of the Robberg Peninsula and the second off Lookout

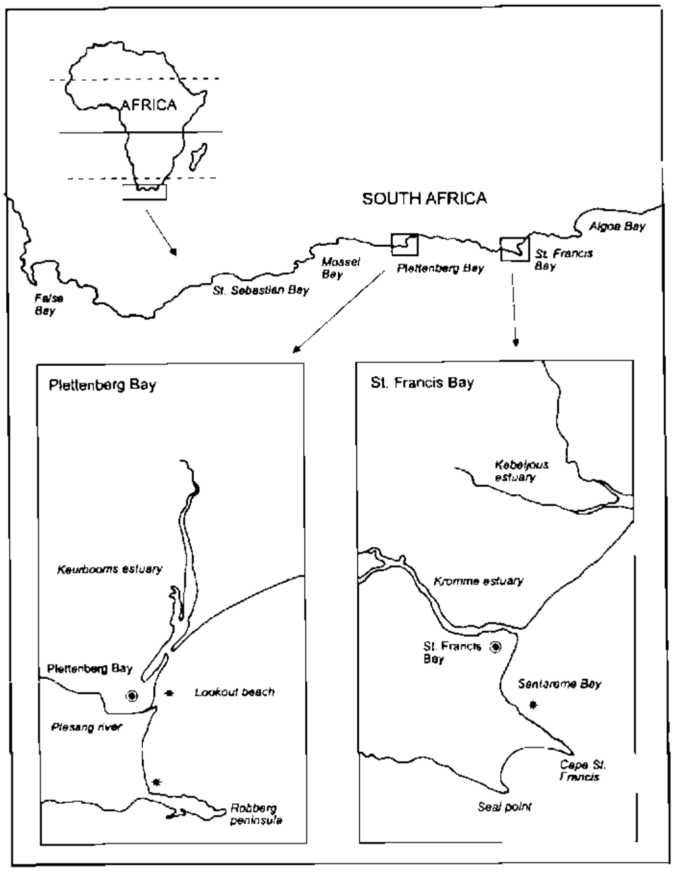

Figure 1 Map of the southern African coastline indicating sampling sites (*) in Plettenberg Bay and St. Francis Bay.

Beach. At the Robberg site extensive ripple fields and mega-ripple formations run parallel to the shore. Ripple patterns at the Santareme Bay and Lookout sites are not as pronounced and mega-ripple formations are seldom visible, while large patches of the substratum are covered by mobile masses of detrital material at the Lookout site, presumably released from the Keurbooms estuary.

Methods

Sampling techniques

Preliminary investigations into the extent of the three populations indicated that five, four and three transects were required at the Santareme Bay, Robberg and Lookout sites respectively. Transects comprised four stations at 2 m depth intervals, ranging from 4–10 m in depth. Sampling was undertaken during June 1990 at the Robberg site only, and during February 1991 and March 1991 at the Robberg, Lookout and Santareme Bay sites. Macrobenthic sampling was performed using SCUBA apparatus from a motorized inflatable dinghy. Samples taken at each station comprised three 0,1 m^2 suction samples using suction sampling apparatus (1 mm mesh) modified from Christie & Allen (1972). Five substratum samples consisting of 11 cm^2 cores were taken at each station using 20 cm lengths of PVC piping (diameter 37 mm) pushed 10 cm into the sediment. Four cores were treated with 7% magnesium chloride for meiofauna extraction before fixation in 10% formalin. The fifth core was preserved in 10% formalin for analysis of sediment parameters. Sand dollars were counted using eight replicate 0,25 m^2 quadrats per station dropped at random on to the sediment surface. The area within each quadrat was hand-sifted to a depth of 10 cm. The number of individuals (eight quadrats) was summed and converted to a value per m^2 of sediment.

Laboratory analysis

Macrofauna were identified to species level where possible. Species abundance values from each individual sample were pooled and converted to numbers per m^2. Dry biomass values were calculated using mean individual dry mass estimates from McLachlan, Cockcroft & Malan (1984) for common species, whereas all other species were oven-dried at 70°C and weighed to 10^{-3} g. Dry mass estimates for gastropods and pelecypods included shell mass.

Meiofauna were extracted from the sediment by three decants through a 45 μm screen. A 10 ml subsample of this extracted material was used to count taxa and determine numeric diversity. Taxa were counted in a counting tray under a stereomicroscope and multiplied by 1,1 to correct for 90% extraction efficiency (McLachlan *et al.* 1984). Abundance values for major taxa were converted to numbers per 10 ml of sediment. Meiofauna biomass estimates were calculated from the following mean individual dry mass values: nematodes, 0,5 μg; harpacticoids, 0,4 μg; turbellarians, 0,5 μg; oligochaetes, 1,6 μg and others, 0,4 μg (McLachlan 1977).

For analysis of sediment parameters, 50 g of oven-dried sediment (70°C) was passed through a computerized settling tube to determine sediment size distribution, mean particle size (graphic mean = M = Q3 + Q1/2) and sorting coefficient (QDa = Q3 – Q1/2) where Q1 is the first quartile and Q3 is the third quartile (Dyer 1979). A 2-g sample was dried at 90°C until attainment of constant weight and ashed at 500°C for 6 h to estimate organic content.

Data analysis

Macrofauna parameters were subjected to Generalised Linear Model (GLM) multifactor analysis of variance (ANOVA) using site and depth as grouping factors (SOLO statistical package, Hintze 1988). A Fisher's LSD comparison test was then performed to determine patterns of statistical difference. The same analysis was then performed using sand dollar presence or absence as grouping factors.

The abundance values (no transformation made) of 83 species at 65 stations were analysed using multivariate data analysis. A Detrended Canonical Correspondence Analysis (DCCA) was performed (Ter Braak 1987) to assess the effect of environmental variables on station groupings. Six sets of environmental data were included in the analysis. Biplots were constructed of species and station data together with these environmental variables (Ter Braak 1987). A cluster analysis was also carried out (BIOSTAT statistical package, Pimentel & Smith 1985) using the Bray-Curtis similarity index together with a flexible clustering strategy (C = 0,25).

Results

Sediment parameters

All stations exhibited similar sedimentary features, possessing fine (M = 181–234 μm), well-sorted (QDa = 0,28–0,48

Table 1 Sediment parameters obtained from the three sites sampled. Stations are represented by transect (A–D) and depth (4–12 m), and MPS = mean particle size; S/C = silt/clay fraction; Sort = sorting coefficient; O/C = organic content

	Robberg (Winter)				Robberg (Summer)				Lookout (Summer)				Santareme (Summer)			
Sta Dpt	MPS (µm)	S/C (%)	Sort (Phi)	O/C (%)	MPS (µm)	S/C (%)	Sort (Phi)	O/C (%)	MPS (µm)	S/C (%)	Sort (Phi)	O/C (%)	MPS (µm)	S/C (%)	Sort (Phi)	O/C (%)
A4	204	2,4	0,35	0,49	213	0.8	0,30	1,10	204	2,3	0,34	1,10	190	1,5	0,40	1,70
A6	232	1,3	0,36	0,48	197	1,7	0,30	0,90	201	1,4	0,33	1,00	203	2,2	0,39	2,10
A8	199	1,9	0,31	0,42	199	2,0	0,30	0,90	190	3,4	0,31	1,60	204	1,7	0,38	1,40
A10	192	1,6	0,29	0,39	213	2,6	0,33	1,20	191	3,4	0,32	1,60	203	2,2	0,38	1,80
B4	216	2,1	0,34	0,32	226	2,3	0,37	1,60	232	2,5	0,38	1,70	219	2,7	0,48	5,60
B6	206	1,9	0,33	0,37	191	1,9	0,29	1,20	222	2,4	0,37	1,80	200	3,1	0,45	3,90
B8	195	2,3	0,30	0,44	195	1,7	0,30	0,90	205	1,0	0,34	1,90	206	1,6	0,37	1,70
B10	187	1,8	0,29	0,39	207	2,5	0,31	1,30	202	2,4	0,33	1,20	203	2,3	0,38	2,10
C4	218	1,4	0,37	0,52	213	2,1	0,32	1,40	229	1,4	0,35	1,10		–	–	
C6	217	2,1	0,35	0,58	206	2,0	0,32	1,70	229	1,4	0,35	1,10	–		–	–
C8	196	0,7	0,33	0,51	204	1,1	0,30	2.10	226	2,5	0,38	1,30	200	0,0	0,44	2,90
C10	181	1,1	0,28	0,55	198	1,5	0,29	1,50	205	2,6	0,29	2,20	183	1,3	0,44	1,40
D4	221	1,5	0,34	0,39	234	2,3	0,37	1,30	–	–	–	–	209	3,7	0,39	2,70
D6	214	1,7	0,32	0,57	214	3,1	0,33	1,70	–	–	–	–	179	2,4	0,48	4,60
D8	200	1,5	0,32	0,48	214	2,9	0,33	1,40	–	–	–	–	172	2,1	0,43	1,80
D10	189	0,0	0,29	0,37	213	2,3	0,32	1,30					179	2,0	0,40	1,80
E4	–	–	–		–	–	–		–	–		–	186	3,0	0,42	1,70
E6	–	–	–		–	–	–	–	–	–	–	–	182	2,2	0,43	1,50
E8	–	–	–	–	–	–					–	–			–	–
E10			–	–	–	–	–	–	–	–	–	–	–	–	–	–

phi) sediments with low silt/clay fractions (0–3,7%) (Table 1). Without exception, all stations gave unimodal particle size structures with 60–90% of particles falling within the 125–250 µm size class.

GLM ANOVA analysis of seasonal data at the Robberg site indicates organic content ($p < 0{,}0001$), mean particle size ($p < 0{,}05$) and silt/clay fraction ($p < 0{,}01$) all to be significantly lower during winter sampling.

Macrofauna

A total of 83 macrofauna species (Table 2) were identified (27 polychaetes, 31 crustaceans, 12 molluscs, 4 echinoderms and 9 other species) and site diversity was relatively uniform with 34 (Lookout), 43 (Robberg summer and winter), and 49 (Santareme Bay) species identified, 21 of these species being common to all three sites.

Macrobenthos was dominated by infaunal species with only two epifaunal species encountered — the asteroid *Astropecten* sp. and the hermit crab Diogenes brevirostris. At all sites the majority of the station faunal assemblages were dominated by crustaceans and echinoderms, these two components comprising more than 60% of total abundance in most cases (Figure 2). Total abundance per station (Table 3) increased with depth from the 4 m to the 10-m stations and ranged from 16,5– 462,1 m^{-2}, With the Lookout site showing the highest mean abundance values over all stations. Corresponding biomass values (Table 3) ranged from 0,2–147,8 g.m^{-2} and generally increased with depth. Total biomass was dominated by the relatively large echinoderms *Echinocardium cordatum* (2.5 g mean individual dry mass) and *E. bisperforatus* (5 g mean individual dry mass), which comprised 70–99% of total biomass. Species richness (Table 3) showed a similar pattern, increasing with depth on most transects and ranging from 2–21 species per station. In all cases crustaceans dominated, constituting > 50% of the species complement at most stations.

Results of GLM ANOVA and Fishers LSD tests (Tables 4a, b) reveal that echinoderm and total abundance were both significantly higher at the Lookout site, owing to the large number of ophiuroids found at this site. In terms of seasonal differences at the Robberg site, crustacean abundance was higher during summer sampling ($p < 0{,}0001$) and total biomass was higher during winter ($p < 0{,}005$), owing to greater densities of sand dollars during winter sampling. The significant differences found according to depth (crustacean, echinoderm and total abundance, *E. bisperforatus* and total biomass and species number) show a general separation of shallow 4 m and 6-m stations and the deeper 8 m and 10-m stations.

Table 2 Macrofauna species recorded during suction sampling at the Robberg, Lookout and Santareme Bay sites. * indicates species presence; W = winter, S = summer

Species		Robberg W	Robberg S	Lookout S	Santareme S
Polychaeta					
Antinoe lactea	Sp 1				*
Aricidea capensis	Sp 2		*	*	
Aricidea curviseta	Sp 3		*		*
Aricidea longobranchiata	Sp 4		*	*	
Armandia leptocirrus	Sp 5	*	*	*	
Cirriformia tentaculata	Sp 6	*		*	
Diopatra cuprea punctifera	Sp 7		*		
Glycera benguellana	Sp 8		*	*	
Glycera convoluta	Sp 9		*	*	
Glycera longipinnis	Sp 10	*			
Goniada emerita	Sp 11	*			*
Goniadopsis incerta	Sp 12	*	*	*	*
Harmothoe sp.	Sp 13				*
Magelona papillicornis	Sp 14	*			*
Marphysa depressa	Sp 15			*	
Nephtys capensis	Sp 16	*	*	*	*
Nephtys paradoxa	Sp 17				*
Notomastus fauveli	Sp 18		*	*	*
Onuphis eremita	Sp 19	*	*		
Ophelia agulhana	Sp 20		*		*
Pectinaria capensis	Sp 21				*
Phylo capensis	Sp 22		*		*
Prionospio cirrifera	Sp 23	*			
Sigalion capense	Sp 24	*	*	*	*
Sthenelais boa	Sp 25	*			*
Sthenelais limicola	Sp 26			*	
Unidentified polychaete	Sp 27	*	*	*	*
Amphipoda					
Ampelisca brachycerus	Sp 28	*			*
Ampelisca brevicornis	Sp 29	*	*	*	*
Atylus homochir	Sp 30				*
Colomastix keiskama	Sp 31	*			
Cunicus profundus	Sp 32		*	*	*
Heterophoxus opus	Sp 33				*
Hippomedon longimanus	Sp 34	*	*	*	*
Hippomedon onconotus	Sp 35		*	*	
Mandibulophoxus stimpsoni	Sp 36	*	*	*	*
Monoculodopsis longimana	Sp 37			*	
Paradexamine pacifica	Sp 38	*			
Perioculodes longimanus	Sp 39				*
Podocerus hystrix	Sp 40				*
Urothoe elegans	Sp 41		*	*	
Urothoe pinnata	Sp 42	*			*
Unidentified amphipod	Sp 43		*	*	*

Table 2 Macrofauna species recorded during suction sampling at the Robberg, Lookout and Santareme Bay sites. * indicates species presence; W = winter, S = summer (Continued)

Species		Robberg W	Robberg S	Lookout S	Santareme S
Isopoda					
Apanthura sp.	Sp 44	*			
Cirolana hirtipes	Sp 45	*			
Cirolana pilula	Sp 46		*	*	*
Cirolana virilis	Sp 47	*			
Eurydice longicornis	Sp 48	*			
Idotea ziczac	Sp 49	*		*	
Leptanthura laevigata	Sp 50		*	*	*
Decapoda					
Betaeus jucundus	Sp 51				*
Callianassa kraussi	Sp 52		*	*	*
Diogenes brevirostris	Sp 53			*	*
Hexapus stebbingi	Sp 54	*			
Ogyrides saldanhae	Sp 55		*	*	*
Ovalipes trimaculatis	Sp 56	*	*	*	*
Philyra punctata	Sp 57		*		*
Thaumastoplax spiralis	Sp 58				*
Pelecypoda					
Crassatina sowerbyi	Sp 59	*			
Donax sordidus	Sp 60	*	*	*	
Loripes clausus	Sp 61	*	*		*
Mactra glabrata	Sp 62		*	*	
Solen capensis	Sp 63		*		*
Tivela compressa	Sp 64	*	*		*
Gastropoda					
Ancilla fasciata	Sp 65		*		
Armina sp.	Sp 66	*			
Bullia annulata	Sp 67	*	*		
Phalium zeylanicum	Sp 68	*		*	*
Philine aperta	Sp 69	*	*		
Volvarina zonata	Sp 70	*			*
Echinodermata					
Ophiuroidea	Sp 71	*	*	*	*
Asteropecten sp.	Sp 72	*	*	*	*
Echinocardium cordatum	Sp 73	*	*	*	*
Echinodiscus bisperforatus	Sp 74	*	*	*	*
Cephalochordata					
Branchiostomata capensis	Sp 75			*	*
Cumacea	Sp 76			*	*
Gstrosaccus psammodytes	Sp 77			*	*
Lysiosquilla capensis	Sp 78				*

Table 2 Macrofauna species recorded during suction sampling at the Robberg, Lookout and Santareme Bay sites. * indicates species presence; W = winter, S = summer (Continued)

Species		Robberg W	Robberg S	Lookout S	Santareme S
Nemertea	Sp 79	*			
Nymphosis cuspidata	Sp 80	*			
Ostracoda	Sp 81	*	*	*	*
Pennatula sp.	Sp 82	*			*
Sipunculida	Sp 83	*	*	*	*

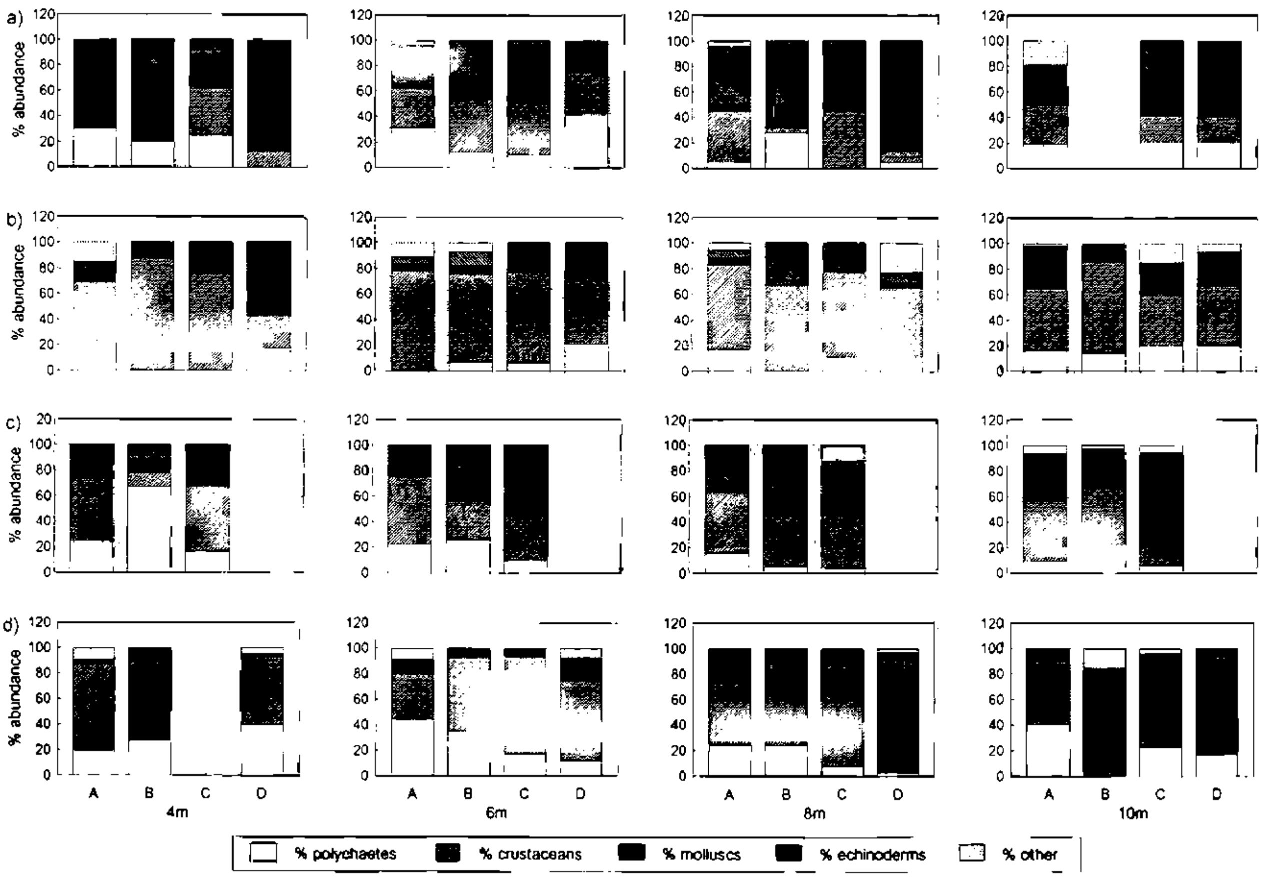

Figure 2 Histograms representing percentage abundance by taxa of macrofauna sampled at the three sites. (a), (b), (c) and (d) represent the Robberg winter, Robberg summer, Lookout summer and Santareme Bay summer sampling sessions respectively.

Meiofauna

Total meiofauna abundance ranged from 744 individuals per 10 ml of sediment ($7 \times 10^5 - 44 \times 10^5$ m^{-2} to a depth of 10 cm) while total biomass ranged from 3,75–21,75 μg per 10 ml of sediment. Nematodes dominated all samples at all sites both in terms of abundance and biomass, comprising 80–90% of total meiofauna values. Harpacticoids and turbellarians made up the bulk of the remaining abundance, comprising 10–20% of total meiofauna numbers. Oligochaetes and other phyla were either present in low numbers or absent from the meiofauna of many stations.

A significantly higher abundance of nematodes was found in sediments during winter sampling at the Robberg site ($p <$ 0,001) than during summer sampling.

Multivariate analysis of community structure

The BIOSTAT dendrogram (Figure 3) shows the affinities between stations based on the abundance scores of the 83 species in the data set. At a 25% faunal similarity level five station groupings are delineated (Groups I–V). The Robberg winter stations (Group I and II) are separated from the summer stations (Groups III, IV and V) at the 0% similarity level, whereas the Robberg, Santareme Bay and Lookout summer stations are separated from each other near the 10% level.

Table 3 Total abundance, biomass and number of species of macrofauna together with *E. bisperforatus* numbers sampled at the three sites in Plettenberg Bay and St. Francis Bay

	Transect A				Transect B				Transect C				Transect D			
	Depth (m)				Depth (m)				Depth (m)				Depth (m)			
	4	6	8	10	4	6	8	10	4	6	8	10	4	6	8	10
Robberg — Winter																
Total biomass (g.m^{-2})	1,0	75,6	50,8	34,7	0.4	85,3	109,5	-	0,6	74,0	110,1	101.3	0,2	147,8	64,7	
Total abundance (m^{-2})	33.0	96,0	66,3	52,9	16,5	55,6	84,0	--	26,6	32,5	66,3	64,2	26,4	70,0	75,3	49.0
Total No. species	05	09	07	11	03	11	12	–	06	06	07	13	02	10	07	08
No. *E. bisperforatus*	00	00	00	00	00	06	08	08	00	06	10	08	00	04	06	06
Robberg — Summer																
Total biomass (g.m^{-2})	10,9	9,2	11,9	67,7	13,4	18,6	13,7	10,3	18,5	45,9	22,7	25,1	60,0	18,9	10,3	02,2
Total abundance (m^{-2})	62,7	59.5	115.8	122,5	37,3	48,2	19,8	23,1	21,9	51,0	59,7	66,4	38.3	31.7	86,0	49.7
Total No. species	12	12	18	18	05	10	04	05	07	08	10	16	07	08	15	09
No. *E. bisperforatus*	00	00	00	00	01	02	00	00	02	08	00	00	02	02	00	00
Lookout — Summer																
Total biomass (g.m^{-2})	33,5	32.5	21,2	31,0	9.3	45,6	51,4	15,7	0.6	18,8	38,1	38,5	–	–	–	–
Total abundance (m^{-2})	53,8	75.0	41,7	145,5	59,6	192.3	258,4	118.9	19,9	65.7	462,1	320,4	–			–
Total No. species	11	14	10	16	09	13	13	13	05	08	11	16	–	–	–	--
No. *E. bisperforatus*	04	02	02	00	00	04	04	00	00	03	00	00		-	-	-
Santareme Bay -- Summer																
Total biomass (g.m^{-2})	7,2	6,2	14,0	12,3	13,4	11,8	20,5	26,5	·	54,6	74,2	28,9	8,2	56,4	31,6	36,2
Total abundance (m^{-2})	34,0	37,3	40,6	33,0	48,2	57,1	69,3	62,7	–	98,7	216,5	72,6	67,0	84,5	198.0	231,3
Total No. species	07	09	10	07	11	08	11	12	–	08	21	12	11	16	15	13
No. *E. bisperforatus*	01	01	01	00	02	01	00	00	–	03	05	00	01	02	00	00

In the Detrended Canonical Correspondence Analysis axes I and II represent 42,5% and 19,1% respectively of the variance associated with the ordination plot and therefore are most important in discerning community patterns related to the data (Figures 4 and 5). Although the station biplot (Figure 4) showed all stations to be closely associated, indicating a relatively homogeneous habitat throughout all sites and depths, a separation of the Plettenberg Bay and Santareme Bay stations according to axis I is evident with the latter stations clustered to the right of the plot. The environmental variables best correlated with this axis are particle size, sorting and meiofauna abundance. There is also a separation along the second axis, representing depth, with deeper stations positioned at the top and shallower stations at the bottom of the plot especially within the Plettenberg Bay sites. Similar trends are evident in the species-environment biplot (Figure 5) with species found solely at the Santareme Bay site positioned to the right of the plot and those species restricted to the Plettenberg Bay sites found to the left. Species found at both locations are positioned between these two extremes. Also visible from this plot is a gradient according to depth, with shallow water species (e.g. *D. sordidus*) positioned at the bottom and deep water species (e.g. *Urothoe elegans* and *Philine arperta*) at the top of the plot.

Sand dollar abundance and distribution

All *E. bisperforatus* individuals were found in the top 5 cm of the sediment. No individuals were found roaming the sediment surface. Sand dollars were found in random associations, except at shallow depths at the Robberg site where they were found in relatively large numbers in the lee of megaripples. The largest densities of *E. bisperforatus* were recorded during the Robberg winter sampling where values ranged from 4–10 m^{-2} (mean 6 m^{-2}) compared to 1–8 m^{-2} (mean 3 m^{-2}) at the Robber s site in summer, 2–4 m^{-2} (mean 3 m^{-2}) at the Lookout site and 1–5 m^{-2} (mean 2 m^{-2}) at the Santareme Bay site.

Sand dollars were found over a 4–10 m depth range at all sites. Distribution patterns at all three sites were extremely patchy, with areas of relatively high density interspersed with areas of low or zero density. Sediment features at the Robberg shallow stations, in the form of depressions and megaripples, normally visible only after storm activity, are responsible for a certain amount of this patchiness, owing to clumping of individuals (up to 10–20 individuals m^{-2} within these features. From GLM ANOVA results only mollusc biomass ($p < 0,05$) was found to be significantly different between stations containing sand dollars and those without.

Table 4 GLM ANOVA and Fisher's LSD tests of macrofauna parameters using site and depth as grouping factors. S indicates a statistically significant difference between the two depths or sites indicated

(a) Parameter	Site	Depth	Site × Depth
Crustacean abundance		p = 0,0160	
Mollusc abundance			p = 0,0148
Echinoderm abundance	p = 0,0003	p = 0,0374	
Echinoderm biomass			
E. bisperforatus biomass		p = 0,0392	
Total biomass	p = 0,0096	p = 0,0036	p = 0,0168
Total abundance	p = 0,0419	p = 0,0076	
Species number		p = 0,0172	

(b)	Echinoderm abundance				Total abundance				Total biomass			
	RW	RS	LS	SS	RW	RS	LS	SS	RW	RS	LS	SS
RW	*	*	S	*	*	*	S	*	*	S	S	S
RS	*	*	S	*	*	*	S	*	S	*	*	*
LS	S	S	*	S	S	S	*	S	S	*	*	*
SS	*	*	S	*	*	*	S	*	S	*	*	*

	Crustacean abundance				Echinoderm abundance				Total abundance			
	4 m	6 m	8 m	10 m	4 m	6 m	8 m	10 m	4 m	6 m	8 m	10 m
4 m	*	*	S	*	*	*	S	S	*	*	S	S
6 m	*	*	S	*	*	*	S	*	*	*	S	*
8 m	S	S	*	*	S	S	*	*	S	S	*	*
10 m	*	*	*	*	S	*	*	*	S	*	*	*

	E. bisperforatus biomass				Total biomass				Species number			
	4 m	6 m	8 m	10 m	4 m	6 m	8 m	10 m	4 m	6 m	8 m	10 m
4 m	*	S	*	*	*	S	S	S	*	S	S	S
6 m	S	*	*	S	S	*	*	*	S	*	*	*
8 m	*	*	*	*	S	*	*	*	S	*	*	*
10 m	*	S	*	*	S	*	*	*	S	*	*	*

Discussion

Results from the three sites studied here compare well with data from other studies of similar environments (Sanders 1968; Christie 1976; McLachlan 1977; McLachlan; Winter & Botha 1977, McLachlan *et al.* 1984; Morin *et al.* 1985; Cockcroft & van der Merwe 1988). The subtidal regions investigated correspond to the surf zone (4-m stations) and transition zone (6–12-m stations) of McLachlan *et al.* (1984). There are also similarities with the zonation scheme of Morin *et al.* (1985) in which their middle zone commenced where major sand shifting ceased (6,5–9,1 m) and turbulence was reduced. This zone was also characterized by an abundance of sand dollars.

The sedimentary characteristics recorded here changed in keeping with the wave-induced turbulence gradient and are similar to those recorded for subtidal high energy sandy areas of Algoa Bay (McLachlan *et al.* 1984). They are also similar to sediments recorded for other sand dollar species. Lane (1977) found sediments in a bed of *Mellita quinquiesperforata* at Mullet Key, Florida to consist of particle sizes with a median of 242–255 μm, sorting coefficients of 0,24–0,28 phi and organic contents of 0,02–0,58%. Smith (1981) found organic content within sediments of a bed of *Dendraster excentricus* off the Californian coast to range from 0,22–0,56% while mean particle size fell within the range from 1,48–2,64 phi, sorting coefficients ranged from 0,3–0,84 phi and silt/clay fraction ranged from 0,1–2,4%.

Meiofauna abundance values correspond to averages (10^6 m $^{-2}$) for soft sediments recorded elsewhere along the southern African coastline (McLachlan 1977; McLachlan *et al.* 1984). Dominance of nematodes in meiofauna samples from fine marine sediments has been found by many authors (McLachlan 1977; McLachlan *et al.* 1984; McIntyre 1969 and Morin *et al.* 1985) and this fact may also partly explain the higher nematode abundance at the Robberg site during winter when mean particle sizes were lower. The low harpacticoid densities recorded in this study are related to the medium-to-fine sediments sampled at most sites, harpacticoids being associated primarily with coarser sediments (McLachlan *et al.* 1977).

Macrofauna assemblages increased in diversity and biomass with depth, as recorded elsewhere for similar habitats

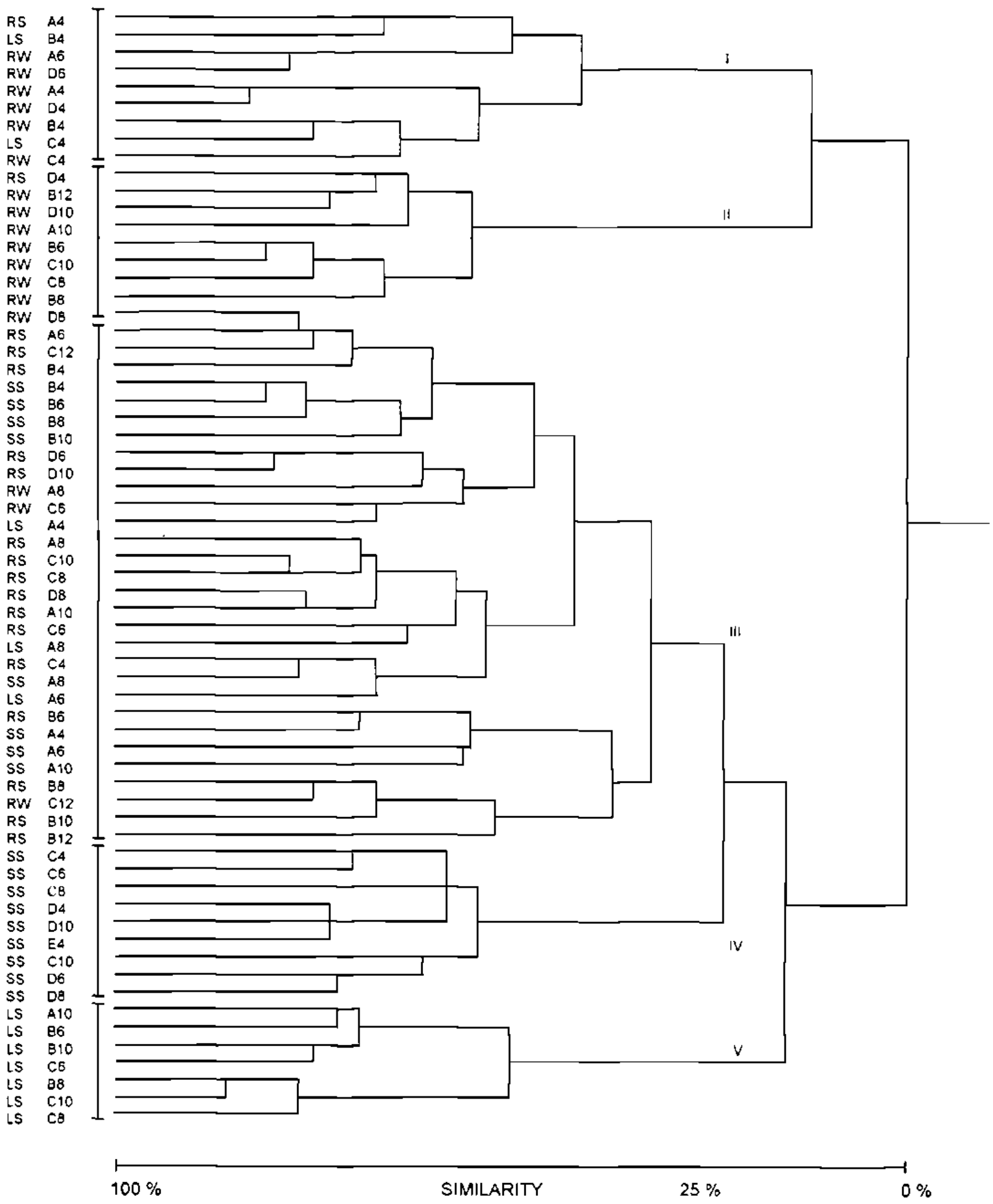

Figure 3 Dendrogram produced from BIOSTAT using a Bray-Curtis similarity matrix and a flexible clustering strategy ($\alpha = -0{,}25$). RW = Robberg winter, RS = Robberg summer, LS = Lookout summer, SS = Santareme Bay summer. Dotted line represents 25% similarity on linear scale bar.

(McIntyre & Eleftheriou 1968; Day, Field & Montgomery 1971; Field 1971; Masse 1972; Gray 1974; Rhoads 1974; Christie 1976; McLachlan *et al.* 1984; Morin *et al.* 1985).

Hughes, Peer & Mann (1972) used multivariate techniques to show that substrate characteristics accounted for 46% of the variance in the frequency of occurrence of polychaetes and echinoderms in St. Margaret's Bay, Nova Scotia. Similar studies indicate that substrate parameters, influenced by exposure to wave action, are instrumental in structuring communities of shallow soft-bottom organisms (Whittaker 1967; Field 1971; Day *et al.* 1971; Hughes & Thomas 1971; Hughes *et al.* 1972; Christie 1976; Shin 1982). Physical environmental parameters, influenced by the turbulence gradient, appear to be the major factors structuring the macrobenthic communities associated with *E. bisperforatus* in Plettenberg Bay and St. Francis Bay (Figures 3 & 4). However, no single abiotic variable emerged as the dominant influence on community patterns. Physical factors are ultimately controlled by wave exposure, and its influence on shallow subtidal community structure would probably become more evident if quantified in some way. Biological interactions probably play a minor role in structuring this community. The major difference between the three communities studied here and those of other studies along the southern Cape coast (Christie 1976; McLachlan *et al.* 1984) is the presence of fairly large numbers of *E. bisperforatus* in these sheltered habitats.

The distribution and abundance of echinoderms has been termed 'notoriously patchy' (Hedgpeth 1957). This patchy distribution appears to be true of echinoids in general (Moore, Jutare, Bauer & Jones 1963; Buchanan 1966; Kitching & Ebling 1967; Ebert 1968; Merrill & Hobson 1970; Ebert &

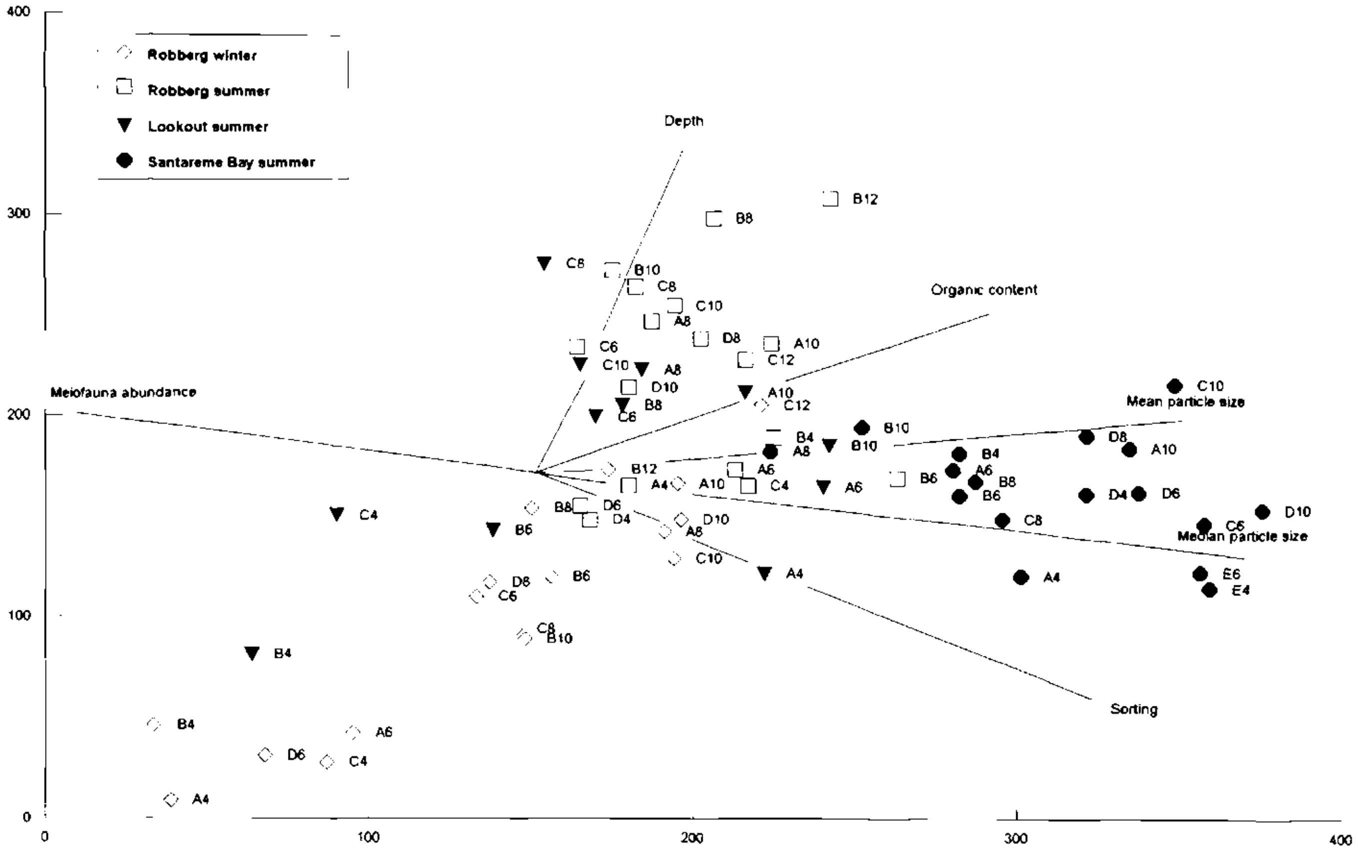

Figure 4 CANOCO DCCA ordination biplot of sites, stations and the six most important environmental variables according to axes I and II.

Table 5 Total abundance (T/A), mean abundance of nematodes (Nem) and all other taxa (Other) (No.10 ml⁻¹ sediment), as well as total meiofauna biomass (T/B) (µg.10 ml⁻¹ sediment) from three sites. Stations are represented by transect (A–D) and depth (4–12 m)

	Robberg (winter)				Robberg (Summer)				Lookout (Summer)				Santareme (Summer)			
Sta	Nem	Other	T/A	T/B	Nem	Other	T/A	T/B	Nem	Other	T/A	T/B	Nem	Other	T/A	T/B
A4	7,24	1,20	8,44	4,15	15,69	6,30	21,9	10,63	9,83	1,52	11,35	5,63	7,98	0,32	8,30	4,12
A6	9,63	1,19	10,82	5,41	10,07	4,70	14,77	7,10	9,50	2,02	11,52	5,64	11,87	2.20	14,07	6,95
A8	10,36	2,39	12.75	6,35	10,09	5,04	15,13	7.22	9,68	1,69	11,37	6,06	14,90	2,25	17.15	8,49
A10	16,00	4,36	20,36	9,92	10.10	6,50	16,60	7,91	7.78	2,24	10,02	4,90	10,36	3,12	13.48	6,55
B4	27,73	1,88	29.61	14,67	15,44	7,40	22,84	11,01	15,84	2,29	18,13	8,96	17,65	2,70	20,35	10.12
B6	19,48	3.63	23,12	11,40	16,38	7,18	23.56	11,31	14,55	2,25	16,80	8,30	6,37	1,11	7,48	3,75
B8	38,09	5,83	43,92	21,75	18,04	7,71	25,75	12,42	9,06	1,29	10.35	5,59	6,83	0,96	7,79	3,84
B10	17,46	2,53	19,99	9,89	13,29	5.72	19,01	9.15	11,44	2.81	14,25	7,04	17,74	1,42	19.16	9,46
C4	18,93	1,87	20,80	10,38	8,33	3,37	11,70	5,04	10,32	0,84	11,16	5,51	-		-	-
C6	30,07	5.68	35,75	17.69	9.40	4,35	13,75	6,59	11,88	2,24	14.12	6,93	7,84	1,06	8.90	4,44
C8	18.15	5,05	23.20	11,45	7,98	4,63	11,75	6.03	20.47	4,55	25,02	12,28	16,78	2,62	19,40	9,66
C10	22,60	3,62	26,22	12,91	15,59	6.10	21,69	10,51	24,93	3,10	28,03	13,91	20,30	2,85	23,15	11,47
D4	23.05	1.75	24,80	12,31	12,52	3,89	16,41	7,96	–	–	–	–	–	–	–	–
D6	20,35	3,53	23.88	11.88	8,63	4,70	13,33	6,38	–	–	–	–	9,58	0,87	10,45	5,19
D8	19,57	4,96	24,53	12,10	13,39	5.14	18,53	8,99	–	–	–	–	16,45	1,61	18,06	9,00
D10	18.29	2.89	21,18	10,42	14,23	3,41	15,65	8,61	–	–	–	–	7,93	0,19	8.12	4,04
E4	–	–	–	–	–	–	–	–	–	–		–	7,70	1,24	8.94	4,43
E6		–	–	–	–	–	–	–	–	–	–	–	19,39	1,70	21.09	10,49
E8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
E10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

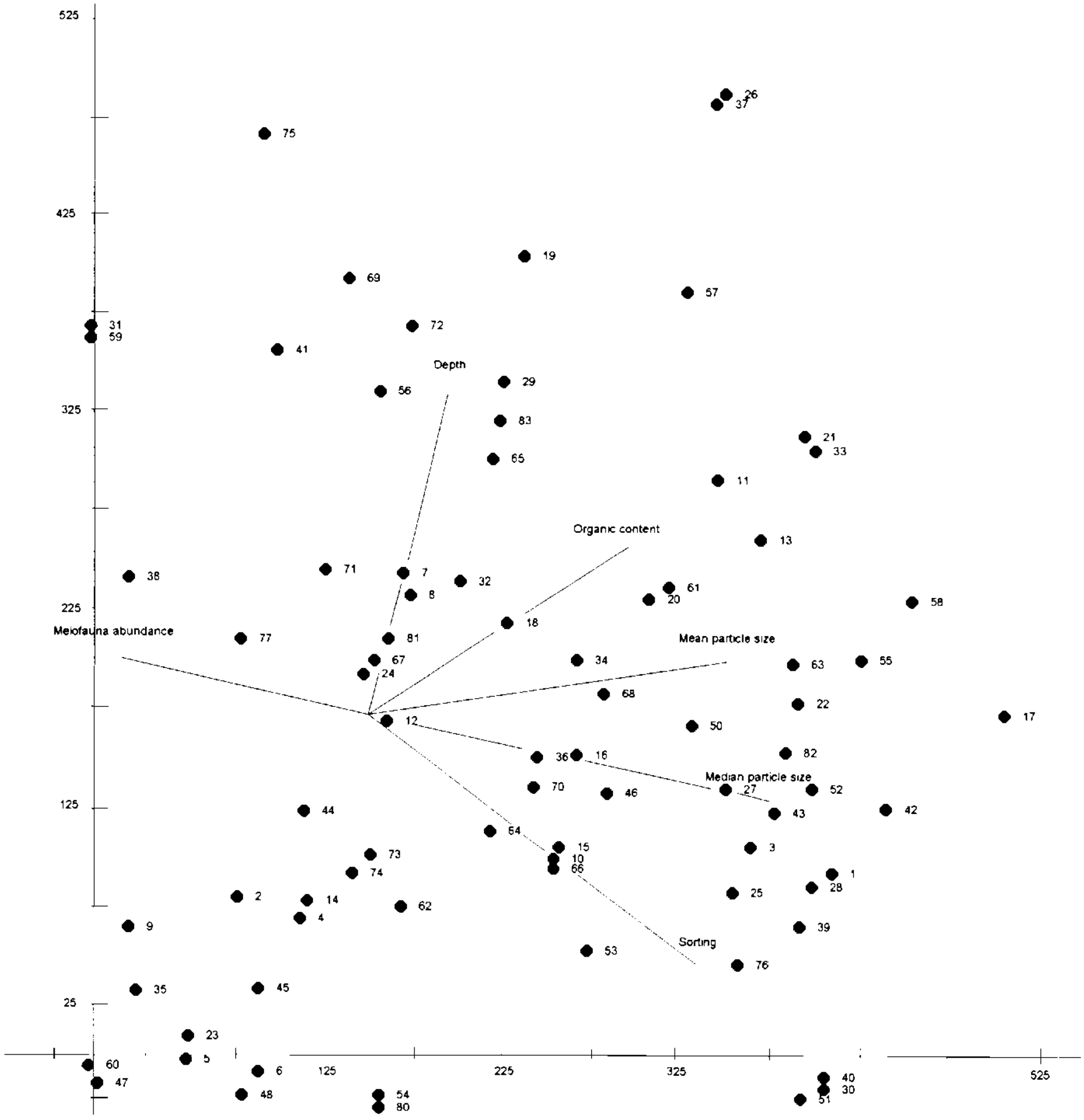

Figure 5 CANOCO DCCA ordination biplot of species and the six most important environmental variables according to axes I and II. Species numbers correspond to those in the species list in Table 2.

Dexter 1975) and sand dollars in particular (Salsman & Tolbert 1965; Bell & Frey 1969; Merrill & Hobson 1970; Timko 1975; Lane 1977). Sand dollars can function as keystone species (*sensu* Paine 1969) in subtidal sands by dominating habitat and detrital food use (Steimle 1990). Stanley & James (1971) concluded that *Echinarachnius parma* was the second most important factor, after major storms, in reworking surface sediments, while Salsman & Tolbert (1965) observed *Mellita quinquiesperforata* completely level a ripple field 6–10 cm high in a single night.

Smith (1981) and Creed & Coull (1984) found that high density aggregations of sand dollars substantially altered benthic macrofauna community structure, especially for tube-dwellers and meiofauna. Brenchley (1978) indicated that epifaunal burrowers in general and sand dollars in particular (*Dendraster excentricus*, with densities in excess of 900 m^{-2}) can restrict the distribution of tube builders by mechanically disrupting the sediment. Two studies of community structure of sand dollar beds (Merrill & Hobson 1970; Smith 1981) have, however, shown that no species were found exclusively inside or outside of sand dollar beds. In this study, a test of macrofauna and meiofauna parameters revealed that only mollusc biomass ($p < 0,05$) was shown to be significantly lower at those sites having sand dollars compared to those without. This may be due to the disruption of surface sediments by these relatively large (85 mm maximum diameter) shallow infaunal burrowers.

Sanders (1968) suggested that shallow-water soft-bottom communities were organized largely by their response to the physical environment. Environmental rigour in such systems inhibits significant biological interactions such as competition and predation. McLachlan *et al.* (1984) concluded that wave energy was instrumental in controlling both the physical environment and the distribution of organisms within these environments. The instability and turbulence caused by wave energy places physical constraints on the ability of organisms to colonize areas such as the surf and transition zones. It is only when sediments become relatively more stable that biological interactions between species become apparent.

Thus wave exposure, through its control of the physical environment, is considered the most important factor shaping shallow subtidal community structure on the sand substratum communities studied. Sand dollar populations are selectively settling in sheltered areas characterized by specific sedimentary parameters. However, the distribution and abundance of populations will ultimately be determined by recruitment success and the absence of sand dollars from habitats with similar environmental conditions may be explained by large scale factors affecting recruitment events in these areas, such as current regimes, sea temperature and storm–calm cycles which will all contribute to the distribution patterns of this species. Current research into aspects of the biology (reproduction, larval development times, and dispersal, recruitment, migration, etc.) of this species will hopefully shed light on this problem.

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