Interstitial meiofauna of Namib sandy beaches

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Interstitial meiofauna were sampled across the intertidal zone and into the sublittoral region on two exposed sandy beaches on the Namibian coast, Langstrand and Cape Cross. A transverse bar-rip beach configuration at Langstrand allowed a comparison between the distribution and abundance patterns at the horn and within the bay of the cusp formation on this beach. Of the eight major meiofauna groups, nematodes were widely distributed and always dominant. The crustaceans, harpacticoid copepods and mystacocarids, were prominent in the mid-shore at Cape Cross but occurred in low numbers at Langstrand , where archiannelids were abundant at mid-tide level. Notably high numbers of gastrotrichs (> 1000 per 100 cm^3) were found sublittorally at both beaches. Non-selective deposit feeders accounted for at least 58% of those nematodes examined from all stations, suggesting an abundant particulate food supply in coastal waters off South West Africa. Cape Cross supported the highest total meiofauna biomass followed by the Langstrand cusp horn and then cusp bay. A slightly elevated slope over a wide beach face, promoting rapid drainage and optimal oxygenation and food input, appeared as characteristics promoting meiofaunal colonization. These Namibian beaches could mark a zone of decline in the abundance of interstitial meiofauna which, from published work, appears to reach a maximum farther to the south.

Interstisiële meiofauna is oor die intergetygebied tot in die sublittoraal op twee blootgestelde sandstrande op die Namibiese kus, naamlik Langstrand en Cape Cross gemonster. 'n Strand- en brandersone met sandbanke loodreg met die strand en skeurstrome tussenin, was die heersende toestand by Langstrand. Hierdie konfigurasie het 'n vergelyking tussen die volopheid en verspreidingspatrone by die punt en die inham van die 'tand'-formasie by hierdie strand moontlik gemaak. Van die agt hoof meiofauna-groepe, was die Nematoda wyd verspreid en altyd dominant. Crustacea, Harpacticoida en Mystacocarida was prominent in die middestrand by Cape Cross, maar min het by Langstrand voorgekom waar Archiannelida by die mid-getyvlak volop was. Merkbare hoë getalle van Gastrotricha (> 1000 per 100 cm^3) is sub-littoraal by albei strande gevind. Nie-selektiewe bodemvoeders het minstens 50% uitgemaak van die Nematoda wat by al die stasies ondersoek is. Dit dui op ryk organiese voedselbronne langs die Suid-Wes Afrikaanse kus. Die hoogste totale meiofauna-biomassa is by Cape Cross gevind, gevolg deur die Langstrand 'tand'-punt, en dan die 'tand'-inhamgebied. 'n Effense helling oor 'n wye strand, wat vinnige dreinering en optimale suurstofbinding en voedseltoevoer bevorder, blyk eienskappe te wees wat kolonisasie van meiofauna begunstig. Volgens werk wat reeds gepubliseer is, blyk hierdie Namibiese strande te dui op 'n sone van afname in meiofauna volopheid, wat verder suidwaarts 'n maksimum bereik.

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Beaches around the southern tip of Africa are in general high energy, moderately sloping shores whose predominant surf zone/ beach morphologies are of the intermediate type (Short & Wright 1983). Northern east coast beaches are typically steep. Towards the southern and south-western coasts, more prominent surf zones, accompanied by strong wave action, tend to produce beaches with broad intertidal regions, sometimes backed by extensive dune systems.

Distribution patterns of intertidal organisms of southern African beaches have been well documented. Oliff, Gardner, Turner & Sharp (1970) and later Dye, McLachlan & Wooldridge (1981) described the meiofauna of some Natal beaches. Wooldridge, Dye & McLachlan (1981) published the only record of macro- and meiofaunal zonation on Transkeian beaches. The sandy beach fauna of Algoa Bay has been exhaustively studied by a research group at the University of Port Elizabeth who have reported on faunal distribution and abundances (McLachlan 1977a, b; 1980; McLachlan & Furstenberg 1977), behavioural adaptations (McLachlan, Wooldridge & Van der Horst 1979), as well as the biology of individual groups (McLachlan, Cooper & Van der Horst 1979; McGwynne 1984; du Preez 1983). Along the west coast, Brown (1964; 1971), Koop & Griffiths (1982), Bally (1983; 1987) and Griffiths, Stenton-Dozey & Koop (1983) recorded the faunal composition of local beaches. Those north of the Orange River, probably owing to their remoteness have largely been neglected. A faunal list for the Sandwich Bay harbour area was drawn up by Kensley & Penrith (1977) and later McLachlan (1985) and Tarr, Griffiths & Bally (1985) surveyed macro- and meiofauna on beaches around Walvis Bay and along the northern Skeleton coast up to the Kunene River respectively.

The initiation of a project on the wedge clam *Donax serra* by the Directorate of Sea Fisheries, South West Africa/Namibia, prompted research on the ecology of beaches harbouring them. A survey of two beaches near Swakopmund, designed to meet these needs, was conducted by a team of scientists from the Institute for Coastal Research at the University of Port Elizabeth. Patterns in the distribution and abundance of beach meiofauna, both intertidal and sublittoral, formed part of the larger project.

This paper reports on the findings of the meiobenthic

surveys and relates these trends to meiofauna distribution profiles previously recorded on beaches around southern Africa. This is the first study along the west coast where sampling for meiofauna has been continuous from the drift line out into the surf zone.

Study area

Sandy beaches constitute more than half of the Namibian coastline (McLachlan 1986). Upwelling occurs predominantly in three localized regions (Shannon 1985) which did not include the beaches of this study. Tides are subequal semidiurnal. The tide range is about 2 m at springs, averages 1,4 m and is 0,7 m at neaps. The annual temperature range of the water is 14–16°C (McLachlan 1986).

Two beaches, north and south of Swakopmund, were selected as study areas (Figure 1). Cape Cross (21°50′S / 14°02′E) is a relatively undisturbed high-energy beach supporting a well developed surf zone and bordered landwards by a berm which extends into a vast salt pan. Langstrand (22°04′S / 14°10′E) is a long, easily accessible, moderate-energy beach partly protected by Pelican Point, which forms the eastern tip of Walvis Bay. Its proximity to the city renders it vulnerable to heavy human disturbance. It is backed by a road and public facilities, behind which large dunes blend with the desert.

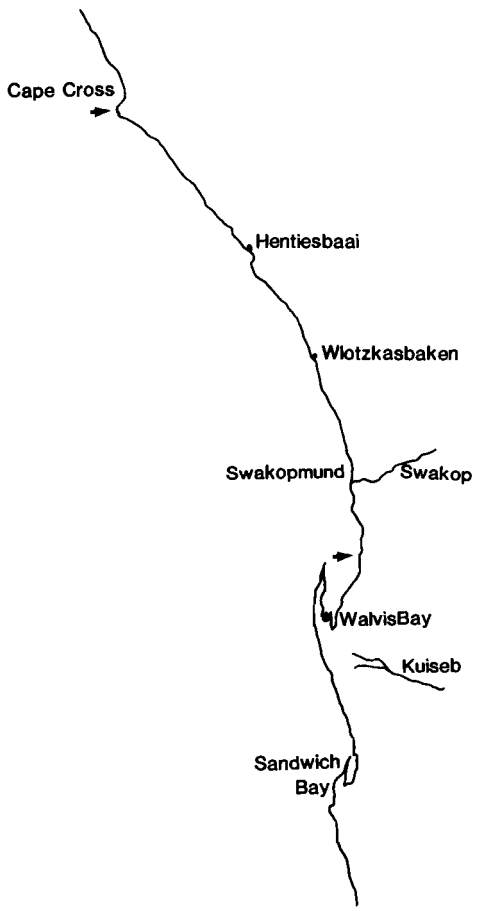

Figure 1 Map of the Namibian coastline indicating the position of the study beaches.

At the time of sampling, the beach state at both Cape Cross and Langstrand was intermediate (Knoop, Talbot & Bate 1986). Strong wave action at Cape Cross created a crescentic bar beach with megacusp embayments and horns situated approximately 200–400 m apart. The intertidal zone appeared as a fairly uniform stretch of beach. At the less exposed Langstrand site the general morphology and inshore surf zone circulation pattern was a transverse bar-rip system tending towards a low tide terrace. Alternating transverse sand bars and rip channels in the surf zone produced an uneven intertidal topography. Crescent-shaped cusps were characterized by wide scalloped bays and high, narrow, flanking horns, the latter approximately 100 m apart.

Patterns of distribution of intertidal macrobenthos were similar at both study beaches. Scavenging isopods *Excirolana natalensis* and *Tylos granulatus* and the amphipod *Talorchestia quadrispinosa* dominated the upper regions, whereas the mid-reaches supported the polychaete *Scolelepis squamata* and isopods *Eurydice longicornis* and *Pontogeloides latipes*. The lower intertidal and shallow sublittoral zones were occupied by the mysid *Gastrosaccus namibensis* and two phoxocephalid amphipods. The wedge clam *Donax serra* fluctuated its position between the low and mid intertidal (Donn 1986).

The distribution of sublittoral macrobenthos at Cape Cross is unknown owing to difficulties caused by heavy seas at the time of sampling. At Langstrand the macrobenthos included three polychaete species, *Diopatra n. neopolitana, Glycera convoluta* and *Nepthys hombergi,* nemertean worms, amphipods, isopods and mysids; two species of mollusc were also present (Cockcroft 1986).

Methods

The regular beach morphology at Cape Cross allowed the selection of a single representative transect, 30 m long in the intertidal zone, divided into six equidistant stations from HWS (high water spring tide) to LWS (low water spring tide). Rough seas permitted sublittoral meiofaunal sampling to a water depth of 3 m only. The cuspate morphology of the intertidal zone at Langstrand necessitated sampling both within the bay and at the horn of a single cusp. Two transects, 24 m and 15 m in length from HWS to LWS with stations every 6 m and 3 m respectively, were chosen at this beach. These transects extended into the sublittoral zone to a water depth of 3 m opposite the horn and 5 m opposite the bay of the cusp. Stations selected below LWS corresponded to water depth intervals of 1 m instead of horizontal distance from LWS.

Sampling was conducted during LWS. Intertidally, four replicate sediment cores were taken at 15 cm vertical intervals into the sand reaching down to the water table. In the sublittoral zone, cores 10 cm long extended to a depth of 20 cm. Corers with internal cross-sectional areas of 10 cm^2 and 6 cm^2 were used for sampling in the intertidal and sublittoral zones respectively. Two of the four cores from each sampling

Table 1 Physical characteristics of the study beaches. Intertidal stations were measured as distances below HWS and sublittoral as water depth intervals. Substrate particle size parameters are given in phi-units.

	Station	Beach slope	Md Ø	Qd Ø	Skq Ø	Mz Ø	i Ø	Sk_i Ø	Org. (%)	Porosity (%)	Water table depth (cm)
Cape Cross											
Intertidal	HWS	1/14	1,55	0,33	–0,03	1,53	0,46	–0,03	0,28	23,0	145
	24 m		1,65	0,30	–0,05	1,63	0,45	–0,05	0,25	21,7	100
	18 m		1,35	0,43	–0,03	1,30	0,65	–0,17	0,23	22,0	67
	12 m		0,95	0,53	–0,02	0,93	0,70	0,02	0,22	20,6	50
	6 m		0,65	0,75	0,10	0,82	0,78	0,34	0,27	17,3	24
	LWS		0,60	0,63	0,03	0,70	0,66	0,28	0,24	19,6	13
	Beach mean (μm)		457			451					
Sublittoral	1 m	1/40	1,18	0,87	–0,11	1,01	1,13	–0,25	0,10	16,1	
	2 m		2,38	0,28	0,01	2,37	0,42	–0,06	0,12	20,9	
	3 m		2,47	0,26	0,07	2,41	0,46	–0,21	0,15	21,3	
	Beach mean (μm)		248			262					
Langstrand (Horn)											
Intertidal	HWS	1/10	1,70	0,35	0,00	1,68	0,49	0,04	0,24	20,6	88
	12 m		1,80	0,30	0,05	1,82	0,44	0,06	0,38	21,5	62
	9 m		1,80	0,35	0,00	1,78	0,50	–0,03	0,22	20,3	32
	6 m		1,95	0,40	0,00	1,97	0,70	0,21	0,25	20,1	17
	3 m		1,65	0,45	–0,05	1,65	0,64	0,02	0,24	19,6	14
	LWS		1,35	0,50	0,10	1,42	0,67	0,17	0,23	18,7	8
	Beach mean (μm)		306			303					
Sublittoral	1 m	1/40	2,01	0,42	0,04	1,98	0,62	–0,11	0,40	17,3	
	2 m		1,85	0,47	0,04	1,80	0,57	0,15	0,39	17,3	
	3 m		1,80	0,50	–0,02	1,77	0,68	–0,06	0,35	17,4	
	Beach mean (μm)		270			277					
Langstrand (Bay)											
Intertidal	HWS	1/16	2,10	0,33	–0,03	2,13	0,53	0,12	0,23	19,8	73
	18 m		2,05	0,30	0,00	2,07	0,52	0,04	0,25	20,4	40
	12 m		2,00	0,27	0,02	1,98	0,46	–0,07	0,23	20,6	27
	6 m		1,95	0,33	0,02	1,97	0,48	0,00	0,27	18,1	17
	LWS		1,70	0,45	–0,05	1,63	0,64	–0,11	0,24	20,4	10
	Beach mean (μm)		259			259					
Sublittoral	1 m	1/39	1,49	0,43	0,02	1,51	0,61	0,06	0,33	16,6	
	2 m		1,63	0,48	–0,02	1,61	0,66	–0,01	0,32	17,4	
	3 m		1,49	0,48	0,04	1,51	0,64	0,08	0,21	16,4	
	5 m		2,61	0,21	–0,03	2,57	0,41	–0,19	0,21	20,8	
	Beach mean (μm)		285			287					

level were pooled to reduce sample numbers and 100 cm^3 was taken from each pooled core for analysis. Meiofauna were killed with 5% formalin and extracted by four decants through a 63 μm screen, stained in Rose Bengal and counted to major taxa. Counts were corrected for 90% extraction efficiency (McLachlan 1978). Dry biomass was calculated by using mean individual dry mass values for the main taxa determined for similar sands (McLachlan, Wooldridge & Dye 1981). The values used were: nematodes 0,8 μg; harpacticoid copepods 0,4 μg; turbellarians 1,0 μg; oligochaetes 1,0 μg; archiannelids 1,0 μg; gastrotrichs 0,3 μg; polychaetes 0,5 μg and mystacocarids 0,5 μg.

Sub-samples of nematodes from each station (7–236

worms) were classified into feeding groups based on the structure of their buccal cavities (Wieser 1953; Warwick 1981). The categories were 1A: selective deposit feeders with no buccal cavity; 1B: non-selective deposit feeders with an unarmed buccal cavity; 2A: epigrowth feeders with a buccal cavity armed with small teeth and 2B: predators with a large strongly armed buccal cavity often with hooked teeth. This last group may not be exclusively carnivorous and has been considered omnivorous with a capacity for predation (Heip, Vincx, Smol & Vranken 1982).

Sand samples were also analysed for porosity (mass of water required to saturate 100 cm^3 dry sand), organic content (mass loss of dried sand on ashing at 500°C for 6 h) and particle size parameters by sieving and plotting phi-cumulative curves (Folk 1974).

Results and Discussion

Physical features

The slope of the intertidal zone at Cape Cross was moderately steep (1/14) while sublittorally the profile declined gradually seawards with a slope of 1/40. The beach sediment was moderately well-sorted, slightly coarse-grained sand with a mean particle diameter of 451 μm. At Langstrand the slope of the cusp horn was steep at 1/10 and the bay moderately steep (1/24). The mean particle size within the bay (259 μm) was slightly finer than at the horn (303 μm). The chief physical characteristics of each study site are shown in Table 1.

Cusp horns are generally characterized by coarse sand, steep slopes, maximum swash up-surge at high current velocities, low water tables and high sediment percolation rates (McLachlan & Hesp 1984). Cusp bays, in contrast, have fine sand, shallow slopes, maximum backwash surge resembling a mini-rip, higher water tables and low sand percolation rates. For Cape Cross and Langstrand, the mean porosity of the sand was 19%. Salinities at the water table were always that of the sea; no freshwater drainage occurred from the land.

Meiofauna: Taxonomic composition

Eight meiofaunal taxa were identified on each beach viz. nematodes, harpacticoid copepods, mystacocarids, archiannelids, polychaetes, turbellarians, gastrotrichs and oligochaetes. The mean densities of the major groups are shown in Table 2. Nematodes were almost always dominant except in the surf zones at Cape Cross and Langstrand horn, where harpacticoids and gastrotrichs respectively were well represented.

Harpacticoid copepods are usually the second most abundant meiofaunal taxon in marine sediments (Hicks & Coull 1983) with free-living nematodes regularly ranking first (McIntyre 1969). At Paaltjies (a beach a few kilometres south of Walvis Bay) and Langstrand, McLachlan (1985) recorded proportions of the major meiofaunal groups similar to those presented here, despite the differing degrees of exposure. At three sites along the northern Skeleton Coast, Toscanini, Hoarusib and Bosluisbaai, Tarr *et al.* (1985) found low numbers of nematodes and platyhelminths in surface sand samples and only small isolated groups of harpacticoids, acarines and isopods.

The 'average' South African beach has a median particle size of 350 μm and a taxonomic composition of 38% nematodes, 38% harpacticoids, 10% turbellarians, 6% mystacocarids, 3% archiannelids, 2% oligochaetes and 3% minor groups (McLachlan *et al.* 1981). The proportions of the major meiofaunal groups appearing on the Namibian beaches studied here show some deviation from these.

The only records of sublittoral distribution of meiofauna around the southern African coast are those of McLachlan, Winter & Botha (1977), McLachlan, Cockcroft & Malan (1984) and Malan & McLachlan (1985) at King's and Sundays River beaches. Nematodes made up the major part of the meiofauna (80%) with turbellarians and harpacticoids contributing less than 10%.

Distribution and abundance

Distribution profiles are shown in Figures 2–4. Where densities in the sublittoral are very low, profiles for a particular group extend only to the LWS mark. At Cape Cross (Figure 2) the lower reach of the beach, which comprised coarse-grained sediment with a mean particle size range of 525–616 μm, was almost devoid of meiofauna. Immediately above this area (346–406 μm),

Table 2 Mean densities (100 cm^{-3} ± *SE*) of the major meiofaunal groups at each transect

Beach	Nematodes	Copepods	Turbellarians	Mystacocarids	Gastrotrichs	Oligochaetes	Nauplii
Cape Cross							
Intertidal	152 ± 91	61 ± 41	24 ± 11	110 ± 100	1 ± 0,5	57 ± 28	–
Sublittoral	168 ± 46	1213 ± 573	75 ± 17	–	305 ± 108	2 ± 1	176 ± 66
Langstrand (Bay)							
Intertidal	514 ± 107	61 ± 24	8 ± 2	31 ± 25	7 ± 5	185 ± 113	–
Sublittoral	757 ± 259	38 ± 22	140 ± 34	–	554 ± 224	79 ± 47	–
Langstrand (Horn)							
Intertidal	659 ± 78	176 ± 42	22 ± 7	213 ± 133	5 ± 2	115 ± 75	–
Sublittoral	349 ± 33	6 ± 0,8	91 ± 30	–	865 ± 128	21 ± 4	–

animals appeared clustered around the 18 mark. Other groups on the beach included gastrotrichs, archiannelids, turbellarians and polychaetes. In the sublittoral zone, nematode numbers never attained the densities of the beach populations. Although only the top 20 cm of sediment was sampled, it is probable that at least 75% of the meiofauna were included in the samples (Tietjen 1971; McIntyre & Murison 1973; Emmerson, McLachlan, Watling & Watling 1983). Minor groups here included nauplii larvae, oligochaetes and turbellarians.

At Langstrand along the steeply sloping cusp horn (Figure 3) three groups, nematodes, archiannelids and oligochaetes appeared to each dominate the intertidal zone in a step-wise gradation from HWS towards LWS.

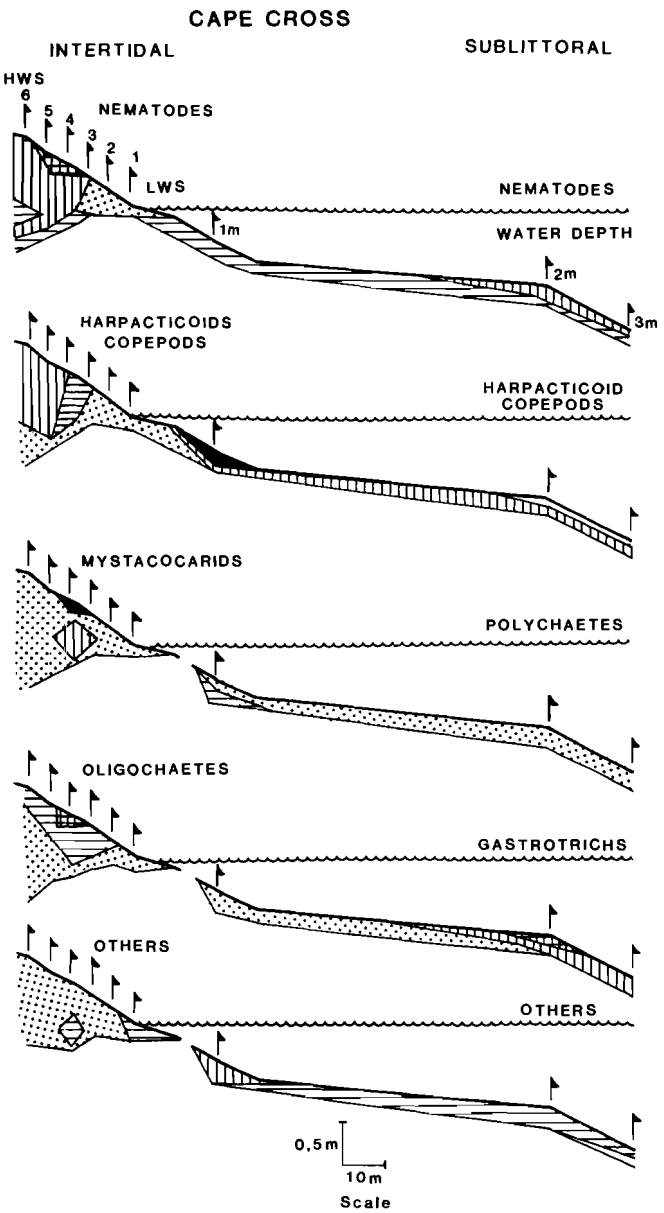

Figure 2 Distribution and abundance profiles of the major meiofaunal groups at Cape Cross from HWS to the sublittoral extremity during spring low tide. Note that these profiles are not always continuous owing to the low numbers of some groups either on the beach or below LWS. Flags indicate sampling stations. Key represents numbers per 100 cm^3 sand.

Within the bay (Figure 4), meiofauna were more evenly distributed. Profiles generally followed the zonation and stratification scheme described by McLachlan (1980). Total meiofauna numbers at the cusp horn were estimated at 33,8 × 10^6 m^{-2} compared to 15,5 × 10^6 m^{-2} within the bay. The horn thus supported more than double the meiofauna found in the bay. Sublittoral densities between these regions were similar (mean 8,69 ± 0,06 × 10^6 m^{-2}).

In a study of meiofaunal distribution and abundance patterns on a cuspate beach in Western Australia, McLachlan & Hesp (1984) found all groups to exhibit the lowest densities at the cusp horn and maximum abundances in the surface sand on either side of the rip axis line bisecting the bay. The location of maximum density zones differed between taxa. These patterns were attributed to an active avoidance of the cusp horn and a weaker but still marked avoidance of the bay midline. At Langstrand, the transects chosen in the

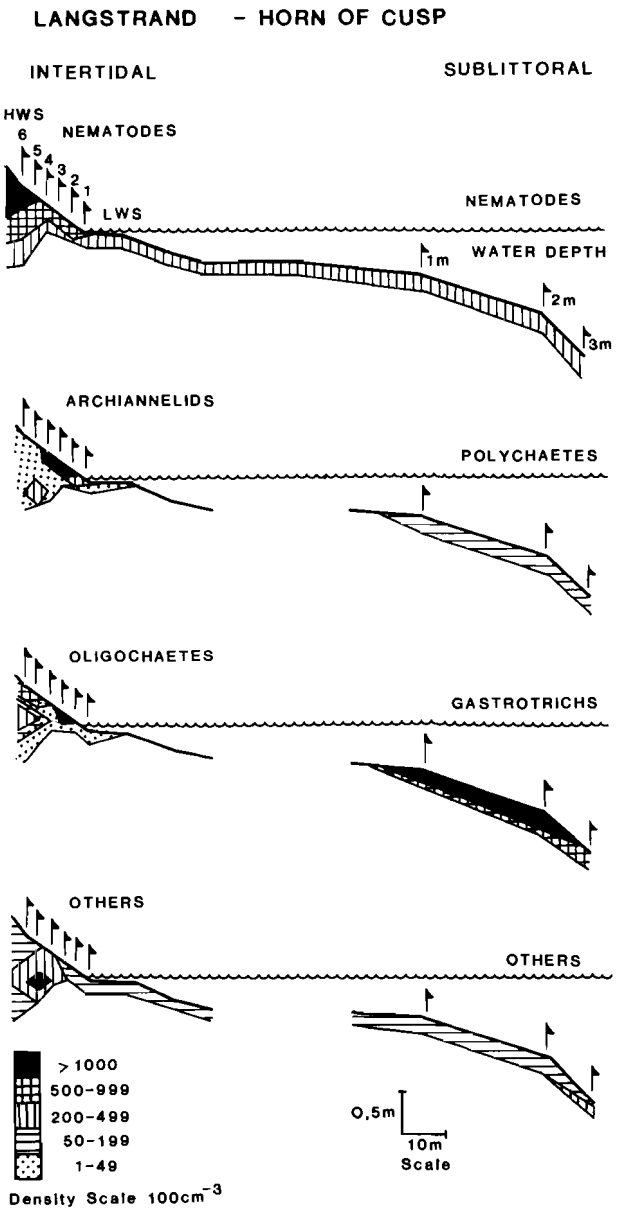

Figure 3 Langstrand, horn of cusp. Legend as for Figure 2.

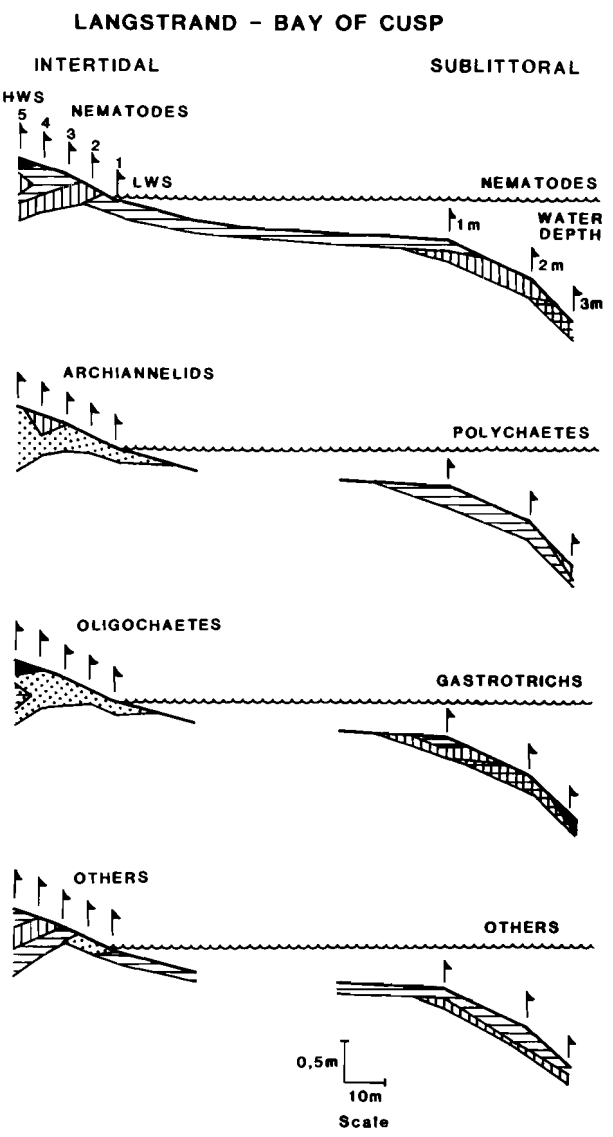

Figure 4 Langstrand, bay of cusp. Legend as for Figure 2.

centre of the cusp bay and along the ridge of the horn prevented the detection of any preferential zones. However, the greater abundance of organisms along the cusp horn does present a situation contrary to that of McLachlan & Hesp.

Water circulation patterns and current speeds associated with beach cusps probably play a major role in determining the distribution of interstitial meiofauna. Backwash from the two adjacent horns, following a swash surge, meets in the centre of the cusp bay and flows seawards as an intense mini-rip current, generating water speeds probably excessive for meiofaunal habitation. The optimal zone seemingly depends on a web of inter-related factors.

Accumulations of seaweed wrack (4,68 g m^{-2} dry mass) were recorded at the drift line of the bays (Van der Merwe 1986). Particulate organic matter emanating from wrack decomposition probably provides a large food input into the upper reaches of the bay region so concentrating meiofauna higher on the shore and away from the midline to an area where current surges are less vigorous. Organic detritus and phytoplankton particulates from the open ocean pumped into the interstices via swash action would constitute an additional food resource to the bay, while probably acting as the primary source of nutriment at the horn. Horns receive on average 1,3 times the number of swashes as bays (McLachlan & Hesp 1984) and generally support coarser sediment which faciliates rapid drainage. These areas pose as zones of greater agitation, although probably receiving a larger water-borne food supply. A balance between water infiltration rates, residence times and food content probably operates within specific zones of the cusp formation, which regulates the distribution and abundance patterns of the interstitial organisms.

Nematode feeding types

Deposit feeders, particularly non-selective ones, were generally the most well-represented group (Table 3). No discernible trend in feeding type occurred with horizontal or vertical space on the beaches. The predominance of deposit feeders could indicate an abundance of particulate food in inshore waters off the Namibian coast or may signify the importance of wrack decomposition products as a major food source. McLachlan & Furstenberg (1977) found epigrowth and then non-selective deposit feeders most abundant on two South African east coast beaches.

Biomass

From LWS, biomass at each beach increased dramatically up the shore (Figure 5) whereas seawards the increase was slow and gradual, never reaching that of the intertidal zone. This point of lowest biomass seemed to demarcate a boundary between the intertidal and sublittoral meiofauna communities, not only in terms of total biomass, but also in taxonomic composition. The communities characterizing each environment appeared to be distinct entities with few groups successfully exploiting both areas.

The availability of oxygen has been indicated as the 'super parameter' affecting the abundance of interstitial meiofauna (McLachlan 1977b, 1978). LWS is a band where sand is saturated and drainage and thus oxygen and food input into the sand interstices are sufficiently low to limit the meiofauna carrying capacity of the sediment. This zone is thus generally characterized by low faunal biomass (McLachlan 1977b, 1980) which increases sometimes dramatically landwards and more gradually seawards of this point. The biomass maxima for sublittoral meiofauna at the Namibian sites are within the range of values measured off other South African sandy beaches (Malan & McLachlan 1985).

The total meiofaunal biomass across a 1-m strip of the intertidal zone was the highest at Cape Cross (71,4 g m^{-1}) while at Langstrand, the total biomass estimate at the short steep horn (62,1 g m^{-1}) was greater than that within the bay (50,8 g m^{-1}). At a third steep (1/13) Langstrand transect, McLachlan (1985) measured a total biomass of 77,0 g m^{-1}, an estimate considerably lower than the 193,0 g m^{-1} recorded at Paaltjies, a broad, gently sloping (1/24)

Table 3 Percentage relative abundance of the four nematode feeding groups at the upper and lower shores of each study beach

Beach	Station	Deposit feeders		Epigrowth	Predators	*n*
		Selective	Non-selective			
Cape Cross						
Intertidal						
	upper shore	25	69	1	5	345
	lower shore	30	30	15	25	20
Sublittoral		10	59	17	14	237
Langstrand (Horn)						
Intertidal						
	upper shore	14	54	24	8	650
	lower shore	24	68	7	1	270
Sublittoral		17	60	9	13	399
Langstrand (Bay)						
Intertidal						
	upper shore	10	60	3	27	589
	lower shore	8	85	7	0	168
Sublittoral		14	56	5	25	304

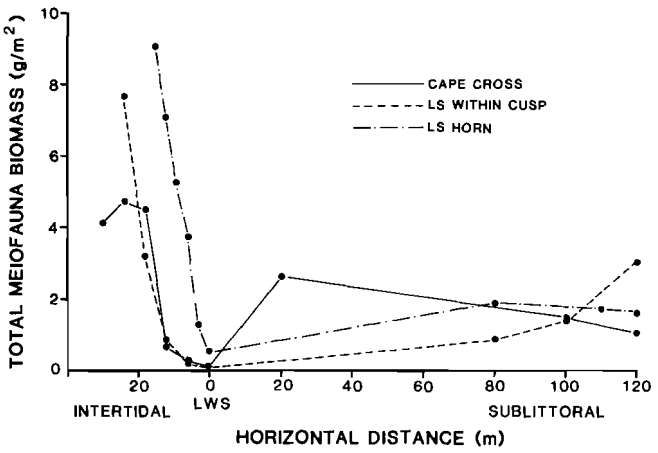

Figure 5 Distribution of the total biomass of all meiofauna groups across the three study sites from HWS to a water depth of 3 m.

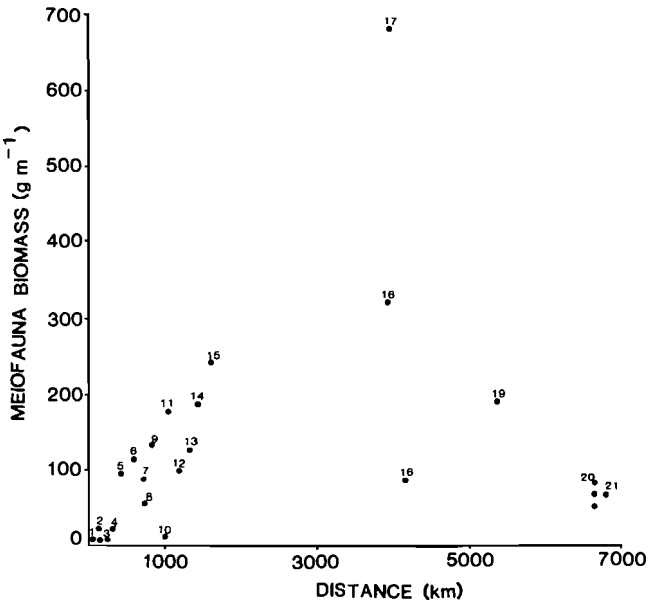

Figure 6 Meiofauna biomass estimates from the intertidal zone of beaches around the southern African coast. Beaches 1–5, 19 and one site at 20 were studied by McLachlan *et al.* (1981) and McLachlan (1985) and beaches 16–18 by Bally (1981); numbers 20 and 21 are the sites of this study. Values represent biomass estimates across a 1 m wide strip of beach from HWS to LWS extending down to the water table. Spacing on the x-axis marks the approximate distance between beaches. Bhanga Nek at the north-eastern extremity is the starting point at distance = 0. The beaches are as follows: 1. Bhanga Nek, 2. Sodwana Bay (2 sites), 3. St Lucia, 4. Blythdale, 5. Kelso, 6. Thompsons lagoon, 7. Mpande, 8. Cebe, 9. Gulu, 10. Kings, 11. Maitlands, 12. Keurbooms, 13. Wilderness, 14. Still Bay, 15. Struisbaai, 16. Melkbosstrand, 17. Ysterfontein, 18. Rocherpan, 19. Paaltjies, 20. Langstrand (3 sites), 21. Cape Cross.

beach. Differences between these five estimates, all within the vicinity of Walvis Bay, serve to re-emphasize the significance of the delicate balance between beach length and slope to provide adequate drainage and, therefore, sufficient oxygenation and food input into the interstitial environment. This balance appears to dictate the meiofauna carrying capacity of the intertidal sediment. In atidal or sublittoral sands, biological interactions such as competition and predation probably play a more determinative role (McIntyre 1971; Hulings & Gray 1976).

Conclusion

Sandy beaches of the southern African coastline appear in a wide range of slopes, mean grain sizes and exposure. McLachlan *et al.* (1981) noted an apparent increase in

interstitial meiofaunal biomass towards the west coast (Figure 6) which they attributed to a potentially higher concentration of dissolved and particulate organic matter in inshore waters of this region. The intertidal deposition and subsequent decomposition of algal wrack and the presence of epipsammic phytoplankton are also potential sources of food for interstitial organisms, particularly oligochaetes and nematodes (Giere & Pfannkuche 1982; Heip, Vincx & Vranken 1985). Ignoring factors such as predominant food source and beach length, the observation of McLachlan *et al.* (1981) is further supported by high biomass estimates subsequently recorded by Bally (1981) on three beaches north of the Cape Peninsula.

Although the biomass recorded at Paaltjies beach in Namibia (McLachlan 1985) was relatively high, the consistently lower values (mean 65 ± 10 g m^{-1}, $n = 4$) measured on other Namibian beaches suggest that the interstitial biomass carrying capacity of the sediment starts to decline northwards of the mid South West African coast. A considerable degree of variation exists between published estimates and an extensive gap in meiofauna records is prominent north of St Helena Bay on the west coast. Meiofauna surveys of beaches in this region could establish the validity of the apparent distribution trend.

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