The ecology of sandy beaches in southern Africa

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The physical features, macrofauna and meiofauna of four exposed sandy beaches along the southern coast of South Africa were quantitatively investigated. All beaches had medium to fine sands with relatively poor to moderate macrofauna and very rich meiofauna. The results are compared with the present knowledge of the southern African coastline. Sandy beaches types around the southern African coastline are summarized according to geomorphology and wave action and three zoogeographic provinces are recognized. The macrofauna is dominated by crustaceans, mostly scavengers, on the warmer east coast and by molluscs, mostly filter-feeders, on the temperate south coast. Relationships between diversity and abundance of macrofauna, beach slope and particle size are analysed in detail. Intertidal zonation of macrofauna is described and a zonation scheme based on crustaceans proposed. Relationships between meiofauna composition and particle size are described as well as intertidal distribution patterns of the meiofauna. The role of surf circulation patterns and macrofaunal food sources in determining beach trophic structure is emphasized.

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'n Algemene ekologiese opname van die sandstrande van die suidkus van suidelike Afrika het die verspreiding en getalle van makrofauna en meiofauna kwantitatief bepaal. Opnames van die supragetysone en brandersone was ingesluit asook belangrike fisiese parameters. Die resultate word vergelyk met die huidige kennis van sandstrande in suidelike Afrika. Die makrofauna het matige biomassawaardes getoon en Mollusca was die belangrikste groep. Drie intergetysones is onderskei en word deur Crustacea gekenmerk. Veranderinge in die makrofauna as gevolg van blootstelling aan branderaksie word genoem. 'n Ryk meiofauna het op alle strande voorgekom en was gedomineer deur nematodes en Harpacticoida. Strandtipes om die Suid-Afrikaanse kus word opgesom ten opsigte van fisiese parameters, soögeografie en trofiese struktuur en die effekte van strandhelling en sandpartikelgrootte en ander faktore op die samestelling en rykheid van die fauna word bespreek. Die belangrikheid van sirkulasiepatrone in die brandersone en voedselbronne vir die makrofauna word beklemtoon as 'n bepalende faktor vir die trofiese struktuur van die strande.

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Until comparatively recently very little was known of the exposed sandy beaches which make up about 70% of the coastline of southern Africa. Brown (1964, 1971) published the first papers dealing with the general ecology of sandy beaches around the Cape Peninsula. Subsequently some quantitative surveys have been undertaken in the East Cape near Port Elizabeth (McLachlan 1977a, b, c) and more recently along the coasts of Natal (Dye, McLachlan & Wooldridge 1981) and Transkei (Wooldridge, Dye & McLachlan 1981) in the east. Workers at the University of Cape Town are presently investigating sandy beaches on the west coast of South Africa. The ecology of sandy beaches along the 700 km south coast has not been reported on in the literature and the main aim of this study was therefore to investigate the area between Cape Agulhas in the west and Cape St Francis in the east. It is also the purpose of this paper to draw some relevant general conclusions from the present knowledge of southern African sandy beaches, which are the only well-studied beaches in the southern hemisphere. Particular attention will be given to the distribution of physical beach types, zoogeography, abundance and energetics of the psammolittoral fauna.

Materials and Methods

Although a number of beaches were visited, only four were sampled intensively. Spaced at roughly 150 km intervals, these beaches are shown in Figure 1. Struisbaai (34°65′S/20°10′E) lies inside a bay about 1 km from a small river mouth and is fully exposed to the sea. Still Bay (34°33′S/21°40′ E) also lies inside a bay about 1 km from a small river mouth and is open to the sea. Wilderness (34°01′S/22°59′E) is a very exposed beach about 5 km from a small river mouth and Keurboomstrand (34°02′S/23°39′E) in Plettenberg Bay is about 3 km east of the Keurbooms River mouth and fully exposed. Along this whole coast swell is generally heavy (>1 m) and approaches mainly from the south and south-west. The coastline mostly takes the form of long, south-east facing bays which experience very vigorous wave action against rocky headlands at their eastern ends and slightly less vigorous wave action towards their western ends. Mossel Bay, Plettenberg Bay and St Francis Bay are typical of this. Tides are semidiurnal and mean spring tide range is 1,6 m.

Sampling was done during spring low tide in early sum-

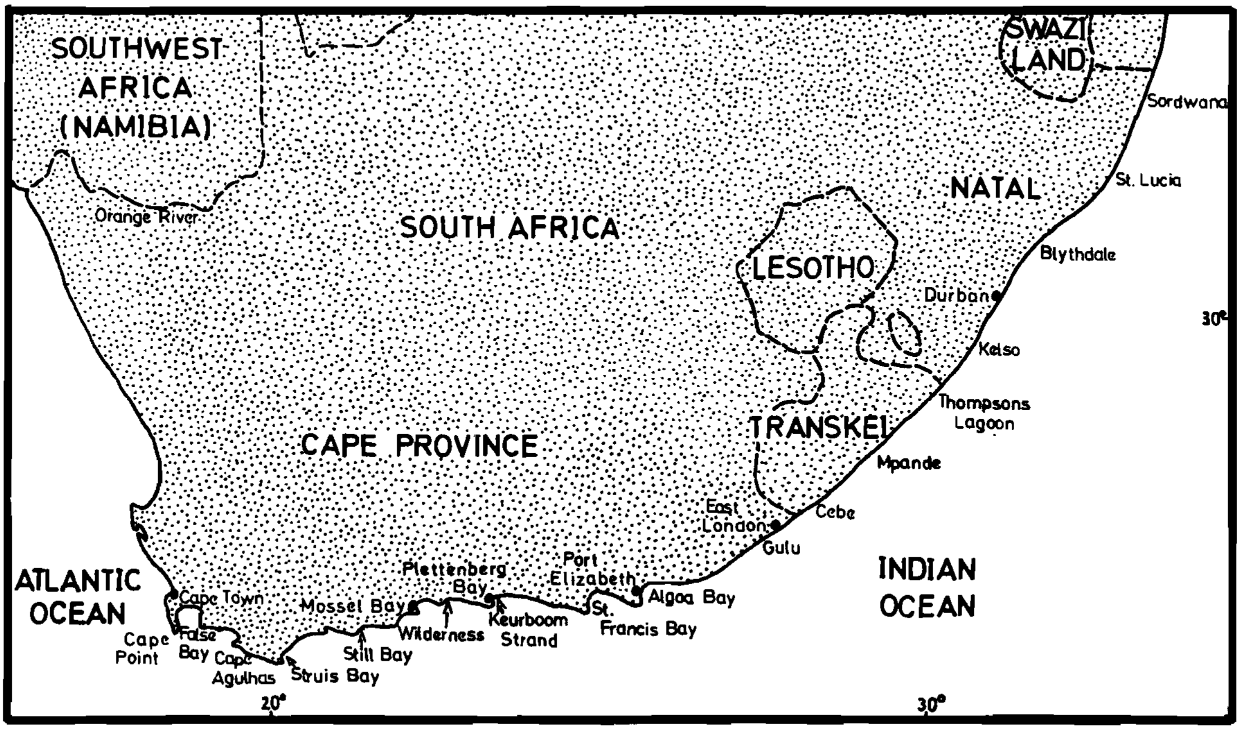

Figure 1 Southern Africa showing beaches surveyed (with arrows) and other localities mentioned in the text.

mer, a routine procedure (Dye *et al.* 1981) being followed on each beach. Beach profiles were measured and at three representative tide levels (the driftline (HW), mid-tide level (MW), and spring low-tide swash line (LW)) temperature, Eh, moisture and salinity were measured at a series of depths in the sand. Sand samples from the upper 30 cm were taken for particle size analysis by wet sieving and estimation of calcium carbonate content by acid treatment.

Macrofauna was sampled quantitatively at a series of points along each transect using both a dredge of 1,5-mm mesh and by digging 2 – 4 quadrats of 0,25 m^2 and passing the sand through a 4-mm mesh. Dry mass of this macrofauna was determined by drying at 90 °C for 24 h after removal of mollusc shells. Mysids were collected with a sled with 1,5-mm mesh which was used to make a series of 10-m hauls from the swash line out to nearly 1-m depth. For biomass determinations mysids were dried to constant mass at 60 °C and weighed on a Sartorius microbalance.

Meiofauna was sampled at the three tide levels where physical measurements were taken. Four replicate series of cores were taken stepwise to below the water table with a 30-cm corer of 10-cm^2 internal cross-sectional area. At the highest tide level (HW), however, only duplicate samples were taken due to the considerable depth to be sampled. Meiofauna was narcotized with 7% $MgSO_4$ solution, killed with 10% formalin and extracted by decanting four times and trapping on a 45-µm screen. The procedure is about 95% efficient for all the major groups. Dry mass values for important taxonomic groups were obtained by drying batches of specimens for 24 h at 60 °C and weighing on a Sartorius microbalance. Exposure was assessed using a 20-point rating scale proposed by McLachlan (1980a).

Results and Discussion

Beaches

Results of substratum analyses and measurements of interstitial water characteristics are presented in Table 1 and beach profiles are given together with macrofauna distribution patterns in Figures 2 – 5. On a 20-point exposure scale (McLachlan 1980a) these beaches rated as follows: Struisbaai 15,0; Still Bay 13,5; Wilderness 15,0 and Keurboomstrand 14,0; which classifies them all as exposed. All had steep to moderate slopes (1/12 – 1/23) and very well-sorted fine to medium quartz sands with very high $CaCO_3$ contents. They were well drained and well flushed and oxygenated by wave action, as indicated by the great depths of the spring low tide water tables and the high Eh values. Salinities were all close to 35‰ indicating no significant seepage of groundwater from the backshores or dunes, and temperatures ranged from 16 to 35 °C. An exposed beach visited at Hermanus, west of Cape Agulhas, had fine sand high in $CaCO_3$ (Table 1) and supported a large population of *Donax serra*, but was not surveyed further.

Surf zones were generally 100 – 200 m wide and all exhibited some evidence of phytoplankton blooms which are an important feature of exposed sandy beach environments (McLachlan 1980b; McLachlan, Erasmus, Dye, Wooldridge, van der Horst, Rossouw, Lasiak & McGwynne 1981). Drift lines were 2,5 – 3,0 m above the spring low-tide swash line (LWS) and generally contained very small quantities of organic debris. None of these beaches had berms between the intertidal zone and the foredunes. Foredunes had a sparse vegetation consisting of *Ammophila* sp., *Scaevola thunbergii, Gazania rigens, Arctotheca nivea* and others and were usually backed by higher stable dunes vegetated with coastal bush.

Table 1 Physical measurements of beach conditions. Substrate particle size parameters given in phi units

Beach and tidal level		Md	Qd	Sk	Mz	GI	Sk	Water table (cm)	% Carbonate	Eh (mV)	Moisture %
Struisbaai	HW	1,60	0,45	0,00	1,58	0,62	−0,03	135		+430	11−28
	MW	1,40	0,60	−0,05	1,33	0,90	0,11	30	93,1	+400	22−26
	LW	1,35	0,65	0,06	1,48	1,00	0,06	0		+450	30
Beach mean	(μm)	367			364						
Still Bay	HW	2,10	0,43	0,08	2,16	0,53	0,10	118		+410	9−23
	MW	2,30	0,35	0,00	2,30	0,46	−0,04	38	40,6	+350	12−28
	LW	2,10	0,45	0,00	2,07	0,64	−0,12	0		+300	30
Beach mean	(μm)	223			222						
Wilderness	HW	1,05	0,50	0,00	1,02	0,62	0,02	160		+380	4−17
	MW	1,55	0,34	−0,04	1,51	0,46	−0,11	40	29,5	+330	15−25
	LW	1,65	0,33	−0,08	1,57	0,48	−0,19	0		+390	22
Beach mean	(μm)	381			394						
Keurbooms Strand	HW	1,75	0,20	0,00	1,75	0,32	0,00	140		−	4−25
	MW	1,75	0,20	0,00	1,77	0,34	0,08	40	31,8	−	7−23
	LW	1,65	0,35	0,00	1,65	0,57	−0,08	0		−	24
Beach mean	(μm)	305			304						
Hermanus	MW	2,25	0,40	−0,10	2,13	0,59	−0,29		60,2		
	(μm)	210			229						

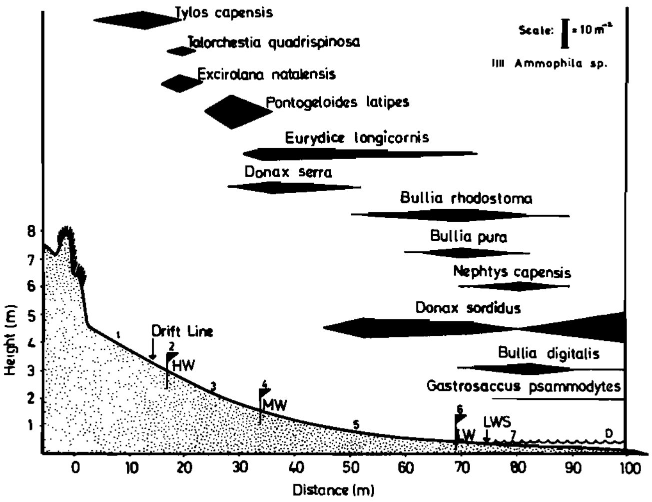

Figure 2 Struisbaai beach with sampling sites in the intertidal (1−6) and subtidal (7, D = dredge). Macrofaunal distribution is indicated quantitatively except for *Gastrosaccus psammodytes*.

Macrofauna

Distribution and abundance of macrofauna is summarized in Figures 2−5 and Table 2. On all four beaches *Tylos capensis* and *Talorchestia quadrispinosa* occupied the supralittoral although *Excirolana natalensis* also extended to the drift line. *Talorchestia quadrispinosa* was concentrated around the drift line and *Tylos capensis* occurred from the drift line into the foredunes. The penetration of *Tylos capensis* into the dunes increased eastwards: at Struisbaai it just reached the seaward slopes of the foredunes, at Keurboomstrand it penetrated well above the foredunes to near the start of coastal bush and near Port Elizabeth, further eastwards, it has been recorded several hundred metres into high shifting dunes.

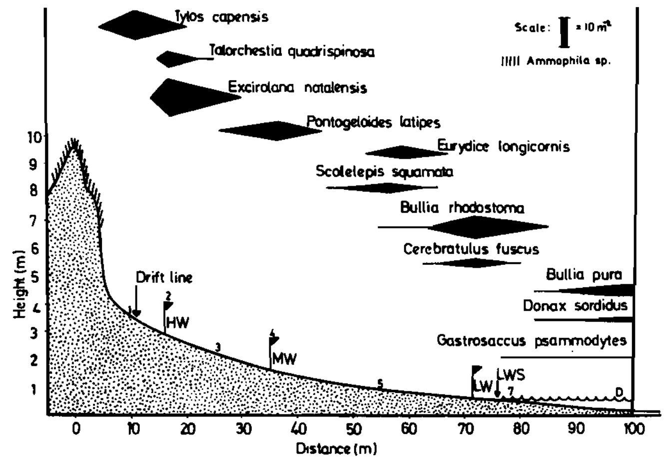

Figure 3 Still Bay beach with details as in Figure 2.

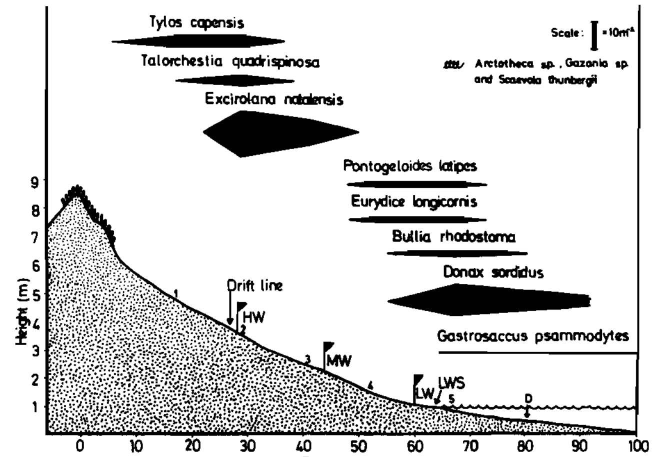

Figure 4 Wilderness beach with details as in Figure 2.

Table 2 Abundance and biomass of the macrofauna in 1-m transects of shoreline from about 1-m depth to the foredunes. Species are listed in order of occurrence from the upper shore out into the surf zone

	Beach							
	Struisbaai		Still Bay		Wilderness		Keurboomstrand	
Species	Abundance (m^{-1})	Biomass ($g \cdot m^{-1}$)	Abundance (m^{-1})	Biomass ($g \cdot m^{-1}$)	Abundance (m^{-1})	Biomass ($g \cdot m^{-1}$)	Abundance (m^{-1})	Biomass ($g \cdot m^{-1}$)
Cerebratulus sp.	–	–	23	0,42	–	–	–	–
Scolelepis squamata	–	–	23	0,31	–	–	–	–
Nephtys capensis	20	1,00	–	–	–	–	–	–
Gastrosaccus psammodytes	1684	2,17	154	0,33	64	0,31	896	4,29
Tylos capensis	10	2,49	8	1,47	114	8,58	82	5,54
Excirolana natalensis	38	0,13	109	0,38	943	3,30	134	0,47
Eurydice longicornis	98	0,39	29	0,12	29	0,11	–	–
Pontogeloides latipes	165	0,99	62	0,37	29	0,17	14	0,08
Talorchestia quadrispinosa	12	0,07	26	0,09	28	0,13	38	0,06
Donax serra	72	61,20	–	–	–	–	–	–
Donax sordidus	314	21,71	14	1,00	268	18,02	204	15,88
Bullia rhodostoma	74	15,90	144	18,05	12	6,30	142	9,71
Bullia digitalis	40	1,23	–	–	–	–	–	–
Bullia pura	28	1,00	32	0,74	–	–	–	–
Total	2555	108,28	624	23,28	1309	36,92	1510	36,03

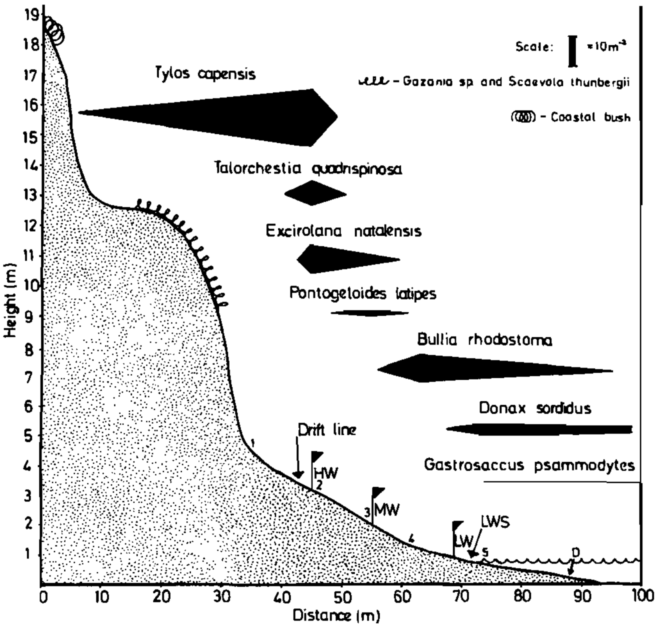

Figure 5 Keurbooms beach with details as in Figure 2.

Talorchestia quadrispinosa has also been found up to 300 m into the dunes at the latter locality. No ghost crabs (*Ocypode* spp.) were encountered in the supralittoral in this survey, although they are known to reach this area (Day 1969; McLachlan 1980c).

Excirolana natalensis occurred around the drift line and on the upper midshore, forming part of a clear zonation of the four isopod species recorded. Below the zones occupied by *Tylos capensis* and *E. natalensis*, *Pontogeloides latipes* and *Eurydice longicornis* occurred in the midshore. R. Bally (pers. comm.) has found a similar pattern on the west coast except that *Tylos granulatus* replaces *T. capensis*. Also recorded in the midshore were *Scolelepis squamata* and *Donax serra*. Nearer the low-water mark molluscs became more important with three *Bullia* species and *Donax sordidus* appearing. *B. rhodostoma* was concentrated just above LWS and *B. pura*, *B. digitalis* and *D. sordidus* at and below LWS. The nemertean, *Cerebratulus fuscus*, and the polychaete, *Nephtys capensis*, occurred near LWS on the Struisbaai and Still Bay beaches respectively. The bentho-planktonic mysid, *Gastrosaccus psammodytes*, was abundant below LWS and exhibited the same intraspecific zonation as recorded elsewhere (Wooldridge 1981) with gravid females closest inshore, juveniles furthest out and most of the population on the bottom within 30 m of the swash line. Maximum abundance of *G. psammodytes* was 61 m^{-2} at Struisbaai and minimum was 2 m^{-2} at Wilderness. Most of this fauna has been shown to undergo tidal migrations in the East Cape (McLachlan, Wooldridge & van der Horst 1979).

Wilderness was the poorest of the four beaches with only eight species recorded and Struisbaai was the richest with 12 species, the faunal composition generally being similar to that recorded in the East Cape (McLachlan 1977c). Biomass values were all relatively low, ranging from *ca.* 20 to 100 g dry mass per metre shoreline (Table 2). Nowhere were the large *Donax serra* populations, which have yielded such high biomass values elsewhere (McLachlan 1977c), encountered. Nevertheless molluscs, particularly *Donax sordidus* and *Bullia rhodostoma*, were the most important component and accounted for at least 90% of biomass in all cases.

Meiofauna

Figures 6 – 9 illustrate the distribution in the sediment of total meiofauna and the dominant meiofaunal taxa. On all beaches maximum densities occurred just below the surface near MW and numbers generally dropped more rapidly towards LW than HW. Abundant meiofauna oc-

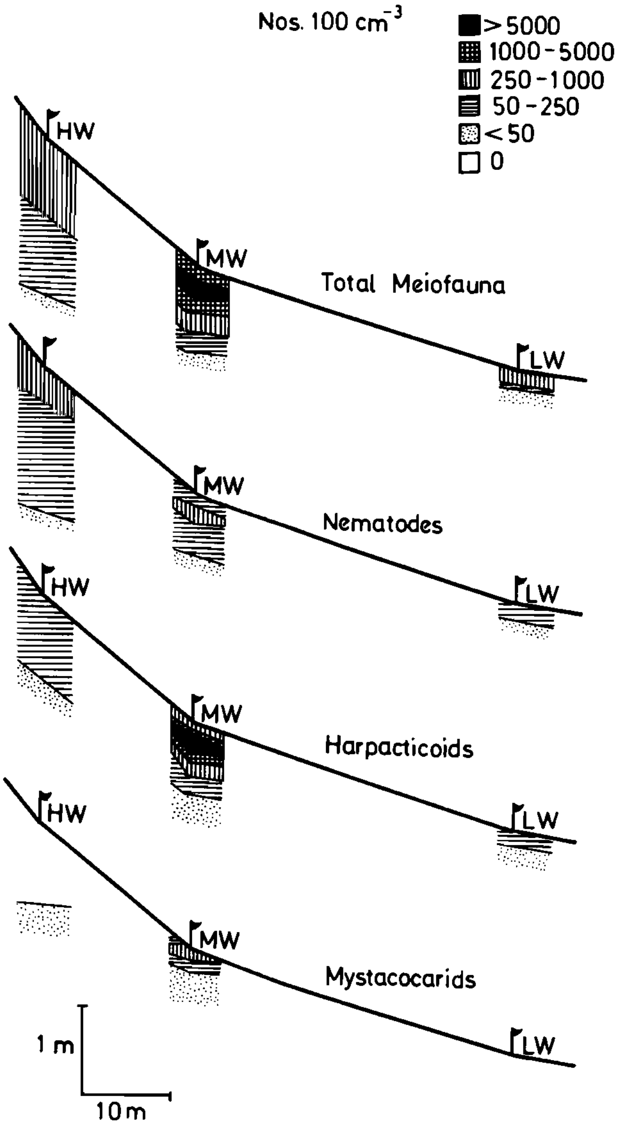

Figure 6 Intertidal distribution of total meiofauna and dominant taxa on Struisbaai beach.

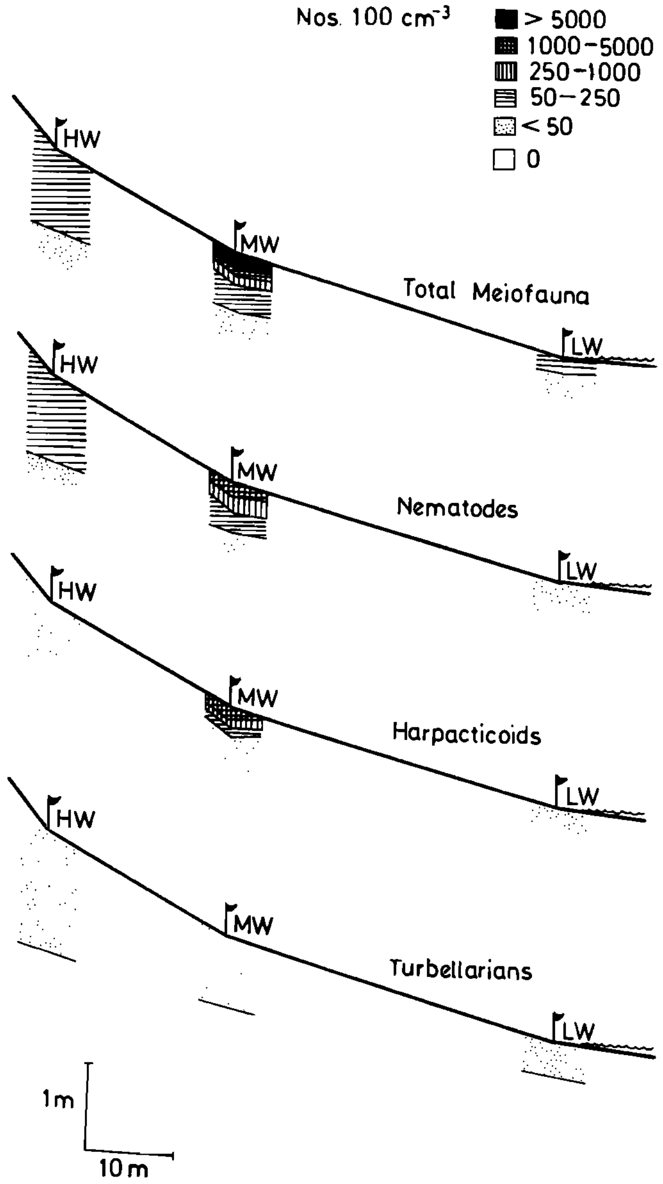

Figure 7 Intertidal distribution of meiofauna on Still Bay beach.

curred to considerable depth in the sand, penetrating below the permanent water table. Nematodes and harpacticoid copepods were always the dominant groups with mystacocarids and turbellarians less important. Oligochaetes, archiannelids, gastrotrichs, polychaetes, calanoid copepods and acarines were also recorded but were never abundant. The general distribution of meiofauna in these sediments conforms with the stratification scheme proposed by McLachlan (1980d).

Individual dry mass values used for estimating meiofauna biomass were as follows: nematodes 0,8 μg; harpacticoids 0,4 μg; mystacocarids 0,5 μg; oligochaetes 1,0 μg; turbellarians 1,0 μg; archiannelids 5,0 μg and other taxa 1,0 μg. Total biomass and numbers per metre shoreline are recorded in Table 3. This shows a clear increase in numbers and biomass westwards from Keurboomstrand to Struisbaai. Exceptionally high meiofauna densities, up to 7 000 per 100 cm^3, were recorded in the upper layers at MW, particularly at Struisbaai and Still Bay. These are the highest meiofauna densities yet reported from sandy beaches around southern Africa.

Table 3 Abundance and biomass of total meiofauna per 1-m transect from LWS to HWS on four beaches

Locality	Biomass g m^{-1}	Numbers 10^8 m^{-1}
Struisbaai	243	3,84
Still Bay	223	2,58
Wilderness	148	2,36
Keurboomstrand	117	2,00

Conclusions

Beach types

From this survey and the work of Dye *et al.* (1981), Wooldridge *et al.* (1981) and R. Bally (pers. comm.), the geographical and physical variation in sandy beaches along the southern African coastline allows the description of five regions from the Mozambique border to the Orange river. Subtropical beaches from the Mozambique

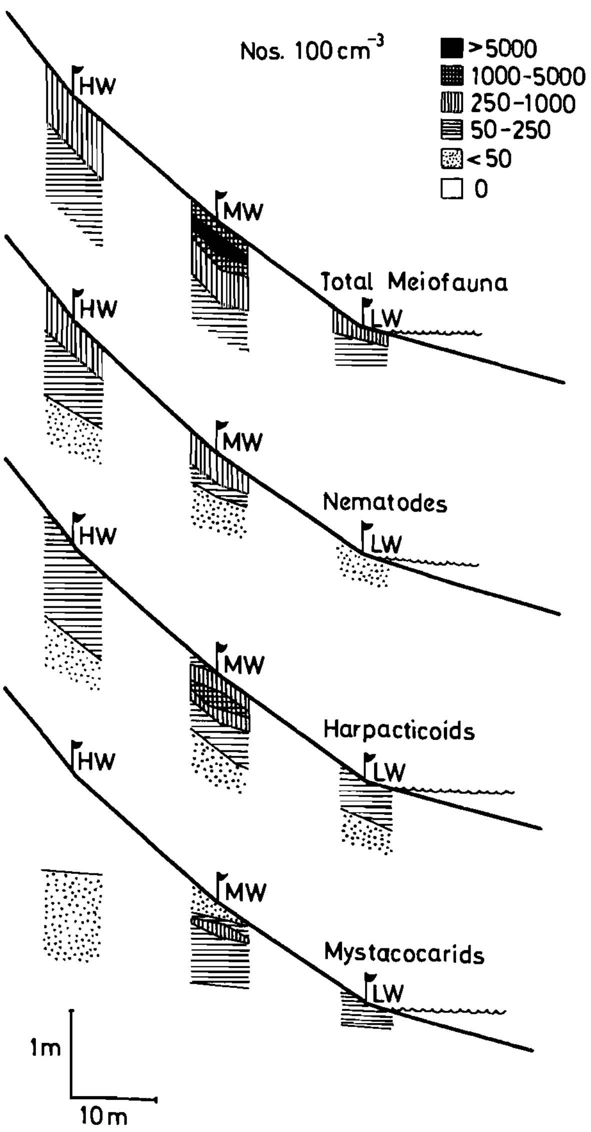

Figure 8 Intertidal distribution of meiofauna on Wilderness beach.

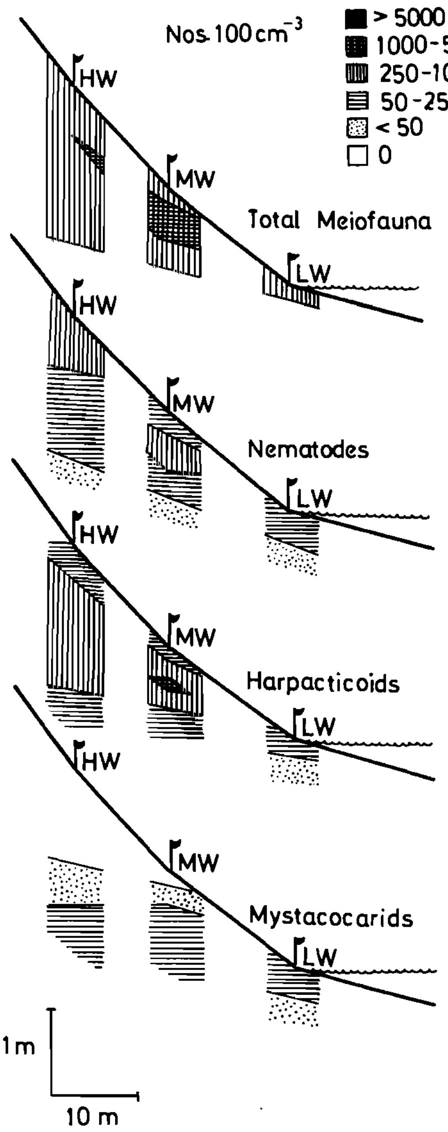

Figure 9 Intertidal distribution of meiofauna on Keurbooms beach.

border to south of St Lucia are exposed (rating ≃ 14) and have fine to medium sand with low calcium carbonate contents, moderate slopes and high, forested back-dunes. Headlands have medium to coarse sands. There is a relatively diverse but sparse macrofauna and meiofauna. From just south of St Lucia to the Transkei border the beaches are very exposed (rating ≃ 17,5), often near rocks and have coarse to very coarse sand, although finer sands may occur in places. Sands are very low in calcium carbonate and there are distinct berms and low, bush-covered dunes. Intertidal macrofauna is sparse or absent but *Ocypode* occurs in the supralittoral. The meiofauna consists of large forms with archiannelids abundant. In the subtropical regions, from the northern border of Transkei to East London, exposed pocket beaches (rating ≃ 13) occur between rocky headlands and are usually associated with small estuaries. They have moderate slopes and fine to medium sands low in calcium carbonate. There is a diverse macrofauna low in abundance and a rich meiofauna. Warm temperate beaches occur between East London and False Bay. They are exposed to very exposed long stretches of beach (rating 12 – 16) usually within large bays which are very exposed at their eastern ends and less exposed at their western ends. There is usually no berm and most beaches are backed by dunes which may be shifting. Slopes are moderate but variable and the sands are fine to medium with high calcium carbonate contents, increasing westwards. A moderately diverse macrofauna can be locally very abundant and is accompanied by a very rich meiofauna. The temperate west Cape coast, from the Cape Peninsula to the Orange River mouth, has long stretches of exposed to very exposed beach (rating ≃ 13 – 18) with moderate to steep slopes and medium to coarse sands high in calcium carbonate. Beaches tend to become steeper and coarser northwards. There is a moderate to poor macrofauna, which may be locally abundant, and a rich meiofauna.

This description is very general and within each region some exceptions may occur. Boundaries may also not be sharp as different beach types are to some extent related to a continuous gradient in wave action along this coastline, but modified by more abrupt geomorphological changes. The largest swell approaches from the south-west and wave action generally decreases up the east coast and to a lesser extent up the west coast (Davies 1972). Despite this, the beaches rating consistently highest on the exposure scale occurred far up the east coast in southern Natal. Their high rating is not a result of very heavy wave action, but rather because they drop off into deep water, causing sizeable waves to break directly onto the intertidal zone, which is steep and has coarse sand.

Using the result of Dye *et al.* (1981) for the Natal coast and Wooldridge *et al.* (1981) for the Transkei coast, in addition to the present results and those of McLachlan (1977b, c), a significant relationship ($P < 0{,}01$) has been obtained between beach slope and sand particle size (Figure 10). This relationship can also be expressed as $\text{Md}\phi = 0{,}95\ln(1/\text{slope}) - 1{,}14$. The interaction between these two factors is related to wave action (Davies 1972; McLachlan 1980a). Consequently the significant relationship obtained from these data suggests that all these beaches fall into a relatively small range of wave action.

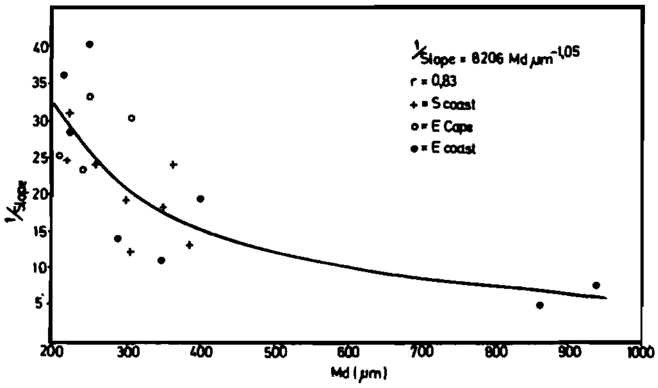

Figure 10 The relationship between sediment particle size (μm) and the reciprocal of slope. Data came from the East Coast (Dye *et al.* 1981, Wooldridge *et al.* 1981), the Eastern Cape (McLachlan 1977a, c) and the present study.

Calcium carbonate levels increased steadily down the east coast to Cape Agulhas, despite the fact that the subtropical and tropical beaches would be expected to have the highest calcium carbonate contents owing to the supply from coral reefs. However, sediment transport along this coast is from south to north, i.e. from Cape Agulhas northwards along the east coast (Davies 1972). It would therefore appear that the source of carbonate may be in the south, possibly offshore on the large continental shelf off Cape Agulhas.

The series of surveys, of which this paper forms part, have been the first to consistently use an exposure rating scale (McLachlan 1980a) for sandy beaches. This has the great advantage that it is relatively independent of subjective assessment based on experience of a limited range of conditions. This scale clearly demonstrates that open sandy beaches around the southern African coastline are fully exposed. A problem when comparing these beaches to those reported in other parts of the world is that many other beaches are labelled exposed when in fact, on a global scale, they do not experience much wave action. If all authors could refer back to one standard reference scale much of this confusion would be alleviated.

Macrofauna

The sandy beach macrofauna of southern Africa falls into the same zoogeographic provinces as described for various other habitats, but particularly for the fauna and flora of rocky shores (Stephenson & Stephenson 1972; Brown & Jarman 1978). A subtropical fauna extends down the east coast to the transition zone between Port St Johns and Woody Cape (just north of Port Elizabeth), with the biggest change at Cebe just north of East London (Wooldridge *et al.* 1981). The warm-temperate south-coast fauna extends westwards from this area to its overlap region with the temperate fauna of the west coast. This latter overlap region lies between Cape Agulhas and the Cape Peninsula, with Cape Point representing the most distinct boundary point. The west-coast fauna extends up the west coast into South West Africa/Namibia. In the northern fringe of Natal a tropical fauna may overlap the subtropical component (Jackson 1976), but this has not yet been documented for sandy beaches.

The distributions of the major sandy beach macrofauna species around the coasts of southern Africa are illustrated in Figure 11. Boundaries between subtropical, warm-temperate and temperate regions are indicated at Cebe and Cape Point respectively and animals are grouped into sublittoral, lower shore, midshore and upper shore species according to their normal position on the shore during spring low tides. Of these 25 species, 12 occur on the west coast, 17 on the south coast and 17 on the east coast. Two are restricted to the west coast, four to the south coast and seven to the east coast. Diversity and endemism thus increase eastwards towards the warmer regions.

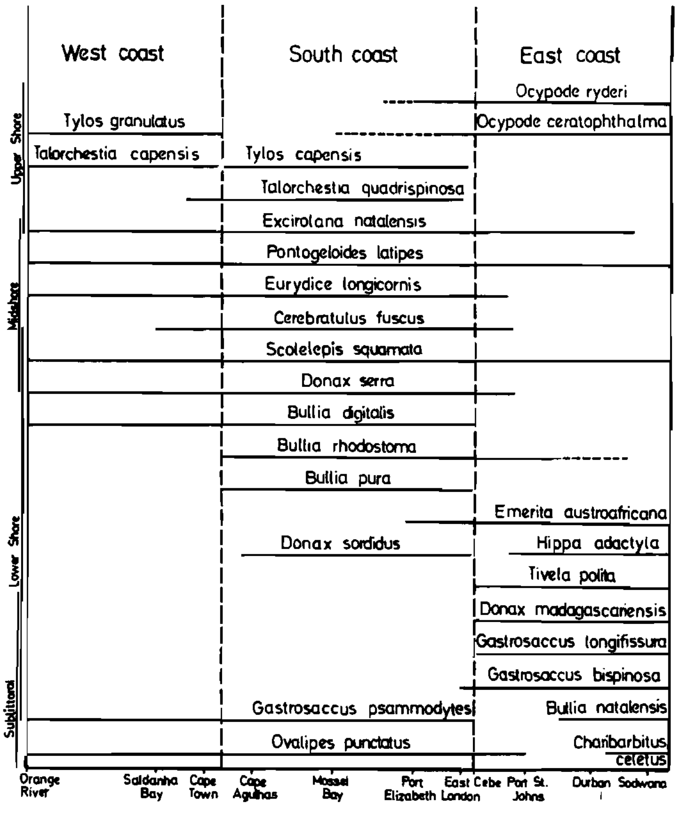

Figure 11 Distribution of major sandy beach macrofauna species around the southern African coastline. The vertical position of each species places it into upper shore, midshore, lower shore or sublittoral categories while horizontal distribution is relative to boundaries of west, south and east coast regions.

Recognizing macrofaunal zones on exposed intertidal sandy beaches has always been difficult because of the dynamic environment and the high degree of motility of the fauna. Dahl (1952) proposed three zones corresponding roughly to the three basic zones found on rocky shores: (1) a subterrestrial fringe characterized by *Ocypode* in warm areas and talitrid amphipods in cold areas, (2) a midlittoral zone on that part of the shore wetted by every tide and characterized by cirolanid isopods and (3) a sublittoral fringe with many species but no reliable indicators. Salvat (1964, 1966, 1967) proposed four zones; a zone of dry sand at the top of the beach, corresponding to Dahl's subterrestrial fringe, a zone of retention and a zone of resurgence, corresponding approximately to the upper and lower parts of Dahl's midlittoral zone and a zone of saturation at the bottom of the shore corresponding approximately to Dahl's sublittoral fringe.

Various workers have found Salvat's scheme to be reliable, particularly for isopods (Withers 1977; R. Bally pers. comm.) and Dahl's scheme has already been applied to East Cape beaches (McLachlan 1980d). The main differences between these two schemes are that Dahl's zones are defined biologically while those of Salvat are defined physically and that Salvat subdivides Dahl's middle zone. Broadly these schemes may be considered equivalent if Salvat's two middle zones are taken as equivalent to Dahl's midlittoral. Two points then warrant discussion. How is this subdivision of Dahl's central zone performed and what species or taxa may be considered indicators of the lowest zone? In answer to the second question it is proposed that benthoplanktonic mysids, of the genus *Gastrosaccus*, are good indicators of the lower shore. They occur on the saturated lower shore and subtidally, and where sampling has been thorough they have generally been recorded (Pearse, Humm & Wharton 1942; Gauld & Buchanan 1956; Brown 1971; Moran 1972; Dexter 1976, 1979; Withers 1977). Hippid crabs (*Emerita*, *Hippa*) may also indicate this zone in warm regions. It is also suggested that air-breathing isopods of the genus *Tylos* may be considered indicative of the subterrestrial fringe in temperate areas where they may often be abundant (Hamner, Smyth & Mulford 1969; Kensley 1974).

The question of subdivision of the midlittoral zone and indicators of this zone is more difficult. Eleftheriou & Jones (1976) have criticized the use of cirolanids as indicators of this zone because different species occupy different tidal levels. However, it can be said that on most open sandy beaches at least one cirolanid isopod will occur over all or part of the midlittoral. Further, within the midlittoral, isopods may exhibit the clearest zonation. In the present survey this has been the case with *Excirolana natalensis, Pontogeloides latipes* and *Eurydice longicornis*, which are clearly zoned from HW down to LW respectively. Molluscs show much less distinct zonation, possibly due to their lower motility. While upper and lower boundaries of the midlittoral can accurately be fixed at the existing drift line (high-tide swash line) and the boundary of saturated sand or glassy layer respectively, a boundary within the midlittoral is less clear. In some cases, particularly on more sheltered shores, faunal zonation may clearly indicate two zones within the midlittoral while in many cases it may be possible to distinguish between Salvat's zones of retention and resurgence only by monitoring pore-water flow and moisture contents.

Whether the midlittoral should be subdivided appears therefore to be a decision that should be made on the merits of each case. The three basic zones are, however, easily distinguishable biologically and physically on most shores and are best indicated by crustaceans. Because crustaceans exhibit the clearest zonation (Dahl 1952; Withers 1977) a simple tripartite zonation scheme is presented for southern African shores on this basis (Table 4). The terms of Lewis (1964) are used for the zones. Because of the dynamic nature of these beach environments this is of necessity a simplified scheme and almost all of the beach fauna undergoes normal tidal migrations as well as semilunar movements (Kensley 1974; McLachlan *et al.* 1979) which constantly alter zones, often resulting in blurring of boundaries.

Some species occupy different intertidal positions on different parts of the coast. *Donax serra* occurs on the lower shore and sublittoral on the west coast (de Villiers 1975) while on the south coast it occurs on the midshore during spring tides and on the lower shore during neaps (McLachlan *et al.* 1979). Further, juveniles occur above the adults on the west coast but below them on the south coast. *Tylos capensis* appears to extend its distribution landwards towards the eastern end of its range while the two eulittoral isopods, *Excirolana natalensis* and *Pontogeloides latipes*, appear to occupy a lower position towards the north-eastern parts of their ranges (Dye *et al.*

Table 4 Zonation scheme for southern African sandy beaches

	Boundaries		Indicator		
Zone	Upper	Lower	Subtropical	Warm Temperate	Temperate
Littoral fringe	Landward limit of supralittoral fauna	Lower edge of drift line	*Ocypode ryderi* *O. ceratophthalma*	*Tylos capensis* *Talorchestia quadrispinosa*	*Tylos granulatus* *Talorchestia capensis*
Eulittoral zone	Lower edge of drift line	Upper edge of saturated (glassy) layer	*Excirolana natalensis* *Pontogeloides latipes*	*E. natalensis* *P. latipes* *Eurydice longicornis*	*E. natalensis* *P. latipes* *E. longicornis*
Sublittoral fringe	Upper edge of saturated layer	No clear boundary; extends into surf zone	*Gastrosaccus bispinosa* *G. longifissura*	*G. psammodytes*	*G. psammodytes*

1981; Wooldridge *et al.* 1981). Further, almost all species studied in detail (*Donax* spp.: de Villiers 1975; McLachlan & Hanekom 1979; McLachlan *et al.* 1979; *Bullia* spp.: McLachlan, Cooper & van der Horst 1979; McGwynne 1980; *Gastrosaccus* spp.: Wooldridge 1981) exhibit a zonation of size classes with juveniles sometimes occurring above and sometimes below the adults.

The range of exposure experienced on open beaches around the southern African coastline is not very great and no beaches can be called sheltered. Beach slopes generally become steeper and sand coarser with increasing exposure. Macrofauna species numbers generally decrease with increasing exposure (Day 1959; McIntyre 1971) and abundance may often follow the same trend. Crustaceans may prefer more exposed localities while molluscs may be abundant at intermediate exposure. Supralittoral forms relying on the presence of a drift line (*Tylos, Talorchestia*) appear to benefit most from increasing exposure.

Some of the physical parameters related to exposure correlate significantly with faunal richness and abundance if data from McLachlan (1977b, c), Dye *et al.* (1981) and Wooldridge *et al.* (1981) are included in the analysis. Species numbers show highly significant correlations ($P < 0{,}001$) with median particle diameter (Figure 12) and the reciprocal of beach slope (Figure 13). Total macrofaunal abundance also correlates ($P < 0{,}001$) with both particle size (Figure 14) and reciprocal of slope (Figure 15). No other significant relationships were found between macrofaunal richness, abundance or biomass and exposure rating or any other beach parameters monitored.

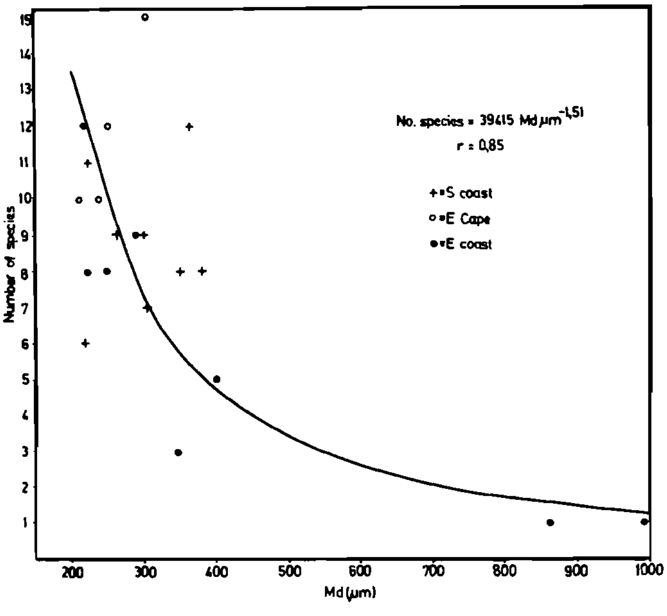

Figure 12 The relationship between macrofauna species diversity and median particle diameter. Details as for Figure 10.

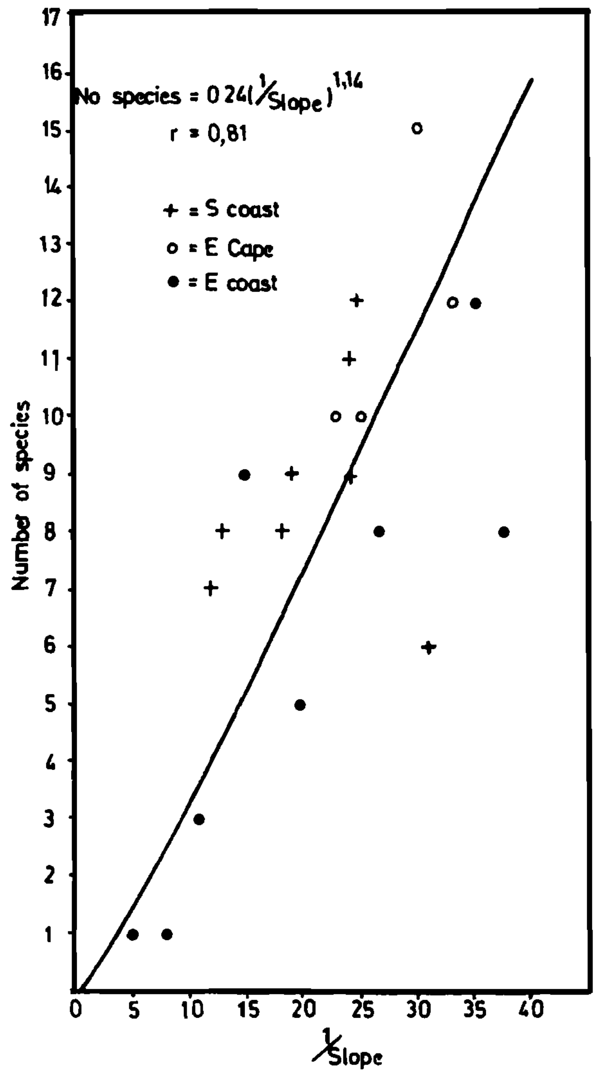

Figure 13 The relationship between macrofauna species diversity and the reciprocal of beach slope. Details as for Figure 10.

For the range of beaches covered in these surveys ('exposed' to 'very exposed') the maximum number of species predicted is 16 at a slope of 1/40 (Figure 13) and 14 at a median particle diameter of 200 µm (Figure 12). Only one species, presumably a supralittoral form, is predicted to occur on beaches with substrate coarser than 1 mm (Figure 12) or slope steeper than 1/5 (Figure 13). This corresponds with the relationship between slope and particle size (Figure 10). In practice the actual number of species present may be higher than predicted as most of the data used in these plots is based on single surveys and repeated sampling might record more species. Maitland River beach (McLachlan 1977c) for example, has been intensively studied over several years and 15 species have been recorded, while Figures 12 and 13 predict only 8 and 10 species respectively.

Macrofaunal abundance shows essentially the same relationship to slope and particle size as does faunal richness; numbers increase markedly below a particle size of 300 µm and at a slope flatter than 1/25. Very low numbers occur when the sand is coarser than 400 µm or the beach steeper than 1/10. At a particle size of 240 µm and slope 1/32 about 3 000 macrofaunal organisms are estimated per metre shoreline. Undoubtedly food availability must be an important factor here but it has not been estimated in this study.

If the increase in abundance with flatter slopes was simply a function of increasing intertidal distance, i.e. available space, a linear relationship would be expected

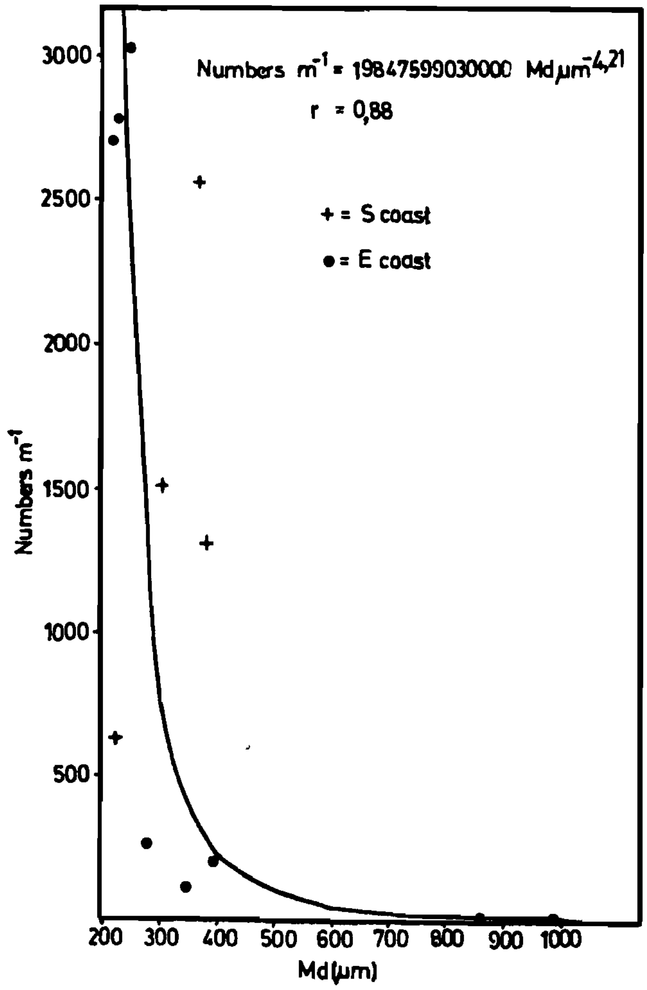

Figure 14 The relationship between macrofauna abundance and median particle diameter. Details as for Figure 10.

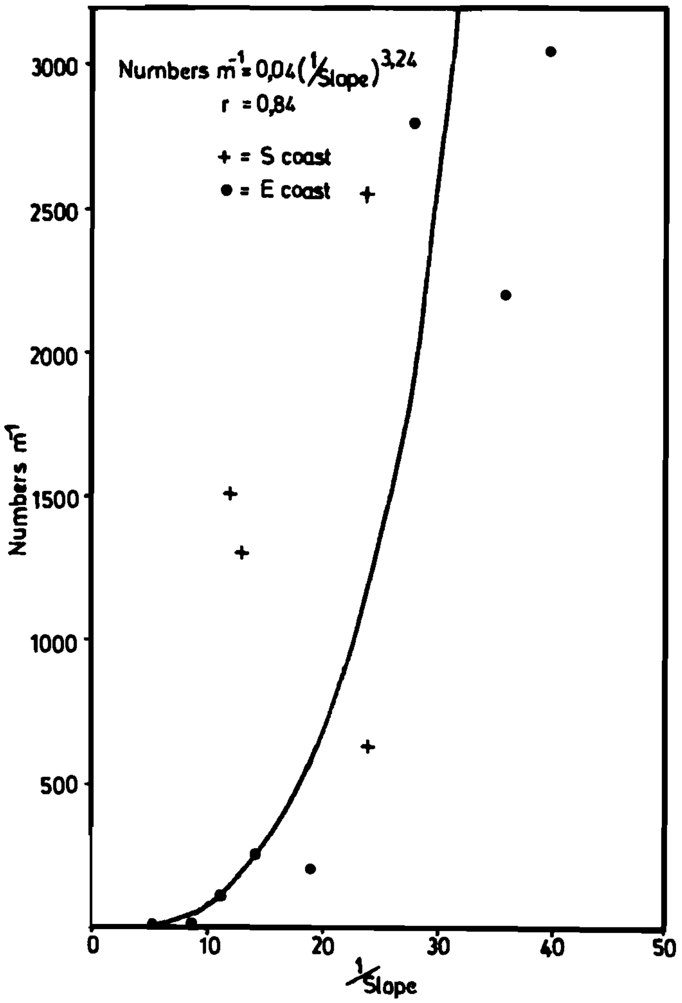

Figure 15 The relationship between macrofauna abundance and the reciprocal of beach slope. Details as for Figure 10.

between reciprocal of slope and numbers per unit area (m^{-2} as opposed to m^{-1}). However, the highly logarithmic nature of this curve (Figure 15) shows this not to be the case. Further, a significant relationship can be obtained even if reciprocal of slope is regressed against numbers per metre square ($P < 0,05$).

McIntyre (1971) recorded a steady decrease in macrofauna with increasing exposure from nearly 35 species and a high biomass at a median particle diameter of 150 μm to less than five species and a very low biomass at a median particle diameter over 300 μm on Scottish beaches. He also found molluscs disappearing first with increased exposure and the more mobile crustaceans being the most persistent. Day (1959) found the same pattern in Langebaan Lagoon. It may therefore be concluded that with increasingly coarser grained and steeper beaches macrofauna becomes poorer in both species and abundance and that molluscs disappear rapidly while crustaceans, by virtue of their greater mobility, decline more slowly. As grain size and consequently steepness tend to increase with exposure this faunal response follows an exposure gradient although it appears that it is not exposure directly so much as coarseness of sand and steepness of slope, i.e. instability, that inhibits macrofauna. Thus Maitland River beach (McLachlan 1977c) for example, although being very exposed (rating = 16), has an extremely rich macrofauna because it has sand that is not too coarse (300 μm) and a slope that is not too steep ($\simeq 1/29$).

The effects of estuaries on psammolittoral animals appear to be minimal and most species penetrate a little way into estuary mouths. Wooldridge (1978) recorded *Gastrosaccus bispinosa* and *G. longifissura* inside the mouth of the Mgazana estuary, Transkei, and Branch & Grindley (1979) recorded *Donax serra, Hippa adactyla, Ocypode* sp., *Pontogeloides latipes* and *Eurydice longicornis* in the same estuary. Further south in Algoa Bay MacNae (1957) found *D. serra* and *D. sordidus* inside the Swartkops estuary mouth. In these cases salinities generally remain high in the mouth regions. Reduced water movement and finer substrates are therefore probably the main factors limiting penetration into the mouth regions of estuaries by psammolittoral fauna.

Meiofauna

Insufficient taxonomic work has been done on psammolittoral meiofauna in southern Africa for generalizations to be made below the levels of higher taxa. Nevertheless some distinct trends in basic taxonomic composition do occur, particularly in relation to tidal level and substratum particle size. Using the data of McLachlan (1977b, c), Dye *et al.* (1981) and Wooldridge *et al.* (1981) the following general patterns emerge for the east and south coast of southern Africa. The average beach has a median particle diameter of 350 μm (or 285 μm if the coarse southern Natal beaches are ignored) and the average taxonomic composition is 38% nematodes, 38% harpacticoids, 10% turbellarians, 6% mystacocarids, 3% archiannelids, 2% oligochaetes and 3% minor groups.

Meiofaunal taxonomic composition bears a significant relationship to substratum grade as the percentages made up by the two co-dominant taxa both correlate with median particle diameter (in phi units);

$$\% \text{ Nematodes} = 8 + 19\phi \quad (r = 0{,}75;\ P < 0{,}01)$$

$$\% \text{ Harpacticoids} = 67 - 18\phi \quad (r = 0{,}60;\ P < 0{,}05)$$

Proportions of nematodes therefore decrease and harpacticoids increase with increasing particle size over the range 200 – 900 μm. Extrapolation of these lines suggests nematodes disappearing above a particle size of 1340 μm and harpacticoids disappearing below 70 μm. However, lower limits of particle size for interstitial harpacticoids, such as those referred to here, have already been set at 160 – 200 μm (Wieser 1959; McLachlan, Winter & Botha 1977; McLachlan 1978), indicating that extrapolation of these regressions outside the limits of the data is not valid. Intrapolation, however, gives median particle diameters of 334 μm and 330 μm for beach sands in which nematodes and harpacticoids respectively make up 38% of the meiofauna. It is therefore postulated that harpacticoids will be the dominant taxon in beach sands coarser than 330 μm, nematodes will dominate in finer sands and these two taxa will be about equally important in sands around 330 μm.

Although McIntyre (1971) suggests an inverse relationship between macrofaunal and meiofaunal abundance with the latter more important on more exposed beaches, abundance of these two groups was significantly positively correlated: meiofauna numbers ($\times 10^8 \text{m}^{-1}$) = 0,3ln (macrofauna numbers (m^{-1})) – 0,31 ($r = 0{,}66$; $P < 0{,}05$) over the beaches analysed. This is because both groups increase in abundance on more stable beaches and where food availability in the water is higher. Meiofauna do, however, tend to be less sensitive to greater exposure and coarser substrata than the macrofauna.

There also appears to be a significant trend for meiofauna to increase from northern Natal towards Cape Agulhas (Figure 16) and high densities are also reported along the west coast (H. Hennig pers. comm.). The most probable explanation for this is increased dissolved and particulate organic matter in the inshore water towards the southern and western coasts of southern Africa.

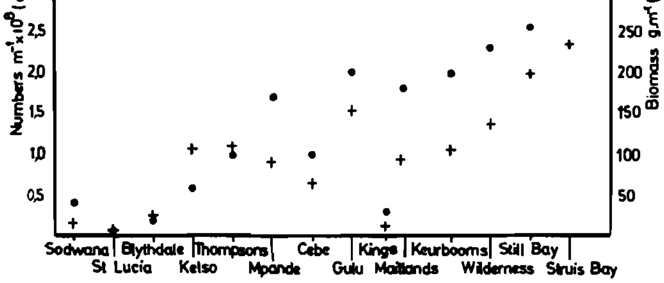

Figure 16 Meiofaunal abundance and biomass along the east and south coasts of southern Africa.

Distribution of the meiofauna within beaches tended to follow the stratification scheme proposed by McLachlan (1980d) although densities were not uniform along strata. The dry-sand stratum, the upper layers above HWN, harbours mostly small nematodes, adapted to living in films of water round the sand grains. In the moist-sand stratum, from here down to the permanent water table, a diverse and abundant meiofauna occurs, usually concentrated near MW where most intense circulation of the interstitial water occurs and here harpacticoids are most abundant. In the water-table stratum, at and just below the permanent water table, larger nematodes become more important and abundance drops. In the deeper low-oxygen stratum, which generally starts about 30 cm below the permanent water table, numbers drop off rapidly although there is usually no trace of reducing conditions and nematodes are the dominant group.

The very steep, coarse-sand beaches of southern Natal are difficult to fit into this scheme because of their very rapid drainage and unusual faunal composition. Basically, however, the strata tend to be compressed downshore. Although the desiccation gradient above the water table and oxygen profile below it basically determine these strata, interstitial water circulation patterns (Riedl 1971; Riedl & Machan 1972; McLachlan 1979) seem responsible for concentrating the meiofauna around that part of the beach where there is maximum percolation and food and oxygen input.

Trophic relations

On the basis of studies conducted on sandy beaches in the eastern Cape it has been proposed that the intertidal and subtidal sand bodies in conjunction with the overlying surf-zone water, out to the perimeter of surf cells of circulation, form a viable ecosystem (McLachlan 1980b; McLachlan *et al.* 1980). Rich surf zone phytoplankton is the major primary producer, macrofauna the consumer, interstitial fauna the decomposer and birds and fishes the transient predators. Southern African beaches may be examined in terms of this approach and the varying trophic structure in different areas.

Macrofauna food chains on exposed beaches fall into two categories: (1) particulate matter, including phytoplankton is consumed by filter feeders which in turn are eaten by birds, fishes and crabs and (2) stranded carrion is consumed by scavenger/predators which are also eaten by birds, fishes and crabs. It is generally assumed that along open beaches particulate food is in more constant and abundant supply than carrion and therefore that filter feeders dominate macrofaunal biomass (Brown 1964; Ansell *et al.* 1972; McLachlan *et al.* In press). Some distinct patterns in the relative proportions of these two trophic components as well as total biomass show the pattern to be more complicated along the southern African coast. This is summarized in Table 5. Filter feeders are absent or relatively sparse in those regions where surf phytoplankton development has not been observed distinctly (S. Natal, Transkei, N. Natal). Where more marked surf phytoplankton blooms have been observed, as on the south and west Cape coasts, filter feeders

Table 5 Macrofauna biomass and feeding types along the southern African coast

	N. Natal	S. Natal	Transkei	S. Cape	W. Cape
Macrofauna dry biomass (g m^{-1} transect)	10 – 90	20 – 30	10 – 100	20 – 7000	10 – >1000
% filter feeders	20	0	5	70	70
% scavenger/ predators	80	100	95	30	30

dominate. Further, biomass tends to increase as filter feeders become more important, suggesting that phytoplankton supply becomes more reliable. From a trophic point of view the sandy beaches of southern Africa may therefore be divided into two components: (1) The east coast (Natal and Transkei) with low biomass and a predominantly scavenging/predatory macrofauna and (2) the south and west coasts with moderate to high biomass dominated by filter feeders which may be fuelled partly by surf phytoplankton blooms. Crustaceans are more important both as scavengers and filter feeders in the warmer east coast regions.

Interstitial faunas, including meiofauna, protozoa and bacteria, generally have lower biomass but much greater activity than the macrofoauna. They are responsible for removing dissolved and particulate organic matter percolating through the interstices and they excrete nutrients which are important for enriching surf water for phytoplankton growth. Investigation of these important processes is one of the most promising lines of sandy beach research for the future. The interstitial fauna probably does not compete with filter feeders for food as it subsists mainly on dissolved organic matter. Although it is not eaten directly by the macrofauna it is important in the macrofauna food chain by producing nutrients that stimulate phytoplankton growth.

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