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PHYSICAL FACTORS REGULATING MACROBENTHIC COMMUNITY STRUCTURE ON A SOUTH AFRICAN ESTUARINE FLOOD-TIDAL DELTA

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Multivariate techniques were used to identify environmental parameters affecting macrobenthic communities on the flood-tidal delta of the Nahoon Estuary and adjacent beach near East London on the south-east coast of South Africa. Water content of sediments, temperature and exposure were identified as important parameters regulating differences in community structure between high-shore and subtidal sites, and between beach sites of varying elevation. High organic content was important for similarity of communities at sites farthest from the mouth and for distinctness of these communities from the others. Sediment particle size, compactness and current velocity contributed to similar communities of channel sites and their variation from those of other sites, and to distinctness of the lowest beach site from higher beach sites. Sites in the mouth and in the middle of the flood-tidal delta, with similarities in community structure, had varying values for all the measured environmental variables and none of these parameters could explain why these sites had similar communities. In summary, no over-riding parameter was shown to dominate the abiotic driving forces at all sampling sites, and different variables were important for structuring communities at different sites.

Key words: benthos, communities, estuary, macrofauna, physical factors, South Africa

Although the benthic macrofauna of sandy environments around tidal inlets has been extensively studied around the world, e.g. sandbars (Holland and Dean 1977), estuarine sandflats (Reise 1985, Dittmann 1995), bays (Jones 1997) and harbours (Parker 1975, Pridmore *et al.* 1990), there is a paucity of data that focuses primarily on benthic macrofauna of estuarine flood-tidal deltas. The term "flood-tidal delta" is not used regularly in the biological literature, but it is encountered in the geological literature in the context of geomorphological, sedimentological and hydrodynamic processes (e.g. Cooper *et al.* 1999, Schumann *et al.* 1999). Flood-tidal deltas are defined as wedge-shaped accumulations of sand on the landward side of an inlet (Hayes *et al.* 1973, Hayes 1977). These areas of marine sand are highly dynamic, regulated by waves, tides and floods, and are a common feature associated with tidal inlets on the south and south-east coasts of South Africa. Given their dynamic nature, flood-tidal deltas are considered to be poor in species (Day 1951, McLachlan and Grindley 1974). However, a recent study identified 106 macrobenthic species (those retained by a 1-mm mesh sieve) on the flood-tidal delta of the Nahoon Estuary and 36 species on the adjacent beach (Bursey and Wooldridge 2002). Species numbers decreased from beach to mouth sites, but in the flood-tidal delta, species richness increased up-estuary.

Several authors have drawn a distinction between fauna of estuarine sandbanks and adjacent wave-swept sandy beaches (Day 1981, Branch and Branch 1983, Junoy and Viéitez 1992), whereas other studies have shown close similarities in the macrofauna inhabiting these adjacent sandy environments (Green 1968, Branch and Grindley 1979, Wolff 1983). On the flood-tidal delta of the Nahoon Estuary and adjacent beach, there was a gradual change in community structure from the beach into the estuary (Bursey and Wooldridge 2002). The flood-tidal delta had a characteristic group of species, some of which were largely restricted to this area, and others more abundant on the beach or in the estuary. Several typical sandy beach species were more abundant in the flood-tidal delta than on the beach. Sites farthest from the mouth were characterized by estuarine species, although community structure differed from typical lower estuarine communities.

Quantitative information on the controlling influence of the physical environment of flood-tidal deltas in South Africa in relation to community structure is lacking. The present study focuses on environmental factors that regulate benthic community structure at different sites on the flood-tidal delta of the Nahoon Estuary and adjacent beach. Environmental variables that influence abundance and distribution of benthic species in estuaries are reviewed by Kinne (1963, 1964), Carriker (1967), Day (1967), Gray (1968), Green (1968) and Day (1981). These variables include sediment water content, organic content, compactness of substratum particles, tidal elevation, exposure (inter-

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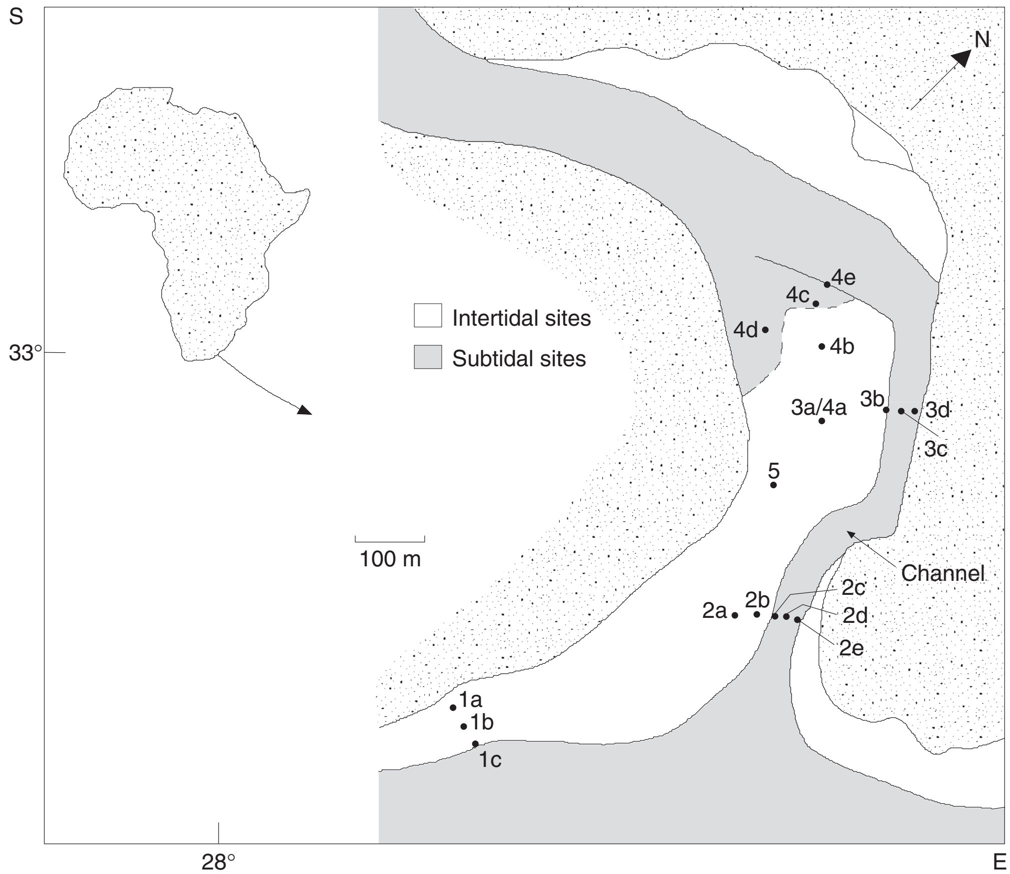

Fig.1: Nahoon beach and estuarine flood-tidal delta, showing positions of sampling sites

tidal sites), current velocity, temperature, water salinity and interstitial salinity, salinity-temperature relations, shelter from wave action and stability of sediment.

MATERIAL AND METHODS

The Nahoon Estuary on the south-east coast of South Africa (Fig. 1) has a well developed flood-tidal delta that merges laterally with the Nahoon beach. Development of the flood-tidal delta is a result of longshore sediment movement in a north-easterly direction and strong flood-tidal currents. The delta extends 900 m into the estuary and is continually changing in configuration (Reddering *et al.* 1986). After varying periods of sand accumulation, occasional floods of sufficient magnitude remove the delta and the cycle begins again.

Field sampling

Environmental measurements were taken at 14 sites in the flood-tidal delta and at three sites on the beach over spring low tides between November 1992 and February 1993 (the same period during which the macrofaunal samples were taken). Sites were located along four transects (1–4), coded according to position down the shore (a, b, c, d and e – Fig. 1). Transects 3 and 4 were perpendicular to each other, with a common origin (3a and 4a). An additional site (Site 5) was located in the middle of the sandflat.

Elevation of each station (relative to mean sea level) was measured using an engineer's level and stadia rod and calculated according to a benchmark of known height (J. S. V. Reddering, University of Port Elizabeth, pers. comm.). Water levels were determined using a graduated pole and the level recorded relative to the benchmark. These data were compared with tidal graphs that were measured at the East London Harbour (5 km away) following the method of Eleftheriou and Holme (1984). Exposure times (between 06:00 and 18:00) of intertidal sites were estimated by noting times when they became exposed or submerged over spring low tides during the sampling period. Water content of the substratum at intertidal sites was calculated from samples of sand (sealed in 10 mℓ phials), taken hourly during spring low tides. Weight of each sample was then measured, before being oven-dried (60°C) and reweighed to calculate percentage water content. Diurnal temperature measurements were taken hourly over spring low tides 50 mm below the surface of the sand. Water current velocity (m s^{-1}) was estimated from knowledge of water flow, using a Kahlsico 005-WA130 flowmeter. At beach sites, two poles were placed 10 m apart, perpendicular to the shore, and the time taken for the swash to travel between the two poles was recorded. Water speed was then calculated in m s^{-1}. Relative compactness of the sediment was measured by dropping a sharpened stainless steel rod (0.266 kg) from a constant height (1.75 m) through a tube of 1.5 cm diameter and measuring penetration into the sediment. This was done 20 times at each site and the mean calculated. Particle size and organic content were analysed in the laboratory from 250 mℓ samples of sediment frozen immediately after collection. Sand particle size was determined using an electronic sediment settling tube. Organic content was calculated from mass loss after ashing in a furnace at 450°C for 8 h. Salinity of water at each site was measured with a hand-held refractometer.

Sampling of benthic macrofauna at most sites was undertaken at high tide using a portable hydraulic suction sampler similar to that described by Brett (1964). A steel ring (355 mm diameter, 190 mm deep, area 0.1 m^2) was driven into the sand and its contents sucked out, deposited and sieved in a net bag (1-mm mesh size). A total of 10 repetitions was combined to provide a total area of 1 m^2. A second replicate sample was taken per site. Standard quadrat sampling was used on the beach and at Site 2a on a receding tide. A square wooden sieve (1-mm mesh) was first used to mark quadrats, and the sediment was removed to a depth of 200 mm and sieved. A replicate sample was also taken at these sites. All samples were preserved in 50% isopropyl alcohol in the field.

The procedure was undertaken during two consecutive spring low tides in November 1992 and repeated over two spring tides in February 1993. Some species could not be sampled using the above methods. Holes of deep-burrowing species, such as the sand prawn *Callianassa kraussi* and pencil bait *Solen capensis*, were counted in a measured area and numbers per m^2 calculated (Forbes 1973). Hermit crabs *Diogenes brevirostris* and gobies *Psammogobius* sp. actively avoided the suction sampler, so individuals on the surface were counted in a measured area and numbers per m^2 calculated.

Multivariate analysis of environmental variables

Environmental data were normalized for each variable by subtracting the mean value and dividing by the standard deviation over all samples for that variable, so that all variables had comparable (dimensionless) scales. Sites were compared to generate a dissimilarity matrix of Euclidean distance. Similarity between sites was expressed using group average cluster analysis and a correlation-based Principal Component Analysis (PCA) ordination (Clarke and Warwick 1994).

Two methods were used to link community patterns to environmental variables:

(i) Visual method: relative values of environmental variables were represented as circles of differing size and were superimposed, each variable at a time, onto a multidimensional scaling (MDS) plot of communities (Bursey and Wooldridge 2002).

(ii) Analytical method: the PRIMER programme BIO-ENV (Clarke and Warwick 1994) was used to select that subset of environmental variables that appeared to affect community structure the most.

RESULTS

There was a gradual change in environmental conditions and community structure down the shore and along the gradient from the mouth into the estuary. The values of the environmental variables measured at each site are given in Table I, with summary comments listed in Table II.

Details of macrofaunal community structure at the same 17 sites under study here are provided in Bursey and Wooldridge (2002). In summary, a total of 118

Table I: Values of environmental variables measured at each sampling site. These values represent the mean (±1 *SE*) of measurements taken on the two sampling occasions, or the maximum/minimum value of frequent measurements recorded at that site. Highest and/or lowest values of each variable are enboldened

Site	Level relative to MSL (m)	Aerial exposure (h)	Minimum sediment water content (%)	Mean maximum temperature of sediment (°C)	Maximum current velocity (m s^{-1})	Measurement of sediment compact-ness (cm)	Mean sediment particle size (mm)	Mean organic content (%)
1a	1.60	8	0.62	33.25 ± 3.75	0.525	13.30	0.171	1.02
1b	0.93	7	3.32	34.50 ± 0.50	0.529	9.35	0.158	0.92
1c	0.72	2.2	10.71	24.85 ± 3.15	0.978	5.15	0.221 ± 0.04200	1.24 ± 0.195
2a	1.90	12	**0.20**	35.25 ± 1.25	0.000	8.49	0.159 ± 0.0010	**0.49 ± 0.115**
2b	1.65	9	1.51	**36.00 ± 1.00**	0.000	10.60	0.156 ± 0.0000	0.90 ± 0.080
2c	0.93	4	11.78	30.10 ± 7.40	0.582	12.57	0.156 ± 0.0005	1.38 ± 0.400
2d	0.25	0	100.00	24.50 ± 0.50	1.131	4.59	0.183 ± 0.0085	0.99 ± 0.255
2e	-0.05	0	100.00	24.50 ± 0.50	**3.101**	**21.43**	0.237 ± 0.0220	1.02 ± 0.210
5	0.99	4.25	6.65	31.75 ± 1.25	0.913	3.80	0.153 ± 0.0045	1.39 ± 0.125
3/4a	1.11	**9.9**	3.73	31.50 ± 0.50	0.071	9.01	0.154 ± 0.0055	0.66 ± 0.010
3b	0.60	5.85	12.10	26.80 ± 1.20	0.483	6.94	0.197 ± 0.0045	0.75 ± 0.160
3c	0.10	0	100.00	23.00 ± 0.00	0.464	8.37	0.251 ± 0.0600	1.03 ± 0.170
3d	*c.*-2.00	0	100.00	23.00 ± 0.00	0.840	13.98	**0.309 ± 0.0965**	1.16 ± 0.545
4b	0.71	6.5	12.01	30.50 ± 1.50	0.008	4.02	0.151 ± 0.0050	1.45 ± 0.080
4c	0.20	0	100.00	23.50 ± 0.50	0.002	3.37	**0.135 ± 0.0035**	1.27 ± 0.250
4d	0.20	0	100.00	23.50 ± 0.50	0.002	4.25	0.153 ± 0.0165	**2.03 ± 0.420**
4e	*c.*-2.00	0	100.00	23.50 ± 0.50	0.149	9.66	0.141	1.61 ± 0.035

MSL = Mean sea level

species was identified, 106 on the flood-tidal delta and 36 on the beach. Major taxa and numbers of species were: Crustacea 60 (Isopoda 24, Amphipoda 17), Mollusca 20, Polychaeta 27, Insecta 6, Pisces 3. Maximum density was 5 171 m^{-2} for the haustoriid amphipod *Urothoe serrulidactylus*. Hill's numbers (Hill 1973) indicated that most of the species collected were not abundant. Species richness decreased from

Table II: Summary comments relating to environmental parameters measured on the Nahoon flood-tidal delta and beach

Exposure time	A trend of increasing exposure time was evident in an upshore direction along each transect. Sites in the mouth and lower region of the flood-tidal delta were exposed for less time than sites at a similar level on the beach, possibly attributable to the narrow inlet causing incoming and outflowing water to build up in the mouth region. Sites farther into the flood-tidal delta were exposed for longer than beach sites of similar level. There is a lag in tidal propagation up the estuary, because the flood tide loses velocity inside the inlet owing to increased frictional resistance as water spills out of the channel and over the intertidal flats
Minimum water content	There was a trend of decreasing water content of sediment up the shore along all transects
Temperature	Temperature was higher at intertidal than at submerged sites. A trend of decreasing temperature from the mouth into the flood-tidal delta was evident
Current velocity	Along all transects current velocity was low at high-shore sites, increasing with depth. Currents were stronger at sites in the estuary than on the beach, being strongest in the channel at the mouth (Sites 2d and 2e)
Compactness of sediment	On the beach, compactness increased down the shore, whereas along other transects the trend was that higher sites had harder, more-compact sand, with looser sand down the slopes and in the channels
Sediment particle size	There was a trend of increasing sediment particle size in a downshore direction along all transects (except Transect 4). The largest particles were in the channels where the currents were strongest. There was no apparent trend from the beach into the estuary
Organic content	Values increased steadily from the beach into the estuary, with Sites 4c, 4d and 4e, farthest from the mouth, having highest values
Salinity	There was no freshwater flow at the time of the study and the salinity of water was 35 at all sites

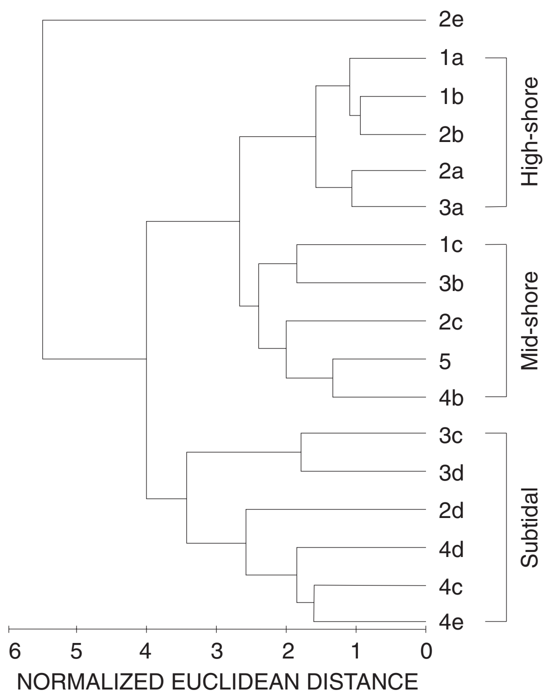

Fig. 2: Dendrogram using group-average linking on normalized data based on a dissimilarity matrix of Euclidean distance to represent similarity of sites in terms of the suite of environmental variables

beach to mouth sites, but in the flood-tidal delta, species numbers increased up-estuary. In all areas, species richness increased from high-shore to low-shore. Multivariate analyses identified four groups of sites, showing a gradual change in community structure from the beach into the estuary. The indicator species of these groups and of some individual sites are listed in Table III. Indicator species were revealed using a combination of techniques, viz. species cluster analysis and multidimensional scaling, breakdown of average similarity and visual examination of the data.

The Nahoon estuarine flood-tidal delta can be considered an ecotone with a characteristic group of species, some of which are largely restricted to the area, whereas others occur more abundantly on the sandy beach or in the estuary. Several typical sandy beach species were more abundant in the flood-tidal delta than on the beach. Sites farthest from the mouth were characterized by estuarine species, although community structure differed from typical lower estuarine communities.

Multivariate analysis of environmental variables

Figure 2 depicts the dendrogram generated by cluster analysis of all the measured environmental variables. The grouping of sites reflected their tidal level, and they were grouped into high-shore sites (1a-1b-2b and 2a-3a), and mid-shore (1c-3b and 2c-4b-5) and subtidal groups (3c-3d and 2d-4c-4d-4e). Site 2e was unique in terms of the complement of measured environmental variables.

Figure 3 illustrates the ordination map of the sites based on Principal Component Analysis. There was a clear separation of intertidal and subtidal sites. Sites were grouped in a similar way to that shown in the cluster analysis (Fig. 2). The first ordination axis represented 49.5% of the total variance and appeared to distinguish intertidal from subtidal habitats. Subtidal sites were separated along axis II, which represented 28.7% of the total variance. Together, the first two ordination axes represented 78.2% of the total variance.

Table III: Indicator species of individual sites or groups of sites

Group/Site	Situation	Indicator species
1a	Beach; upper shore	*Bullia rhodostoma, Excirolana natalensis, Adersia oestroides* (larvae)
1a-2a	Beach and mouth; upper shore	*Talorchestia* sp., *Pontogeloides latipes*
1c	Beach; intertidal	*Donax serra*, *Exosphaeroma hylocoetes*, *Gastrosaccus bispinosa*
2b	Mouth; intertidal	*Pontogeloides latipes*
2c-2d-3b-3c-5	Mouth and flood-tidal delta; mixture of intertidal and subtidal	*Urothoe serrulidactylus*, *Pontogeloides latipes*, *Scolelepis squamata*
2e-3d	Channels; subtidal	*Urothoe coxalis*, *Gastrosaccus brevifissura*, *Nephthys capensis*
3a	Flood-tidal delta; intertidal	*Oxytelus* sp., *Dyschirius* sp., *Pontogeloides latipes*
4c-4d-4e	Flood-tidal delta adjacent to lower estuary; subtidal	*Psammotellina capensis*, *Nassarius kraussianus*, *Lumbrineris tetraura*, *Solen capensis*

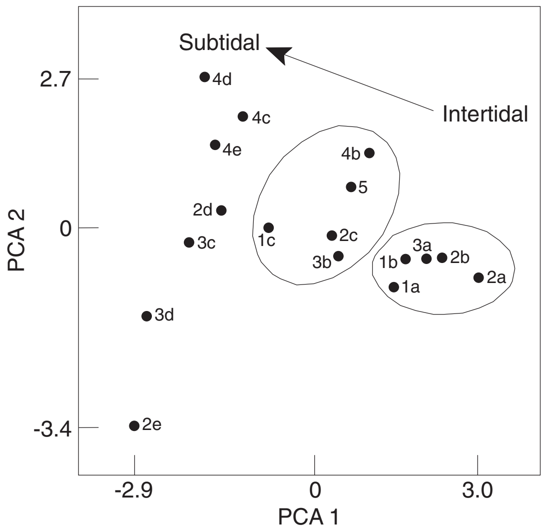

Fig. 3: Principal Component Analysis (PCA) ordination map of the sites in which their positions reflect similarity in terms of the suite of measured environmental variables

Therefore, Figure 3 seems to be a reliable representation of relationships between sites in terms of the suite of measured environmental variables.

Linking community patterns to environmental variables

Ordination plots of species abundance (Fig. 4, top left) and environmental data (Fig. 3 – referred to as biotic and abiotic plots respectively) showed the same broad patterns between sites. These similarities were: a group of estuarine sites (4c, d, e), a group containing high-shore sites, the separation of channel sites, and an association between sites in the mouth and in the central area of the flood-tidal delta.

Visual method of linking community patterns to environmental variables

By superimposing the relative value of each variable (represented as circles of different sizes) on the species plot (Figs 4a–g), it was shown which sites within groups had similar values for a variable. That variable was, therefore, likely to be important in regulating the similarity of species composition within the group(s). It was also possible to distinguish which sites or groups had differing values for a variable, and that variable was, therefore, likely to be important in regulating the difference in species composition.

AERIAL EXPOSURE, WATER CONTENT AND TEMPERATURE (Figs 4a, b, c)

These variables were important in separating Sites 1a-2a from subtidal groups 4c-4d-4e and 2e-3d. Water was likely to be a dominant requirement for the species in the subtidal communities, causing grouping of 4c-4d-4e and 2e-3d. However, exposure, water content and temperature did not explain why these two subtidal groups differed in community structure. Extremes of exposure, low water content and high temperatures at Sites 1a, 2a and 2b were likely to be limiting for marine organisms, explaining the low diversity at these sites. These conditions probably separated these sites as well as Sites 1b and 3a from all the others. However, other environmental factors must have been responsible for causing the observed differences in community structure between these sites, as shown in the MDS plot (duplicated on top left of Fig. 4). Sites 2c, 3b and 5 were intertidal and 2d and 3c subtidal, so water content, exposure and temperature did not explain why these sites showed common patterns in community structure.

CURRENT STRENGTH, COMPACTNESS AND PARTICLE SIZE (Figs. 4d, e, f)

Particle size was the environmental factor most similar in value between 2e, 3d and 3c, suggesting it contributed most to the similarity of their communities and explained their separation from other sites. Site 1c showed greater similarity to 2e and 3d in terms of particle size, although current strength at Site 1c was low. This could have been an artefact of the method of measuring current strength, and not a true reflection of the forces on the animals in the sediment. Although the current was not consistently strong over time, contrary to currents in the channels, the force of the waves was probably considerable on the animals in the sediment. Particle size and compactness differed between the three beach sites and were likely to be important in contributing to the differences in community structure between them. Sites 2c-2d-3b-3c-5 had a mixture of values of these variables, so they did not account for similarity of community structure in this group.

ORGANIC CONTENT (Fig. 4g)

Sites 4c-4d-4e had relatively high values of organic content, so organic content may have been a factor responsible for grouping these sites and separating them

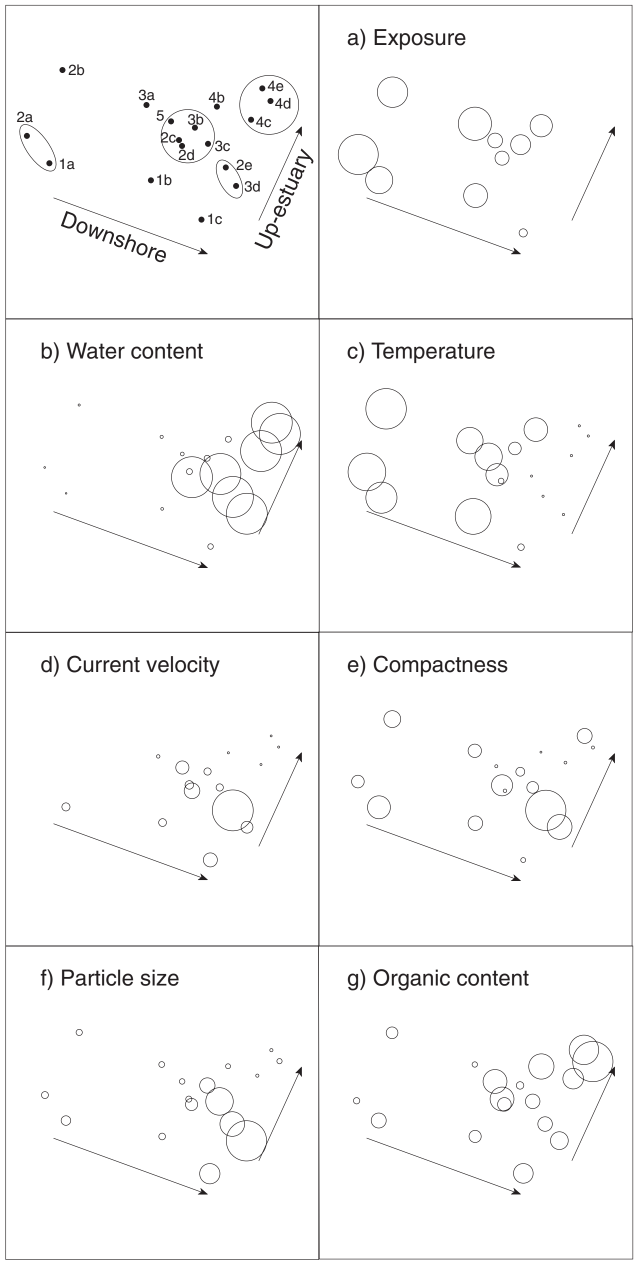

Fig. 4: Multidimensional scaling plot of biological communities (top left), with superimposed circles of different size representing relative values of each environmental variable (a–g)

from the rest. The difference in organic content between groups 4c-4d-4e and 2e-3d was probably an important factor separating these two groups of subtidal sites. Group 2c-2d-3b-3c-5 had varying values, so organic content could not explain their similarity.

This method showed that, at any given group of sites, certain environmental variables had similar values, whereas other variables had differing values. Therefore, it is assumed that the variables with similar values were those that were important in causing the similarity in community structure. Conversely, certain variables had different values between groups of sites and were most likely to be those that caused the differences in community structure. There were also cases in which certain variables had similar values at sites that did not show similarities in community structure, showing that other variables, (measured or not) were responsible for observed differences. Similarly, sites with similar communities did not share similar values of all the environmental variables.

Analytical method of linking community patterns to environmental variables

Table IV displays the correlation between the ordination maps of combinations of environmental variables and the biotic plot (PRIMER programme BIO-ENV). The single variable that yielded the best match of biotic and abiotic similarity matrices was temperature. At p = 0.369, the correlation was not close, an indication of the diverse effects of other environmental variables. The best two variable combination was temperature and organic content (p = 0.366). Table IV shows that the parameters that reflected the intertidal gradient, i.e. temperature, exposure and water content, played the greater role in structuring the community. Environmental variables associated with water flow (current velocity, particle size, compactness) appeared to have less of a structuring effect at all sites.

DISCUSSION

There was a steady gradation in values of environmental variables across sites, and ordination displayed this in a way that cluster analysis was incapable of doing. In cases where samples were strongly grouped, ordination also revealed the same pattern.

The abiotic and biotic plots showed the same broad patterns; a group of estuarine sites (4c, d and e), a group containing high-shore sites (although in the abiotic plot this group included sites that were separate in the biotic plot), a separation (and grouping in the biotic plot) of channel sites, and an association among sites in the mouth and in the central area of the flood-tidal delta. These patterns represented a gradual change in environmental conditions and community structure down the shore and along the gradient from the mouth into the estuary.

The fact that the abiotic and biotic ordination plots did not contain any major differences in their respective groupings of the sites showed that the environmental variables selected for measurement were likely to be influential in structuring macrofaunal communities. Where the two plots showed a close match, in particular the grouping of sites 4c, d and e, it is presumed that the suite of environmental variables was important in influencing the observed pattern. In the other cases, where the match was not as good, it is presumed that key environmental variables were omitted or variables irrelevant to community structure were included (Clarke 1993).

Each of the three beach sites was more similar in terms of community structure to sites in the flood-tidal delta than to other beach sites: 1a to 2a; 1b to sites in the middle of the flood-tidal delta; 1c to channel sites 2e and 3d. Two-thirds of the species collected on the beach were present in the flood-tidal delta. Characteristic sandy beach species such as the isopod *Pontogeloides latipes* and polychaete *Scolelepis squamata* were indicator species of sites in the flood-tidal delta (Bursey and Wooldridge 2002). In a Spanish estuary, species characteristic of sandy beaches achieved highest densities on midlittoral sheltered sands (Junoy and Viéitez 1992). The presence of species normally associated with exposed beaches in flood-tidal delta areas has been attributed to high salinity and clean sand of marine origin (Green 1968, Branch and Grindley 1979, Wolff 1983). Where rivers have been dammed, open estuaries also become predominantly marine (Allanson and Winter 1999).

The low species diversity at Sites 1a and 2a and the dissimilarity of their communities from those of other sites (Bursey and Wooldridge 2002) appeared to be attributable to extremes of aerial exposure, high temperature and low water content. The distinctness of Sites 1b, 2b and 3a in terms of community structure was not accounted for by any of the measured environmental variables, which were very similar at these sites. Site 1b experienced wave action and Site 2b, on the edge of the channel inside the mouth, experienced periodic flooding by the incoming tide. This was on account of water built up in the mouth caused by the delay in high tide between the sea and the estuary. These factors could contribute to distinct macrobenthic communities.

Water content, sand particle size and compactness of sand differed among the three beach sites, suggesting

Table IV: Combinations of the seven environmental variables, taken *k* at a time, yielding the best matches of biotic and abiotic similarity matrices for each *k*. Bold type indicates overall optima

1	**Temp** **0.369**	Expo 0.337	Water 0.334
2	**Temp, Org** **0.366**	Temp, Expo 0.361	Temp, Water 0.309
3	Temp, Org, Expo 0.353	Temp, Expo, Water 0.316	Temp, Expo, Size 0.304
4	Temp, Org, Expo, Water 0.313	Temp, Org, Expo, Size 0.312	
5	Temp, Org, Expo, Size, Water 0.285	Temp, Org, Expo, Water, Current 0.239	
6	Temp, Org, Expo, Size, Water, Current 0.214		
7	Temp, Org, Expo, Size, Water, Current, Comp 0.175		

Temp = Temperature
Org = Organic content
Expo = Exposure time
Water = Minimum water content
Size = Sediment particle size
Current = Current velocity
Comp = Compactness of sediment

that these factors were important in causing observed differences in community structure. Water content, sediment grain size, beach exposure and sediment stability are recognised as important factors leading to zonation patterns of sandy beaches (Wendt and McLachlan 1985, Brown and McLachlan 1990, Rakocinski *et al.* 1998). Wendt and McLachlan (1985) divided the Sundays River beach on the south-east coast of South Africa into four zones according to percentage moisture.

Sites in the group of mouth and flood-tidal delta sites (2c-2d-3b-3c-5) had differing values for all environmental variables. None explained the similarities in community structure. A possible explanation is that none of the values of the measured variables was extreme enough to be beyond the tolerance of species in the communities. Any one factor may only become important when the limits of tolerance for that factor are reached. It is likely that it is the extreme and not the average conditions that limit distribution and abundance (Day *et al.* 1952). The ranges of different values of the variables suggest that different variables may be important for, or limiting to, different species, and no variable affected the whole community in the same way. Nichols (1970) found that juxtaposition of stations appeared to contribute most to the degree of faunal similarity, despite changing physical conditions. Sites 2c, 2d and 5 were close to each other, as were Sites 3b and 3c. The macrobenthos in an estuary is subject to the combined effect of many environmental variables (Day *et al.* 1952, Nichols 1970, De Villiers *et al.* 1999). On the intertidal sandflats in Manukau Harbour, New Zealand, Pridmore *et al.* (1990) were unable to identify any single factor responsible for shifts between bivalve- and polychaete-dominated communities.

Sites with large sand particle size (i.e. 2e, 3d, 3c and 1c), indicating strong water movement (although this was not always reflected in the measurements of current velocity), showed similarities in their communities. Only species capable of existing under these conditions could survive in the channels, leading to low species richness and biomass (Bursey and Wooldridge 2002). Nichols (1970) suggested that species of benthic polychaete inhabiting unstable areas may be able to contend with shifting sand in relation to tidal activity. Gray (1968) also found low species diversity in areas with high current action and coarse sediments. The sediment was too loose and unstable to allow construction of permanent burrows. Small species may have been washed out of the sediment, and this may explain the relatively low numbers of *U. serrulidactylus* compared to other sites in the flood-tidal delta (Bursey and Wooldridge 2002). Feeding for many species under these conditions would be problematic, because fine particles were washed away and the organic content was low. There was also an absence of small prey for carnivorous species. Sphaeromatid isopods were successful at these sites, probably because they are adapted to roll into a ball to withstand abrasion.

The sites in group 4c-4d-4e were subtidal, which moderated temperature. Current flow was also weak, and there was high organic content in the sediment. Many indicator species in the communities of these sites (Bursey and Wooldridge 2002) rely on detritus, e.g. the deposit-feeding snail *Nassarius kraussianus* and the suspension-feeding sunset clam *Psammotellina capensis* and pencilbait *Solen capensis*. Species of this assemblage cannot tolerate prolonged exposure and are typical of sheltered situations such as estuaries (Kilburn and Rippey 1982). High species diversity could be on account of environmental factors being within the tolerances of many species of marine organisms, and there were also more resources for utilization. Numbers of amphipods, isopods, small crabs and gastropods are known to increase as organic content increases (Day 1981).

Variation in salinity is an environmental factor central to the definition of an estuary (Day 1980), and the components of an estuarine fauna are recognized in terms of salinity tolerance (Day 1981, Wolff 1983). Difference in salinity was not a factor regulating differences in community structure among sites in the Nahoon flood-tidal delta, because salinity was similar to that of seawater.

A possible reason for the weak correlations in the results using the programme BIO-ENV is that different factors were important for separating different groups of sites and for causing similarity within groups. Therefore, each group needed to be examined separately. No one factor or combination explained the entire plot satisfactorily. These details could be seen by superimposing values of each environmental variable as circles of differing size on to the biotic plot. This important information was hidden by the programme BIO-ENV. Another consideration is that environmental variables that showed similar values within a group of sites, and which were important for structuring the community, may also have been shared with other communities that were different, so other factors were important in separating the groups. Also, some sites showed grouping in terms of environmental variables, but their communities did not show patterns. Therefore, it cannot be concluded that these variables were not important for the species in the communities, but other variables or interactions caused separation of sites in terms of community structure. Jones *et al.* (1986) also found that environmental variables did not always explain community structure in a consistent way.

It is concluded that the visual method was preferable to the analytical method for explaining which environmental factors were most important in structuring communities in this study. There were so many different habitats and combinations of environmental parameters at each habitat that the usefulness of trying to find a factor/subset that accounted for community structure at all sites over the whole flood-tidal delta was questionable.

The methods used here cannot prove cause and effect, because they may have been correlated with unrecorded variables that were causal (Gray 1968, Clarke and Warwick 1994). Experiments would require investigating the effects of a single factor or combination thereof on community structure, while the other factors are held constant or controlled.

Much of the experimental work, examining limiting effects of salinity and temperature, determined upper and lower lethal limits on selected organisms (Kinne 1963, Hill 1981). Direct lethal effects are not the only manner in which physical factors can influence survival and distribution of macrobenthos, but sublethal effects may reduce fitness or activity and render a population non-viable (De Villiers *et al.* 1999). Different life-history stages may also respond differently to environmental conditions.

In estuarine habitats, great variability of environmental factors, in addition to physiological tolerance of extremes, may play a role in regulating community structure. Subtidal sites were more stable in terms of the measured environmental variables than intertidal sites. Even if the physical and chemical attributes of a substratum are suitable, it does not necessarily follow that a given species will inhabit all the areas in which it could survive, because biotic interactions may be limiting (Green 1968). Reise (1985) cautions against seeking explanations for patterns of species abundance and distribution entirely in terms of physical factors. Species belonging to different feeding types might respond differently to environmental factors (Beukema 1976, Brown *et al.* 2000). For example, Sanders (1958), Rhoads and Young (1970) and Grange (1977) demonstrated a relationship between sediment grain size and particular trophic groups.

Many recent studies relating macrobenthic community structure to abiotic variables investigate the effects of sediment contaminants or organic pollution on benthic communities (e.g. Ahn and Choi 1998, González-Oreja and Saiz-Salinas 1998, Rakocinski *et al.* 1998, Hyland *et al.* 1999, Brown *et al.* 2000). The methods of linking community patterns to environmental variables used in this study were developed mainly to assess effects of pollution on benthic community structure. In the present context, it was shown that these methods are useful in showing the importance of environmental factors in regulating community structure.

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