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Spatial variation of the intertidal sediments and macrozoo-benthic assemblages along Eighty-mile Beach, North-western Australia

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Abstract

The extensive intertidal flats along Eighty-mile Beach in North-western Australia appear to be monotonous and homogeneous and seem ideally suited to study tidal zonation in macrozoo-benthic communities and their possible correlates with characteristics of the sediment. In October 1999, we sampled benthic invertebrates and sediments at a total of 895 sampling stations distributed over six different locations, each location separated by 15 km of unsampled foreshore along Eighty-mile Beach. To test for the presence or absence of patterns of tidal zonation (distinct height-related zones of specific sediment grain sizes or zoobenthic taxonomic groups) or patchiness (distinct patches of specific sediment grain sizes or zoobenthic taxonomic groups not related to tidal height) each location was divided into three along-shore sections and each section (transect) was examined at two or three tidal heights. Zonation was observed for sediment grain sizes. Sediments were coarser at the highest intertidal level and finer towards the low water line. Benthic assemblages also differed among tidal heights, but in terms of species-composition the differences were not consistent among the locations. Each location supported a unique collection of benthic invertebrates. Therefore the hypothesis of the presence of distinct zones of specific species or zoobenthic taxonomic groups was rejected; the presence of benthic patches was confirmed. The distribution of sediments and the composition of benthic assemblages were surprisingly poorly correlated compared to those reported in 12 previous quantitative studies around the world. One possible explanation might be that super-cyclone Vance, which hit the study-area only six months before this study, contributed to this poor correlation. Alternatively, the poor correlation may indicate that biotic interactions are more important than the assumed abiotic structuring.

Keywords: Beach morphology; Zoobenthos; Sediment; Grain size; Spatial patterns; Zonation

1. Introduction

Animals and plants on intertidal rocky shores often occur in patches or show vertical zonation, i.e. (presumably) tidal-height related bands consisting of a specific assemblage of species (Underwood, 1981, 1984; Peterson, 1991). Except for larger plants (mangroves, seagrasses), zonation is less obvious in intertidal soft sediments. Most intertidal animals live buried in the sediment and, therefore (see references in Peterson, 1991) patterns are harder to recognise. If present, those

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patterns are generally most pronounced in areas where invertebrates are able to modify the physical environment and, in that way, contribute to spatial differences in the composition of sediment and of benthic assemblages. The effects of the ability of biota to modify the environment are most pronounced in sheltered beaches (McLachlan, 1987). Other processes that can contribute to zonation or patchiness are, for example, recruitment or larval preferences (Grosberg, 1982), settlement, selective mortality, and habitat-composition (Raimondi, 1988).

Causes of the existence of zonation or patches in intertidal areas, reviewed by Peterson (1991), can be: (1) the need of some benthic species of invertebrates to be submerged for a relatively long period of the tidal cycle to be able to feed and meet energetic requirements, (2) the inability to cope with physical stress of exposure to air and, therefore, a preference to live at lower tidal levels, (3) the avoidance of particular kinds of predation (fish and crabs vs birds; e.g. Zwarts and Wanink, 1993) (4) the outcome of interspecific interactions among benthic animals themselves. For example, food competition among filter feeders (Peterson and Black, 1987, 1991; Kamermans, 1993; Beukema and Flach, 1995; Thrush et al., 2001) and modification of sediment by bioturbation (Warren and Underwood, 1986; Warwick et al., 1990; Schratzberger and Warwick, 1999) can facilitate or prevent settlement or survival of species (Warwick et al., 1986; Flach, 1996). Finally, there is (5) the dissipation of energy generated by waves which may affect sediments and, hence, the fauna (McLachlan, 1987). Closer to the shore, the waves transfer energy to the seafloor and affect sorting of sediments. Generally, finer sediments are deposited at lower tidal levels where wave action is less severe; coarser particles can only be deposited at higher tidal levels. Some species or groups of species appear to have preferences for a certain distribution of grain sizes (Rhoads and Young, 1970; Levinton, 1972; Gray, 1974; Peterson, 1991; Snelgrove and Butman, 1994).

Although apparent zonation of benthic assemblages in sandy beaches has been reported in many studies reviewed by McLachlan and Jaramillo (1995), testing hypotheses about the composition of assemblages at, for example, different tidal heights is difficult; general processes causing zonation are hard to identify. Due to a confusing suite of inter-and intraspecific interactions among species and/or interactions with abiotic environmental factors (Underwood, 2000), the (assumed) presence of zonation cannot always be confirmed (Underwood, 1978, 2000; Chaloupka and Hall, 1985).

The aim of this study was to see whether there is any evidence for across-shore (tidal zonation) and along-shore gradients in the distribution of sediments and in the composition of benthic assemblages of the intertidal (littoral) zone at Eighty-mile Beach (Western Australia) and if any of the gradients are correlated. This beach, which starts 200 km south of Broome, West Kimberly, is about 150 km long, an almost continuous sandy beach with a wide intertidal area interrupted by only a few, small, muddy bays bordered by mangrove trees. Going seaward, the steep upper slope of the beach gives way to intertidal mud-and sandflats. At very low tides the maximum width of the flats is 4–5 km. So far, it has been relatively little impacted by human activities. The physical appearance of the beach seems homogeneous, making it an ideal location to study subtle gradients in benthic assemblages and characteristics of the sediments. We expected to find coarser sediment close to the reflective upper-shore of the beach and finer sediments at the lower tidal levels, but we have no specific predictions about the composition of the zoobenthic community.

2. Methods

2.1. General description of the study area

Despite a tidal difference of about 6 m and an intertidal zone up to 5 km wide, Eighty-mile Beach can be considered a reflective beach (McLachlan, 1987, 1990). At this type of beach, conditions are generally calm and waves are basically absent. Coarse sand is deposited high in the intertidal, resulting in a characteristic step (about 0.5 m) on the lower shore where the incoming waves collide with the backwash and with a platform of coarse sand above the intertidal slope. The intertidal area is relatively flat and consists mainly of fine sediments except at the highest levels just below the step where sediments consist mainly of medium and coarse sands. Thus, conditions at Eighty-mile Beach can be summarised as a tidal-flat system with a reflective upper shore. We sampled sediments and benthos at the tidal flats from just below the step of the beachfront to the low-water line.

2.2. Sampling and treatment of benthos and sediment

Along Eighty-mile Beach, at six locations (A–F) each ca 15 km apart, blocks of sampling stations were selected (top graph of Fig. 1). Each location consisted of 10–14 transects, starting at the landward side of the intertidal area and going towards the low water level

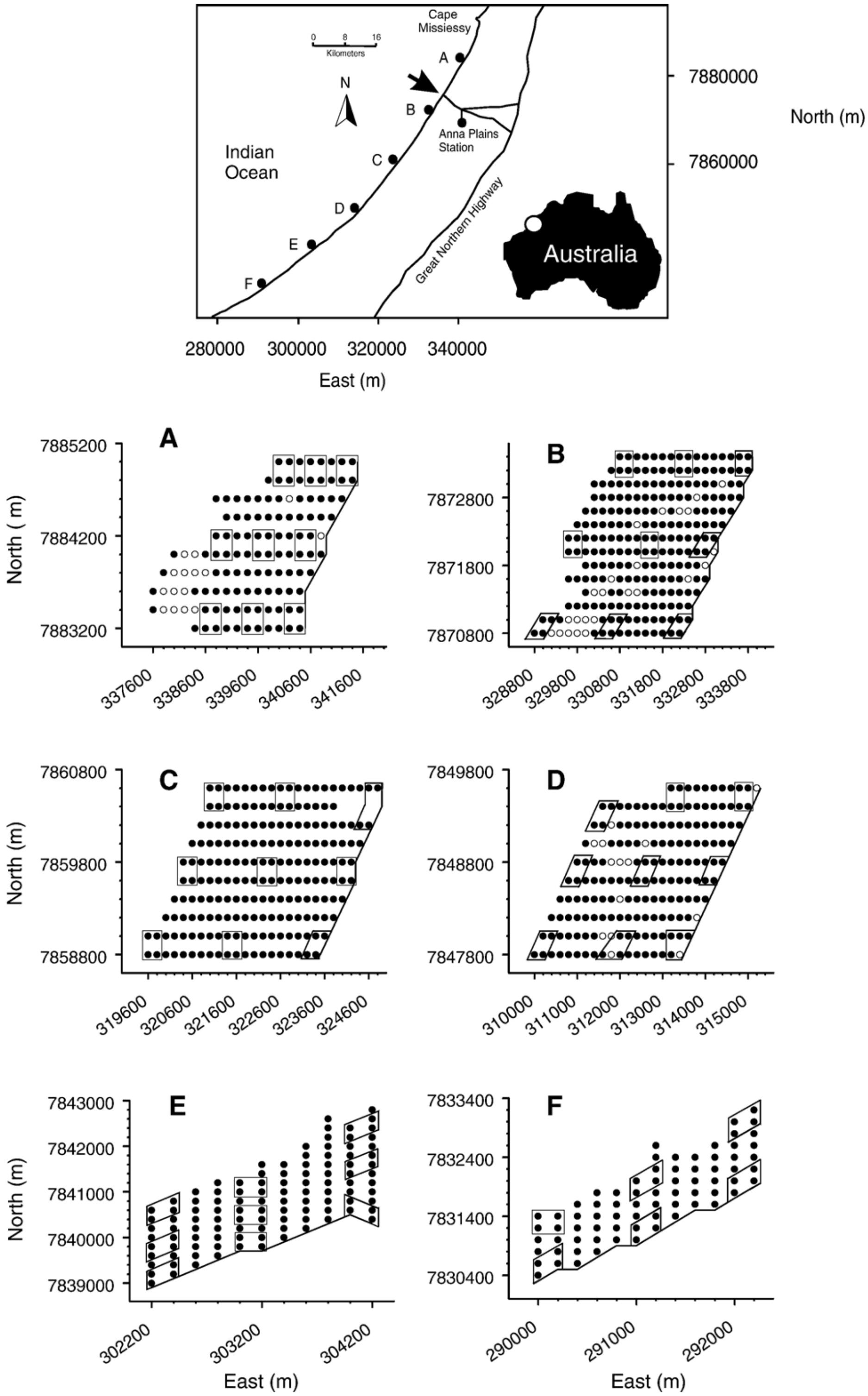

Fig. 1. The top graph is a map of Eighty-mile Beach showing the sampling locations (A–F). The northernmost location was located 10 km north of the entrance to the beach near Anna Plains cattle-station (arrow). The six other graphs represent the individual sampling locations. At each solid point sediment and benthos were collected and processed, from the open points data were missing. Distance between adjacent transects and sampling stations is 200 m. The sampling stations grouped within a small box are the replicates used to test the hypothesis concerning the gradient in tidal height. Geographic co-ordinates are UTM-projections (units in metres).

(six lower graphs of Fig. 1). We located sampling stations using GPS. Sampling at the highest stations took place at the same tidal level, just below the steep upper shore of the beach. Samples at the lowest stations were taken along the low-water line at about 6 m below the highest sampling stations. Transects and sampling stations along transects were 200 m apart from each other, thus forming grids with 200 m intersections. No mangroves occurred near or at the locations.

To quantify the macro-zoobenthos, at each sampling station three cores with a diameter of 10.2 cm (1/120 m^2) were taken to a maximum depth of 30 cm (less if the corer hit a shell or rock layer as no benthos was expected below such a hard barrier). The sediment was sieved on the spot over a sieve with a mesh-size of 1 mm. All material retained on the sieve was transferred to a plastic bag and brought to the laboratory for sorting and identification of benthic fauna. Anthozoans, decapods, gastropods, bivalves, scaphopods, ophiuroids, holothurians and hemichordates were classified to species level, polychaetes and crustaceans to family level and nemerteans, sipunculids and phoronids only to phylum level (Table 1).

At each sampling station, a core with a diameter of 4.4 cm was taken to a depth of 10 cm to collect sediment. Such sediment cores were transferred to a plastic bag, labelled and stored until further treatment. A total of 895 sediment cores were collected, 858 of which could later be properly allocated to a sampling station. The remaining 37 cores had an illegible label or were lost during processing. From the 858 assignable sediment cores, 108, 214, 196, 159, 108, and 73 cores were analysed from locations A, B, C, D, E and F, respectively.

In the laboratory the sediments were removed from the bags and transferred to clean buckets. All aggregates of clay and sand were disaggregated in tap water by swirling and kneading. After disaggregation, the larger particles were allowed to sink. After 30–60 s, the smaller particles were carefully decanted onto preweighed Schleicher and Schuell folded filters (type 595 1/2, diameter 385 mm, retention 4–7 μm). Water was added to the remaining sediment and the content of the bucket was stirred thoroughly. The water was decanted onto the same filter paper and the process repeated until the water remained clear after stirring. After filtration, the filters were folded and allowed to air-dry for 48 h. They were then dried at 80 °C to constant mass. Filters were allowed to cool in a desiccator and weighed to the nearest 0.01 g. The mass of the sediment retained on the filters was the difference between the two weights and was assumed to be <63 μm.

The sediment left in the bucket (grain size >63 μm) was transferred to a beaker and dried at 80 °C for 4 d (constant mass). The dried sediment was then transferred to a stack of sieves with mesh sizes of 63, 125, 250, 500 and 1000 μm. Each sampling unit was sieved for 15 min with an electrical sieve-shaker. The material retained onto each sieve was weighed to the nearest 0.01 g. The mass of the smallest fraction (silt, <63 μm) was added to the mass of the material retained by the corresponding filter paper. Percentages of mass of each size class were used rather than absolute mass. Rather than using the logarithmic millimetre scales of the sieves, a $\log_2$-transformed scale, the phi (ϕ)-scale (Folk, 1980) was used to calculate median grain size.

Table 1
Composition of the grouped taxa used in the statistical analyses

Group	Taxon	Number of finer taxa included
1	Anthozoa	4 species
2	Polychaeta	21 families
3	Other worms	3 phyla (Nemertea, Sipuncula, Phoronida)
4	Decapoda	9 families
5	Other Crustacea	9 species
6	Gastropoda	8 species
7	Bivalvia	13 species
8	Scaphopoda	1 species
9	Ophiuroidea	1 species
10	Holothuroidea	4 species
11	Hemichordata	1 species
Total	11	74

2.3. Statistical analyses

To test hypotheses about an across-shore gradient in distribution of sediment and benthos, data from groups of four adjacent sampling stations were treated as replicate samples (Honkoop et al., 2005). Each transect was divided into three zones according to distance from low water. These were the two sampling stations closest to the sea on each transect, the two farthest from the sea on each transect and two towards the middle of each transect (Fig. 1). In locations A to E, data from these three tidal heights were combined for two transects along each of the edges of the location and for two transects in the middle of each location. At each of the five locations, there were thus nine groups of four stations (i.e. a combination of distance across-shore and distance along-shore); three replicates at each of three tidal levels. Because transects at location F were relatively short, only differences between the highest and lowest tidal levels were examined (Fig. 1).

For multivariate analyses we used software package PRIMER (Plymouth Routines In Multivariate Ecological Research). Across-shore differences of characteristics of the sediment and of benthic fauna were evaluated by comparing the similarity matrices of benthos (Bray-Curtis (dis)similarities) and sediment (Euclidean distances) taken at each tidal height (Clarke, 1993; Clarke and Ainsworth, 1993) and visualised with n-MDS plots. To test the differences in benthos among tidal levels, Non-Parametric Multivariate Analysis Of Variance (NP-MANOVA) of untransformed data was used (Anderson, 2001). This calculation not only tests for main effects (in our case, tidal height and distance along-shore), but also allows evaluation of the interaction between the two main effects. Because a maximum of two factors can be tested in these analyses, they were done for each location separately. The across-shore distance was treated as a fixed factor and transects as a random factor. If significant effects of tidal level on characteristics of the sediments or benthos were observed, a-posteriori comparisons were done to reveal differences between any two levels of the tidal height. Taxa responsible for differences in assemblages at different tidal heights were examined with the SIMPER routine in PRIMER (Clarke, 1993). In this analysis the contribution of each taxon to the dissimilarity between any two pairs of location is evaluated.

To examine differences among the along-shore parts of Eighty-mile Beach, only data from the sampling stations used to test the across-shore gradient (see previous paragraph) were used. Data from each of these four replicate sampling stations were summed and individual species or families were grouped into coarser taxa (Table 1) to reduce the effects of species or families that were found in very small or very large numbers of individuals. Each location, except location F, thus had nine replicates each consisting of the number of species found at four sampling stations. Location F had only six replicates. Along-shore differences among characteristics of the distribution of sediment (grain size) and benthos (numbers of individuals per species or per group of species and presence/absence data) were visualised and analysed using appropriate routines in PRIMER. Because estimating differences among locations did not involve evaluation of an interaction term, they were tested by analysis of similarities. In this test from similarity-matrices (Euclidean distances or Bray-Curtis dissimilarities) that were also used to construct n-MDS plots, the-rank similarities of the within-location replicates are compared to those of all pairs of the replicates between locations (ANOSIM, Clarke and Green, 1988; Clarke, 1993). In this way it is also possible to perform pairwise comparisons of the different locations. However, by running independent pair-wise comparisons, the Type 1 error increases. Any correction to reduce this risk (i.e. reducing significance levels) has the consequence that the Type II error increases. Therefore, the best way to interpret the results (for example those shown in Table 6), is to compare the statistical value (R) of sets of comparisons. If two locations are similar, R is close to zero, if two locations are very different R is close to unity.

The SIMPER routine was then used to identify the relative contribution of different taxa to differences between locations. Across-shore and along-shore differences in median grain size and total number of invertebrates per sampling unit were also examined using standard ANOVA techniques.

The correlation of the patterns found in the distribution of the sediment and of the benthic assemblages in each location was examined using the BIO-ENV routine. In this routine the similarity-matrices of the biota and abiotic ordinations are linked. Matching of the pattern is expressed by a weighed Spearman or Harmonic rank correlation (Clarke and Ainsworth, 1993). Note that the resulting rank correlation does not indicate how much of the change in the benthic assemblages is explained by the change of the characteristics of sediment. It is only a measure of how well the observed patterns of difference among sampling units correlate with each other. Possible gradual differences in sediment and benthos from location to location were tested with the RELATE routine (Clarke et al., 1993). This method measures the degree to which possible differences in assemblages or sediments conform to a linear sequence (i.e. distance between any two locations).

3. Results

At most sampled stations the sediments consisted of silt and clay (median grain size <63 μm in 469 cores) or very fine sand (63–125 μm in 228 cores). Fine sand (125–250 μm) was found in 130 cores, medium sand (250–500 μm) in 12 cores, coarse sand (500–1000 μm) in 9 cores. Only one core contained very coarse sediment (>1000 μm).

3.1. Across-shore gradients in sediment characteristics and benthic communities

Variability among replicate sampling stations in the sediment characteristics was relatively large (Fig. 2).

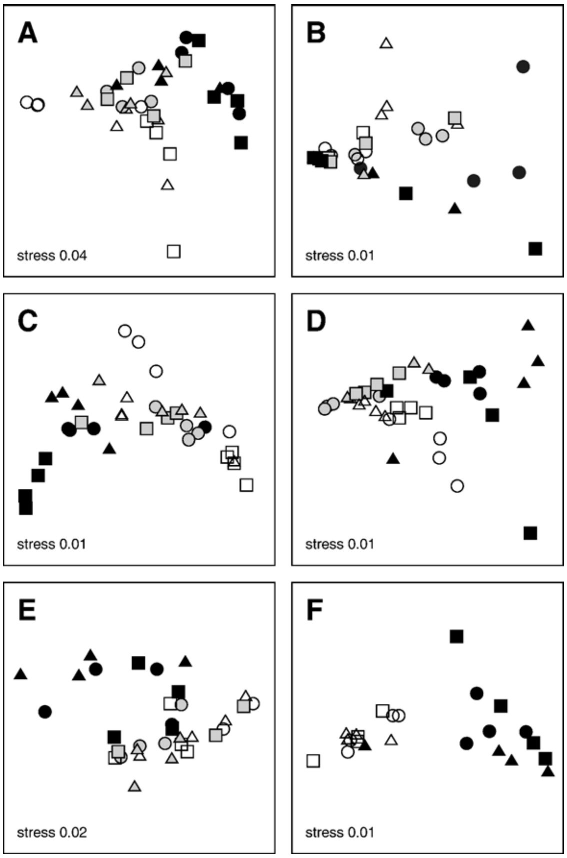

Fig. 2. n-MDS ordinations of the characteristics of sediment at three tidal height and three parts of transects within each location. Solid black symbols: highest tidal level; grey symbols: intermediate tidal level; open symbols: lowest tidal level. Circles: southernmost transect; triangles: middle transect; squares: northernmost transect.

Nevertheless, a separation of the highest and lowest tidal level (solid black and open symbols in Fig. 2, respectively) can be seen in all locations. The stations at the intermediate tidal level (grey symbols in Fig. 2) were generally more similar to stations at the lowest tidal level than to those at the highest tidal level. Non-parametric MANOVA revealed that in most cases the interaction between tidal heights and transect was significant, indicating different across-shore trends along each location (Table 2A). A-posteriori tests for differences among tidal heights within transect were not always conclusive. Generally, they occurred between the characteristics of the sediment at the highest and lowest tidal levels. The only location where the interaction between tidal height and transect was not significant was location F. Here, a consistent difference between the two tidal heights was observed. Because of the significant interaction between tidal height and transect (Table 2A), it was not possible to find the size class or classes of the sediment responsible for the patterns within each location.

The composition of the assemblages of grouped taxa (Table 1) showed similar patterns to those observed for characteristics of the sediment (Fig. 3), but in only one case (location B) was the interaction term significant. In all other cases, assemblages at the different tidal heights were significantly different (Table 2B). Transects within locations A and E were also significantly different, but because the locations are essentially random along-shore locations, there is no logic in exploring those differences any further. A-posteriori tests revealed that the assemblages at each tidal level were significantly different from the assemblages at the other tidal heights in almost all cases. At location C, the assemblages at the higher and intermediate tidal level were similar, but different from those lowest on the shore.

Polychaetes and ophiuroids contributed most to differences between any two tidal heights and, generally, explained more than 60% of the dissimilarity (Table 3). In our samples one species of ophiuroid was found, *Amphiura tenuis*, which was very common at the lower tidal levels (880 individuals found in our samples). Because of the diversity of the group of the polychaetes, it was not possible to generalise the difference among tidal level concerning the polychaetes. For example, if found, polynoids were always associated with *Amphiura tenuis* at the lowest tidal level, cirratulids were mainly found at location E at the highest tidal level, capitellids at F at the lowest tidal level and owenids at location D at the highest tidal level. Occasionally other groups were important. At location C

Table 2

Significance levels (*P*-values) of non-parametric analyses of variance of effects of tidal height and transect on (A) characteristics of the sediment and of (B) benthic assemblages at the different locations

Source	df	Location					
		A	B	C	D	E	F
		P	*P*	*P*	*P*	*P*	*P*
A							
Height	2	**0.02**	0.38	0.06	**0.01**	0.08	<**0.01**
Transect	2	**0.01**	0.11	0.30	0.74	0.23	0.50
Height * transect	4	<**0.01**	**0.04**	**0.01**	<**0.05**	**0.01**	0.48
B							
Height	2	**0.03**	<**0.01**	<**0.01**	**0.01**	<**0.01**	**0.02**
Transect	2	**0.03**	0.11	0.38	0.63	**0.03**	0.10
Height * transect	4	0.12	<**0.01**	0.13	0.34	0.85	0.19

Significant values are in bold. Number of permutations=4999.

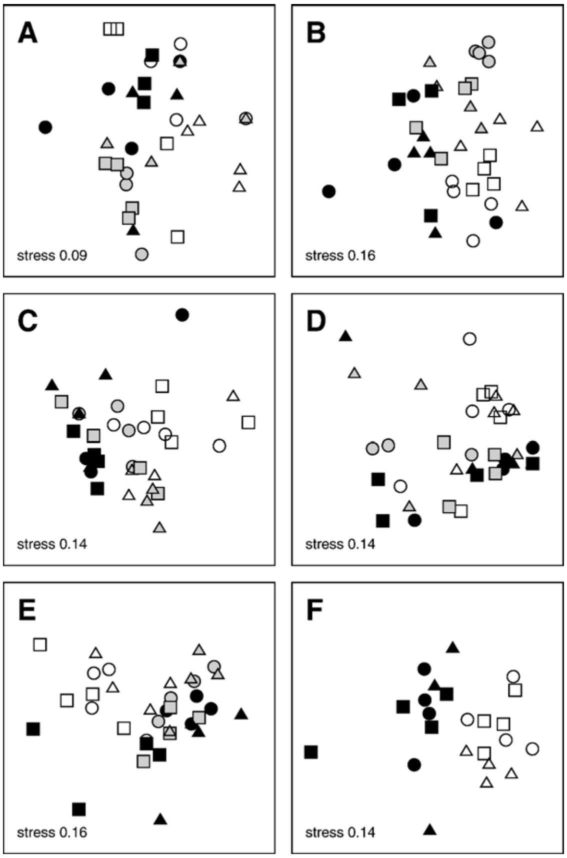

Fig. 3. n-MDS ordinations of the benthic assemblages at three tidal height and three transects within each location. Solid black symbols: highest tidal level; grey symbols: intermediate tidal level; open symbols: lowest tidal level. Circles: southernmost transect; triangles: middle transect; squares: northernmost transect.

many individuals (271) of the bivalve *Siliqua pulchella* were found at the lowest tidal level. From this species only three individuals were found at the intermediate and none at the highest level. At location E many crustaceans, an amphipod *Corophium* spec., were found at the highest tidal level. At location F, phoronids (Other worms, Table 1) were responsible for a relatively large part of the difference between the two tidal levels; most of them were found at the lowest tidal level. Because of the significant interaction between tidal height and transect in location B (Table 2B), it was not possible to examine which taxa differed between tidal heights within this location. Although not contributing to a large difference at any location, holothurians were mainly found at the lowest tidal level, particularly at locations B and C. Of 101 individuals found, only five were found at the intermediate level and one at the highest tidal level. More detailed descriptive information on the species found and their distribution along Eighty-mile Beach can be found in Lavaleye et al. (2005).

Multivariate analyses revealed offshore gradients in sediment characteristics. To examine these gradients, sediment data from each individual sampling station were used to calculate the median grain size, a univariate variable easier to interpret than a multivariate set of data. However, because of the significant interaction between tidal height and transect (Table 4), across-shore and along-shore gradients in median grain size were not easily interpreted. This significant interaction indicated that patterns within a location were not always consistent. An a-posteriori test on the interaction showed that, within each location, the median grain size at the highest tidal level was generally larger than at the lowest tidal level, but that the median grain size at the intermediate tidal level was sometimes similar to that at the highest and sometimes to that of the lowest tidal level. Occasionally, differences in median grain size among the tidal heights within transects were insignificant. Because this pattern was observed, data from each tidal height within a location were pooled and an average value for the median grain size was calculated. The median grain sizes at the lowest tidal level were significantly smaller than at the intermediate and higher tidal level, except in location B, where differences were not significant. At most locations, but not at location A, the median grain sizes were similar at the lowest and intermediate tidal level (Fig. 4A). Because location F had only two tidal heights, data had to be analysed separately. The median grain sizes at the two tidal heights were significantly different, the lowest tidal level having the finer sediment ($F_{1,2}$=107.88, P<0.01). The interaction between tidal height and transect was not significant ($F_{2,18}$=0.41, P>0.05).

The total number of invertebrates per sampling unit was different at each tidal height but, just as for the median grain size, was not consistent between locations, resulting in a significant interaction between locations and tidal height (Table 5A). The number of individuals was significantly smaller at the highest tidal level at locations B and C, while all other comparisons were not significantly different (Fig. 4B). A separate analysis of the effects of tidal height on the total numbers of individuals at location F showed that there was no significant difference between tidal heights ($F_{1,2}$=6.77, P>0.05), nor was there a significant interaction between tidal height and transect ($F_{2,18}$=1.08, P>0.05). Total numbers were generally largest at locations B and C and smallest at locations A and F (Fig. 4B). The patterns of species richness and of

Table 3
Contribution of the four most important taxa (Con. in %) to the dissimilarity between any combination of two tidal heights within each location

Location	A				B			
Tidal level	H		M		H		M	
	Taxon	Con. (%)	Taxon	Con. (%)	Taxon	Con. (%)	Taxon	Con. (%)
M	Ophiuroids	64.89			N/A			
	Polychaetes	19.49						
	Decapods	4.45						
	Bivalves	3.74						
L	Ophiuroids	33.93	Ophiuroids	58.31	N/A		N/A	
	Polychaetes	29.43	Polychaetes	22.77				
	Bivalves	17.31	Bivalves	10.23				
	Decapods	7.78						

Location	C				D			
Tidal level	H		M		H		M	
	Taxon	Con. (%)	Taxon	Con. (%)	Taxon	Con. (%)	Taxon	Con. (%)
M	Polychaetes	42.17			Polychaetes	70.48		
	Ophiuroids	33.72			Ophiuroids	8.23		
	Decapods	11.31			Decapods	7.94		
	Bivalves	4.73			Crustaceans	5.35		
L	Bivalves	36.69	Bivalves	33.20	Polychaetes	38.22	Ophiuroids	33.61
	Ophiuroids	25.58	Polychaetes	25.98	Ophiuroids	30.65	Polychaetes	30.38
	Polychaetes	19.78	Ophiuroids	23.92	Bivalves	8.58	Bivalves	9.90
	Decapods	8.93	Holothurians	7.33	Crustaceans	8.21	Crustaceans	8.45

Location	E				F			
Tidal level	H		M		H		M	
	Taxon	Con. (%)	Taxon	Con. (%)	Taxon	Con. (%)	Taxon	Con. (%)
M	Polychaetes	35.99			N/A			
	Crustaceans	24.81						
	Bivalves	14.71						
	Decapods	14.08						
L	Ophiuroids	40.80	Ophiuroids	52.69	Polychaetes	26.73	N/A	
	Polychaetes	19.84	Polychaetes	17.00	Ophiuroids	21.53		
	Crustaceans	13.45	Decapods	10.55	Crustaceans	21.25		
	Bivalves	12.51	Bivalves	8.63	Other worms	11.32		

H = highest, M = medium and L = lowest tidal height. The taxa can be found in Table 1. Data from location B were omitted from analysis. Location F had only two tidal heights, H and L.

total abundance were similar (Fig. 4C). A significant interaction between height and location was observed (Table 5B). This was caused by the data from location A. At this location there were no differences among the number of species at different tidal heights, whereas in all other locations the number of species was smallest closer to the shore and gradually increasing towards the lower tidal levels. A separate analysis for the data from location F showed only a significant difference for the effect of tidal height ($F_{1,2} = 49.00$, $P < 0.05$), the highest tidal level having fewer species than the lowest tidal level.

Table 4
ANOVA results of the effects of location (Loc), tidal height (He) and transect (Tr) on the Ln-transformed median grain sizes of the sediment

Source	*SS*	df	*MS*	*F*-ratio	*P*
Location	3.6663	4	0.9166	4.29	0.0282
Tidal height	5.4448	2	2.7224	18.13	0.0011
Transect(Loc)	2.1375	10	0.2137	2.99	0.0019
Loc * He	1.2014	8	0.1502	0.87	0.5593
He * Tr(Loc)	3.4651	20	0.1733	2.43	0.0015
Error	9.6421	135	0.0714		

Only locations A, B, C, D and E are included in this analysis. Cochran's test $C = 0.0943$, $P >> 0.05$, n = 4.

Plots of median grain size (Fig. 4A) and total number of individuals of all species per tidal height at each location (Fig. 4B and C) showed a roughly opposite pattern. When median grain size was small

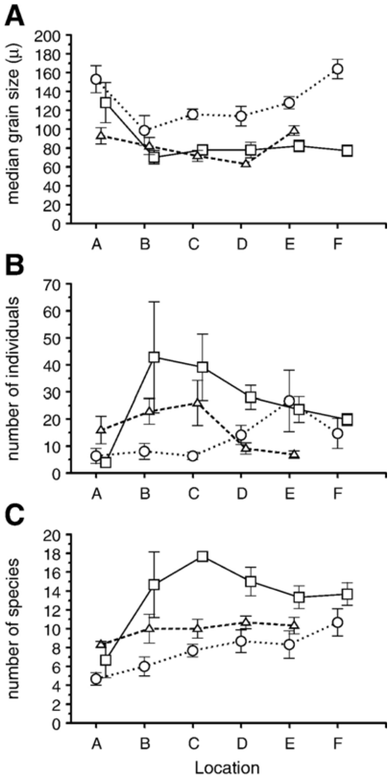

Fig. 4. (A) Median grain-size, (B) total number of individuals of all species, and (C) total number of species at the different tidal heights at the different locations. At each location data from all sampling stations per tidal height were pooled. Mean ± SE. ○=highest, △=in-intermediate and □=lowest tidal level.

(locations B–E), the number of individuals and species was large and when the median grain size was large (locations A and F), the number of individuals and species was relatively small. Plots of the relationship between median grain sizes and the total number of species confirmed this pattern. In both cases there were significant negative correlations between median grain size and numbers of individuals or species, significantly fewer individuals ($F_{1,15}$=4.82, P<0.05, R^2=0.243, Fig. 5A) and species ($F_{1,15}$=8.49, P<0.05, R^2=0.362, Fig. 5B) in coarser sediments than in finer sediments.

3.2. Along-shore gradients in sediment characteristics and the composition of benthic assemblages

In addition to the differences among sediments at the different tidal heights within locations, analysis of similarity revealed that there were also significant differences (Table 6, ANOSIM, P<0.05) *between* many locations. However, because location was a random factor, those differences were not logically interpretable. The differences of the composition of the sediment among locations were significantly related (P<0.05, from RELATE) to the actual distance between any two locations, the further away from each other, the greater the difference.

Benthic assemblages were compared among locations in three different ways. First, the total number of individuals at the finest taxonomic resolution was examined. As a result of the large number of taxa (74, see Table 1) compared with the small number of replicates, the stress value of the 2-dimensional ordination was relatively large (0.20). Observed patterns using untransformed data can be mainly driven by the abundance of a few species in a few sampling units. Therefore, to reduce the impact of patchy and abundant species, data were transformed to only presence (=1) or absence (=0). This transformation resulted in an even larger stress value (0.22) than using abundance, indicating that the description of the assemblages in a 2-dimensional space is a poor one. The smallest stress value (0.18) was obtained by grouping the individuals into coarser taxa (Table 1). Variability within locations was relatively large, especially within location B. Analysis of similarity (ANOSIM) revealed differences among locations (Table 6), but these were difficult to interpret. Generally, location A was different from the other locations, which were similar to each other. The observed pattern was significantly correlated to the spatial distances among the beaches (P<0.05, from RELATE). This correlation is also reflected in the general similarity of the assemblages of two adjacent

Table 5
ANOVA results of the effects of location (Loc), tidal height (He) and transect (Tr) on (A) the total number of individuals of all species combined and of (B) the total number of species

Source	*SS*	df	*MS*	*F*-ratio	*P*
A					
Location	18.66	4	4.67	5.23	0.0155
Tidal height	20.64	2	10.32	3.09	0.1015
Transect(Loc)	8.92	10	0.89	1.19	0.3049
Loc * He	26.75	8	3.34	2.77	0.0306
He * Tr(Loc)	24.11	20	1.21	1.60	0.0599
Error	101.47	135	0.75		
B					
Location	115.86	4	28.96	10.45	0.0014
Tidal height	213.38	2	106.69	10.04	0.0066
Transect(Loc)	27.72	10	2.77	0.61	0.8030
Loc * He	85.01	8	10.63	4.21	0.0043
He * Tr(Loc)	613.25	20	2.52	0.56	0.9361
Error	1105.66	135	4.54		

Only locations A, B, C, D and E are included in this analysis.

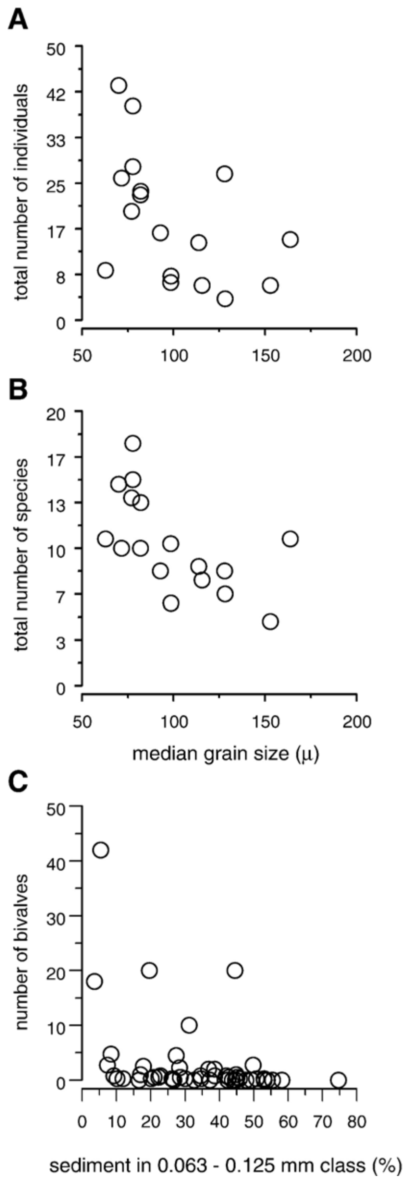

Fig. 5. Relationship between median grain-size and (A) total number of individuals and (B) total number of species per tidal height per location. Each data point represents the average median grain-size and average number of individuals or species at each tidal height at each location. (C) the relationship between the total number of individuals of bivalves and the relative amount (%) of sediment in the 0.063–0.125 mm size class. Each point represents average values of four replicate sampling units (see Fig. 1).

beaches (the exception being location A and location B; Table 6).

The taxa that caused differences between any two locations were examined using the SIMPER routine. It was found that four taxa, ophiuroids, polychaetes, bivalves and crustaceans, mainly caused these differences (Table 7). Generally, the two most important taxa causing the difference explained more than 50% of that difference and the four most important taxa explained more than 85%.

Matching the pattern found in characteristics of the sediment with that found in benthic assemblages (BIO-ENV routine) gave relatively small Spearman rank correlation coefficients for any combination of size-classes. The pattern of the single size-class correlating best with the benthic patterns was the 0.063–0.125 mm fraction of the sediment, but still ρ was only 0.229. Addition of a second size class (0.125–0.250 mm) improved the correlation slightly ($\rho=0.259$). Adding more size-classes improved the correlation only marginally ($\rho=0.269$), or worsened it ($\rho=0.239$) (Table 8).

Thus, four taxonomic groupings were mainly responsible for the patterns observed in the assemblages and the 0.063–0.125 mm class of grain size appeared to be the best variable to summarise sediment characterisation. Therefore, total numbers of individuals of these four taxa were each correlated to the relative amount of sediment in the 0.063–0.125 mm size class and found that the correlations were weak ($R^2=0.02$, 0.01, 0.14 and 0.03 for polychaetes, crustaceans, bivalves and ophiuroids, respectively) and not significant ($P>0.05$), except for bivalves ($F_{1,49}=7.79$, $P<0.05$). Bivalves occurred in significantly larger numbers in

Table 6
Differences among locations in the distribution of size classes of the sediment based on Euclidean dissimilarity measures and of the grouped benthos data based on the Bray-Curtis dissimilarity measures

locations	sediment *R*	grouped benthos *R*
A vs. B	0.239*	0.163*
A vs. C	0.053	0.173*
A vs. D	0.049	0.360*
A vs. E	0.139*	0.111
A vs. F	−0.019	0.309*
B vs. C	0.068	0.059
B vs. D	0.006	0.315*
B vs. E	0.582*	0.091
B vs. F	0.494*	0.102
C vs. D	−0.073	0.064
C vs. E	0.156*	−0.070
C vs. F	0.150	−0.051
D vs. E	0.187*	0.069
D vs. F	0.165	−0.020
E vs. F	0.216*	−0.088

(R=statistical value, * significantly different at $P<0.05$, from ANOSIM, number of permutations=9999). Adjacent locations are in bold. If two locations are similar R is close to zero, if two locations are very different R is close to unity.

Table 7
Contribution of the four most important taxa (Con. in %) on the dissimilarity between any combination of two locations (Loc.)

Loc.	A		B		C		D		E	
	Taxon	Con. (%)	Taxon	Con. (%)	Taxon	Con. (%)	Taxon	Con. (%)	Taxon	Con. (%)
B	**Ophiuroids**	**31.0.0**								
	Bivalves	**26.99**								
	Polychaetes	**13.97**								
	Crustaceans	**10.27**								
C	**Ophiuroids**	**29.69**	Polychaetes	33.26						
	Polychaetes	**29.19**	Ophiuroids	23.38						
	Bivalves	**26.25**	Bivalves	20.12						
	Decapods	**6.17**	Crustaceans	8.04						
D	**Polychaetes**	**46.12**	**Polychaetes**	**32.20**	Polychaetes	30.86				
	Ophiuroids	**31.79**	**Bivalves**	**21.95**	Bivalves	26.22				
	Bivalves	**5.90**	**Ophiuroids**	**21.12**	Ophiuroids	24.63				
	Crustaceans	**5.84**	**Crustaceans**	**9.86**	Crustaceans	6.27				
E	Ophiuroids	36.50	Bivalves	24.76	Bivalves	26.646	Polychaetes	36.63		
	Polychaetes	23.84	Ophiuroids	23.54	Polychaetes	24.81	Ophiuroids	27.47		
	Crustaceans	12.16	Polychaetes	18.70	Ophiuroids	23.66	Crustaceans	12.90		
	Bivalves	10.94	Crustaceans	13.75	Crustaceans	10.16	Bivalves	10.01		
F	**Polychaetes**	**29.22**	Polychaetes	23.41	Polychaetes	24.52	Polychaetes	28.04	Polychaetes	24.54
	Ophiuroids	**27.82**	Bivalves	21.63	Bivalves	20.97	Ophiuroids	24.76	Crustaceans	24.42
	Crustaceans	**21.30**	Crustaceans	18.92	Ophiuroids	19.78	Crustaceans	24.16	Ophiuroids	24.29
	Decapods	**6.41**	Ophiuroids	17.13	Crustaceans	17.69	Bivalves	7.76	Bivalves	9.19

The taxa can be found in Table 1. Data from locations that had a significantly ($P < 0.05$, from SIMPER) different composition of the assemblage are in bold.

areas where the relative amount of the 0.063–0.125 mm grain size class was relatively small (Fig. 5C).

4. Discussion

Sandy beaches are usually divided into three distinct zones, the supralittoral, littoral and sublittoral zones (McLachlan and Jaramillo, 1995). In our study we aimed to find evidence of zonation within the littoral zone as the supralittoral zone and beach front were not sampled quantitatively. Based on our qualitative observations very few species were observed here, mainly crustaceans (one or more members of the ocypodids (ghost crabs), coenobitidae (land hermits), amphipods and isopods). These taxa appear to be a general feature of reflective beaches (Gauld and Buchanan, 1956; Trevallion et al., 1970; McLachlan and Hesp, 1984; McLachlan, 1985).

Table 8
Combination of the six size classes, taken 1–6 (all) classes at a time resulting in the best matching of the abiotic and biotic similarity matrices as measured by the Spearman rank correlation (ρ)

Number of size-classes	Best combination of size classes (d in ϕ)	ρ
1	3.5	0.229
2	2.5; 3.5	0.259
3	0; 2.5; 3.5	0.269
4	0; 1.5, 2.5, 3.5	0.268
5	0; 0.5; 1.5; 2.5; 3.5	0.267
6	All	0.269

Only the size class resulting in the largest rank correlation within each number of combinations is given. Size classes are given as the midpoint (d) of the phi (ϕ) scale (Folk, 1980). The midpoint of the >1 mm class is arbitrarily set to 0.

In this study we aimed to find evidence for the presence of across-shore and along-shore patterns in characteristics of the sediments. Generally, sediment of the studied locations along Eighty-mile Beach was very fine, 55% of all cores containing more than 50% mud and silt (median grain size <63 μ). At reflective beaches it is generally observed that coarser sediments occur close to the beach front and finer sediments closer towards the low-water line (McLachlan, 1987). This also appeared to be the case at the intertidal area along Eighty-mile Beach. A multivariate analysis of variance on sediment data confirmed this pattern (Fig. 2). The small stress values indicated that the multivariate data of grain sizes fitted very well in a two-dimensional space, meaning that a single grain-size class drove the pattern and that similar results would have been obtained if that particular size class was analysed in a univariate sense. Sampling stations at the intermediate tidal level had an intermediate grain-size distribution. Thus, the hypothesis of a tidal gradient in sediment characteristics with coarser sediments closer to shore and finer towards the low-water line was confirmed. In addition to the multivariate tests, the sediment data were transformed to one univariate variable, median grain size. In accordance with the multivariate tests sediments at the higher tidal levels were found to be coarser (i.e. had a larger median grain size) than at the lower tidal levels.

We also aimed to find evidence for the presence of across-shore and along-shore patterns in the composition of intertidal benthic assemblages. Except at location B, benthic assemblages were indeed different among tidal heights, showing a gradual change from the shore towards the lowest tidal level. The species or groups of species causing that difference were not the same at each location (e.g. echinoids at location B and C and polychaetes at D and F, see below), indicating that along the Eighty-mile Beach foreshore there are changes in the composition of the benthic assemblages. This means that tidal height is not the only factor determining the composition of assemblages. Thus, although zonation was expected (see references cited above), a multivariate examination of the composition of benthic assemblages did not confirm its presence along Eighty-mile Beach. Nevertheless, there was one species that was found in large numbers on the lower flats, the ophiuroid *Amphiura tenuis*. Therefore, the lower part of the intertidal zone can be considered to be an ophiuroid zone.

Transforming benthos data to univariate variables, numbers of species and individuals, revealed a few general across-shore patterns. The number of individuals and species was larger at the lower tidal levels than close to the shore. Therefore, within the intertidal area a zone with few species and individuals (the higher tidal level) and a zone with more species and a larger number of individuals (the lower tidal levels) could be identified.

Biological and physical factors that shape the environment and the composition of (benthic) assemblages can operate at similar or different spatial scales ranging from millimetres to hundreds or thousands of kilometres (Underwood and Chapman, 1996; Van der Meer and Honkoop, 1999). Abiotic factors that, generally, correlate well with biotic factors, and do so relatively independently of the studied spatial scale, are usually indicative of sediment type (e.g. median grain size, silt content) and tidal height or water depth. In ten studies dealing with sediment-benthos (either species abundance or species richness or both) relationships in a quantitative way (using the same goodness-of-fit measure, R^2), the value for the relationships between sediment and benthos ranged between 0.12 and 0.91 with an average R^2 of 0.515 (Table 9). In the current study we found that the total number of individuals appeared to be negatively correlated with the median grain size and, consequently, with tidal height (Fig. 5A). Nevertheless, the goodness-of-fit found here (0.243) was smaller that the above-mentioned average of 0.515. A similar relationship was found between median grain size and total number of species (Fig. 5B) with an R^2 of 0.362. These results suggest that both tidal height (Fig. 4) and median grain size (Fig. 5A and B) affect the numbers of individuals and species. It appeared that the total number of bivalves was most influenced by the sediment, as significantly more individuals were found at places where the 63–125 µm fraction was largest (Fig. 5C). At these locations relatively large numbers of the bivalves *Siliqua pulchella* and *Tellina amboynensis* were found.

Along-shore differences in characteristics of the sediment and of benthic assemblages were also observed (Table 6, Fig. 4) and appeared to be related to the distance between locations. As for the across-shore

Table 9
Maximum R^2 of studies in which species abundance (studies 1–4) or species richness (studies 4–10) was related to environmental variables

Study	Spatial scale (km)	Independent variables	Max. R^2	Reference
1	0.5	Shell hash, elevation, shear stress, energy dissipation, water coverage, wave stirring	0.69	Legendre et al. (1997)
2	30	Median grain size, altitude	0.48	Van der Meer (1991)
3	40	Silt, altitude	0.39	McLachlan (1996)
4	50	Mean grain size, beach slope, Dean's parameter	0.43	Jaramillo and McLachlan (1993)
5	1.5	Total and food particle diversity, % Organic material	0.34	Whitlatch (1981)
6	10	Median grain size	0.12	Lie (1978)
7	25	Beach slope, sand particle size, sand sorting	0.85	McLachlan (1996)
8	50	Median grain size, 1/beach slope, Dean's parameter	0.83	Jaramillo (1994)
4	50	Mean grain size, beach slope, Dean's parameter	0.91	Jaramillo and McLachlan (1993)
10	80	Water depth, median particle diameter, silt and clay content, sediment sorting, salinity, area	0.42	Elliot and O'Reilly (1991)

Compiled from Tables 3 and 4 in Van der Meer and Honkoop (1999).

differences in the benthic assemblages, ophiuroids and polychaetes were important, as were crustaceans and bivalves. Surprisingly, the pattern observed for benthic invertebrates was only weakly correlated with the pattern found in sediment characteristics. The largest correlation coefficient found was $\rho=0.269$, a value much smaller than that found in a similar study done in Roebuck Bay two years earlier (Pepping et al., 1999). In that study, distribution patterns of silt (sediment <63 μ) and benthos were better correlated ($\rho=0.553$) than in our study ($\rho<0.229$, see also Table 9). One explanation is that at Eighty-mile Beach the distribution patterns of benthos were influenced or determined by other factors than those measured in this study, one possibility being that biotic interactions are more important than the assumed abiotic structuring.

Alternatively, the expected larger correlation was obscured by the recent passage of severe tropical cyclone Vance, which hit the area in March 1999, only six months before the current study. The fastest wind speeds ever recorded above mainland Australia were measured during this cyclone: 267 km/h (http://www.bom.gov.au/info/cyclone/). It is likely that the sediments were dramatically disturbed during this storm; the intertidal sediments and biotic assemblages might still have been in a recovery phase. Some observations are consistent with this hypothesis. We noticed the presence in some places of a five cm deep layer of coarse sediment on top of muddy sediment, suggesting that some coarse sediments were recently deposited. We also noticed that the huge ridges of shell fragments that are so characteristic of the highest parts of Eighty-mile Beach were not present to any large degree in October 1999. Cyclone Vance may have changed the abiotic environment such that the benthic community was still recovering from this event. Repeat surveys after a long cyclone-free period are requested to test this hypothesis.

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