COMPOSITION, DISTRIBUTION, ABUNDANCE AND BIOMASS OF THE MACROFAUNA AND MEIOFAUNA OF FOUR SANDY BEACHES

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ABSTRACT

The macrofauna and meiofauna have been investigated quantitatively on four exposed sandy beaches of medium quartz sands. Of the 12 macrofauna species recorded, two bivalves (*Donax* spp.) and one gastropod (*Bullia rhodostoma*) made up the bulk of the numbers and biomass values on all beaches. Macrofauna biomass values were 0,01 - 316,46 g/m² on an ash-free, dry mass basis. Diversity index values for the macrofauna were low and on all beaches decreased from LW to HW irrespective of the distribution of densities. Similarity analysis indicated three faunal assemblages, which were less related to tidal heights than to quantities of available food. High meiofauna numbers were recorded (152 - 7056/10 cm²) and these were made up mainly of crustaceans (48%) and nematodes (44%). Meiofauna ash-free dry biomass values were 0,08-3,36 g/m². On all beaches the meiofauna tended to be concentrated at those tide levels where a moderate, but not extreme, degree of desiccation of the sand occurred. Biomass values of macrofauna and meiofauna were extrapolated to 1 m transects of beach giving macrofauna values of 17,5-16553,3 g/transect and meiofauna values of 13,8-76,0 g/transect. Production estimates based on these biomass values indicated that the meiofauna dominated two beaches and the macrofauna two beaches. Two general conclusions are discussed, namely that the meiofauna and macrofauna on these beaches are quite distinct faunal components in all respects, and that the meiofauna, although not part of the macrofauna food chain, are nevertheless of great quantitative importance in the flow of energy.

INTRODUCTION

Sandy beaches are unstable, often very exposed environments that generally have impoverished macrofaunas but abundant, stable and diverse meiofaunas (McIntyre 1968, 1969; McIntyre & Murison 1973; McLachlan 1977b). Renaud-Debyser & Salvat (1963), McIntyre (1968), Nagabhushanam & Rao (1969), Gray & Rieger (1971) and Thomassin *et al* (1976) have studied both the macrofauna and meiofauna of psammolittoral environments but none of these authors has taken comparisons further than abundance in terms of numbers. Comparisons on the basis of numbers favour the meiofauna while biomass comparisons favour the macrofauna and ecologically significant comparisons should be based on production or energy flow values. Such comparisons would necessitate very long term study and for practical purposes the best comparison is on the basis of production values estimated from biomass values and a knowledge of turnover rates (McIntyre 1964; Arlt 1973; McLachlan 1977b). McLachlan (1977b) did this for two beaches and found that the meiofauna made up significant percentages of the total metazoan production in both cases. The present work is an attempt to supplement this data by investigation of a further four beaches, including one beach with an extremely rich macrofauna.

METHODS

The study area

The four beaches investigated are all in the vicinity of Algoa Bay (Figure 1), and consist of medium to fine quartz sands with a high calcium carbonate content. They experience a maximal spring tidal range of 2,1 m and a sea temperature range of 12-25°C. Maitland River beach and Sardinia Bay beach A, both south of Algoa Bay, are very exposed to the southern ocean swells while St Georges Strand and Sardinia Bay B beaches receive some shelter from the headland of Cape Receife and a large offshore reef respectively. Although pollution is not visible, St Georges Strand may be slightly enriched by sewage drifting northwards from outlets near the Port Elizabeth harbour (McLachlan, Winter and Botha 1977). The range of physical and chemical conditions found on Algoa Bay beaches has been described by McLachlan (1977a) and only the most important features will be analysed here.

Sampling

Each beach was sampled during summer (January 1976) and winter (June 1976) as follows. The beach was surveyed and three reference levels, named LW, MW and HW, were marked out at heights of 0,3 m; 1,0 m and 1,9 m above ELWS respectively. Sand samples were collected for particle size analysis following Morgans (1956) and the depths of the water tables and salinities of this water were measured at each tide level. Salinities were read on a refractometer to 1 part per thousand.

At each tide level macrofauna was sampled in four areas of 0,25 m^2 by excavating a hole to 30 cm depth and passing this sand through a screen of 1,5 mm mesh. A number of tests using a nest of screens of 2,1 and 0,5 mm mesh had shown that none of the macrofauna was of a size small enough to pass this screen and it was therefore used in preference to a 1 mm screen because it was easier to operate in the field. On the beaches with high macrofauna densities (St Georges Strand and Maitland River) additional levels were sampled exactly half of the horizontal distance between the LW and MW and MW and HW sampling levels. All specimens were taken back to the laboratory except in cases where very high numbers of the sand mussel, *Donax serra* Röding, were recorded. In such cases specimens were counted and subsamples taken back to the laboratory.

Meiofauna (metazoans passing undamaged through a 1 mm screen) was collected at each level in four replicate series of 10 cm^2 cores. These series of cores were taken in 15 cm steps (Hulings & Gray 1971) to depths of 45 cm at LW, 60 cm at MW and 90 cm at HW where possible. Cores were preserved in 5 percent formalin with rose bengal and taken back to the laboratory for processing.

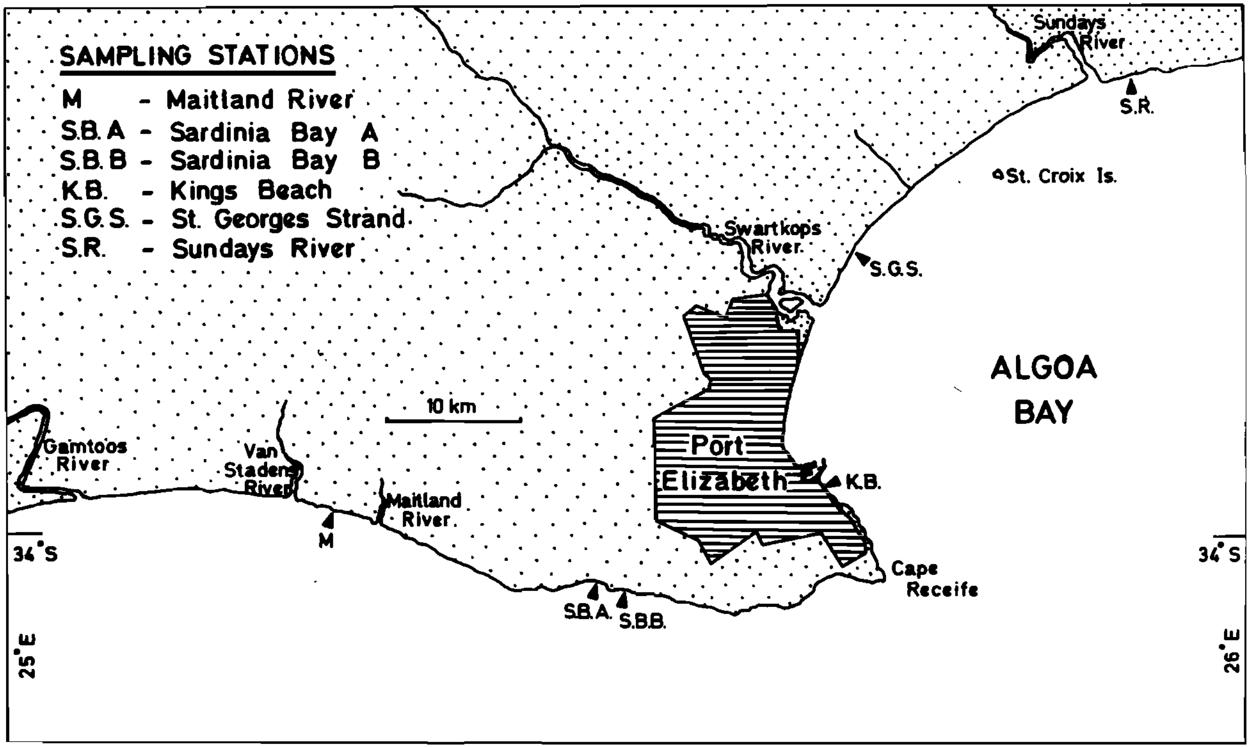

FIGURE 1
Map of the study area showing the four sampling stations used in this study as well as the Kings Beach and Sundays River stations sampled by McLachlan (1977b).

Laboratory analyses

All macrofauna was identified and counted and the ash-free dry mass determined by drying at 100°C for 12-24 hours and ashing at 500°C for 12 hours. In the case of molluscs, shells were first decalcified with hydrochloric acid.

Meiofauna was extracted from the sediment using a modified Oostenbrink extractor that is 80 percent efficient (Furstenberg pers. comm.) and trapped on screens of 75 μm and 45 μm mesh. After further staining in rose bengal all the meiofauna was counted. Individual, ash-free, dry mass was determined for dominant taxa by weighing batches on coverslips to 1 μg on a microbalance. The average, ash-free, dry biomass for a particular taxon was the difference between masses after drying at 55-60°C for 14 hours and ashing at 450-500°C for 12 hours, divided by the number of specimens in the batch. Numerous repeats were done for each taxon and control coverslips were treated in a similar manner.

Analysis of results

As some elements of the meiofauna are lost during extraction and, further, coring never went deep enough to obtain the total meiofauna, it was necessary to correct the numbers and biomass values obtained. Extraction losses could be corrected for by multiplying counts by 1,25. The percentage of the meiofauna that was missed at each tide level due to samples not penetrating deep enough was estimated as follows. Numbers recorded in each 15 cm depth layer were plotted against depth and a curve of numbers against depth in the substrate was fitted by eye and extrapolated to zero numbers. From such a curve the percentage of the population that was missed could be estimated.

Biomass values of the macrofauna and meiofauna were extrapolated graphically to mate the total biomass values for 1 m transects of beach from ELWS to an intertidal ght of 2 m. Similar extrapolations for 1 m wide transects have been done by Ansell *et al* (1972), Hanekom (1975), McLusky *et al* (1975) and McLachlan (1977b). These total beach biomasses were then converted to production estimates by multiplying by a turnover of 10 for the meiofauna (McIntyre 1964; Gerlach 1971) and 2,5 for the macrofauna.

Macrofauna species diversity was calculated using the Shannon index (Odum 1971) which is relatively independant of sample size (Sanders 1968). Indices of species richness and evenness, the two components of diversity, were calculated as done by Boesch (1973) using $\log_2$. Macrofaunal similarity was calculated between all the sampling levels using the Czekanowski coefficient and these were then grouped in dendrogram form using a group average method of sorting (Field 1971).

RESULTS AND DISCUSSION

Abiotic features

Table 1 summarizes the substrate and water-table data for the four beaches. The median particle diameters of all beaches were very similar, ranging from 268 to 308 μm. Very low phi quartile deviation (QDϕ) and zero skewness (SKϕ) values indicate that at all sites a high proportion of the particles fell in a narrow range around the median and that there was equal sorting of particles both larger and smaller than the median. The small differences in median particle diameter belie the great differences in exposure between these beaches. Maitland River beach for example, directly faces the southern ocean swells while St Georges Strand, in Algoa Bay, has only moderate exposure. At Maitland River beach, however, the waves break several hundred metres from the shore while at St Georges Strand they break virtually on the shore as there are seldom offshore bars. Thus, although Maitland River beach is considerably more exposed than St Georges Strand, wave action on the beach is only slightly greater. In terms of wave action and turbulence on the beaches Maitland River is the roughest, followed closely by Sardinia Bay A, St Georges Strand and Sardinia Bay B.

Water table depths are a good indication of the degree of desiccation, and consequently oxygenation, of the interstitial water (McLachlan 1977a). Coarser sands generally have higher permeabilities and therefore deeper water tables, higher desiccation and a greater degree of oxygenation than finer sands (Hulings & Gray 1971). Maitland River and Sardinia Bay A beaches, which had the coarsest sands, nevertheless had the shallowest

TABLE 1

Summary of abiotic factors monitored on the four beaches during 1976.

Beach and Tide Level		*Particle Diameter*					*Water table depth (cm)*	*Salinity at water Table ‰*
		Mdμm	*Mdφ*	*Qdφ*	*Skφ*	*Mean Mdμm*		
Sardinia Bay A	HW	281	1,84	0,12	0,00		47	36
	MW	298	1,76	0,19	0,00	296	17	36
	LW	308	1,72	0,20	0,00		1	35
Sardinia Bay B	HW	268	1,92	0,08	0,00		53	33
	MW	271	1,89	0,09	0,00	276	17	20
	LW	289	1,80	0,13	0,00		1	35
St. Georges Strand	HW	280	1,85	0,13	0,00		70	37
	MW	286	1,83	0,10	0,00	286	19	36
	LW	291	1,79	0,10	0,00		1	35
Maitland River	HW	303	1,74	0,15	0,00		45	13
	MW	295	1,78	0,13	0,00	302	9	26
	LW	307	1,73	0,11	0,00		1	34

water tables. Shallow water tables at Maitland River are explained by the low salinity values which indicate fresh water seepage from the backshore. Shallow water tables at Sardinia Bay A are probably mainly due to the gentle slope of this beach (1/29) as this would slow down drainage. From the water table depths it may be deduced that desiccation of the sand and oxygenation of the interstitial water decrease from St Georges Strand through Sardinia Bay B and Sardinia Bay A to Maitland River beaches.

Beach slope (Figure 2) showed relatively little change between summer and winter as compared to the exposed Cape beaches studied by Brown (1971). There was no relationship

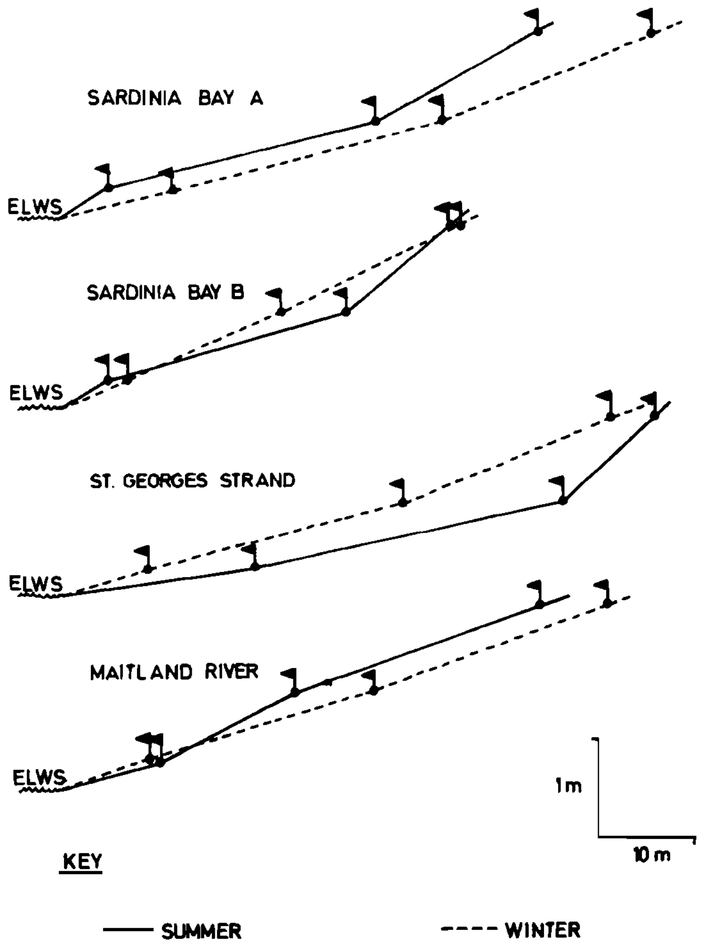

FIGURE 2
Slopes of the four beaches during summer (solid lines) and winter (dotted lines). Flags indicate the LW, MW and HW sampling levels.

between degree of exposure or particle size and beach slope. Brown (1971) has found that exposed beaches do not necessarily have steeper gradients than sheltered beaches and this has been confirmed by McLachlan (1977a) and the present study.

Macrofauna

Table 2 shows the mean numbers of each of the 12 macrofauna species recorded during this study, and Table 3 lists their biomass values. The summer and winter biomass values used to compile Table 3 have been extrapolated to estimate total biomass values in a one-metre wide transect from ELWS to a height of 2 m on each beach and these values are given in Table 4. Sardinia Bay B has an extremely poor macrofauna, both as regards species and

TABLE 2

Macrofauna species and numbers recorded on each beach. Values are means of summer and winter values. Under Isopoda are two species, *Eurydice longicornis* (Studer) and *Pontogeloides latipes* Barnard.

Species	*Sardinia Bay A*			*Sardinia Bay B*			*St. Georges Strand*					*Maitland River*				
	HW	*MW*	*LW*	*HW*	*MW*	*LW*	*HW*	*H-MW*	*MW*	*M-LW*	*LW*	*HW*	*H-MW*	*MW*	*M-LW*	*LW*
Donax serra Röding	—	0,5	—	—	—	—	1,5	18,0	21,0	4,0	2,0	0,5	282,0	123,5	19,0	1,5
D. sordidus Hanley	—	—	—	—	—	—	—	—	—	6,0	7,0	—	—	9,0	23,0	24,5
Bullia rhodostoma Reeve	0,5	5,5	7,0	—	1,0	0,5	—	—	3,0	6,0	—	—	2,0	5,0	62,0	13,5
B. digitalis Meuschen	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,0	2,0
B. diluta (Krauss)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2,0
B. pura Melvill	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,0	8,0
Gastrosaccus psammodytes Tattersall	—	0,5	2,5	—	—	1,0	—	—	—	—	6,5	—	—	0,5	3,0	3,5
Isopoda	1,5	1,0	1,5	0,5	0,5	1,5	5,5	6,0	4,5	2,0	1,0	4,0	4,0	7,5	1,0	1,5
Cerebratulus sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,0	1,0
Lumbrineris tetraura (Schmurda)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2,0	—
Nephtys sp.	—	—	—	—	—	—	—	—	—	—	0,5	—	—	—	—	—
TOTAL	2,0	7,5	11,0	0,5	1,5	3,0	7,0	24,0	28,5	18,0	17,0	4,5	288,0	145,5	113,0	57,5

numbers, and biomass values are very low. Sardinia Bay A and St Georges Strand have moderate macrofaunas with biomass values around 100 g ash-free dry mass per metre transect. Maitland River has the most species (11), highest numbers and extremely high biomass values around 6600 g per metre transect. Ansell *et al* (1972) found maximum wet weight biomass values of 500 g per metre strip, more than an order of magnitude lower than these without correcting to ash-free dry weights. Of the high biomass values recorded on Maitland River beach, 98,5% was due to the white sand mussel, *Donax serra*. Very high population densities are well known for *Donax* spp. (Coe 1955; Nayar 1955; Wade 1955, 1967; Loesch 1957; McLusky *et al.* 1975) but there are no comparable biomass values except those of Hanekom (1975) for *D. serra* also on Maitland River beach. The latter's maximum recorded biomass was 5820 g/1 m transect, slightly lower than the values recorded here. No great biomass changes occurred between summer and winter as occurs after the monsoon on Indian beaches (Ansell *et al.* 1972; McLusky *et al.* 1975).

These beaches thus have an extreme range of macrofaunal biomass values which is probably mainly the result of differing food supplies. Wade (1967) noticed that large *Donax* populations often develop near river mouths which bring large quantities of organic matter into the sea. This can explain the tremendous *Donax* populations at Maitland River beach as there are two small rivers (Maitlands and van Stadens) and one large river (Gamtoos)

TABLE 3

Macrofauna biomass values in g/m². Details as for Table 2.

Species	*Sardinia Bay A*			*Sardinia Bay B*			*St. Georges Strand*					*Maitland River*				
	HW	*MW*	*LW*	*HW*	*MW*	*LW*	*HW*	*H-MW*	*MW*	*M-LW*	*LW*	*HW*	*H-MW*	*MW*	*M-LW*	*LW*
Donax serra	—	0,297	—	—	—	—	0,100	2,402	4,675	0,050	0,030	0,745	315,699	275,533	35,980	0,035
D. sordidus	—	—	—	—	—	—	—	—	—	0,110	0,505	—	—	0,637	1,679	2,424
Bullia rhodostoma	0,060	3,584	0,772	—	0,084	0,449	—	—	1,250	0,150	—	—	0,730	0,114	1,785	1,150
B. digitalis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,090	0,231
B. diluta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,215
B. pura	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,090	0,924
Gastrosaccus psammodytes	—	0,015	0,029	—	—	0,013	—	—	—	—	0,080	—	—	0,010	0,035	0,047
Isopoda	0,038	0,011	0,095	0,010	0,011	0,012	0,090	0,040	0,062	0,040	0,015	0,038	0,033	0,050	0,010	0,010
Cerebratulus sp.	—	—	—	—	—	—	—	—	—	—	—	—	-	—	0,038	0,025
Lumbrineris tetraura	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,185	—
Nephtys sp.	—	—	—	—	—	—	—	—	—	—	0,030	—	—	—	—	—
TOTAL	0,098	3,907	0,896	0,010	0,095	0,474	0,190	2,442	5,987	0,350	0,660	0,783	316,462	276,344	39,892	5,061

TABLE 4

Macrofauna biomass values (ash-free dry mass in grams) per 1m transect of the four beaches from ELWS to a height of 2m.

Beach and Species	*Summer Biomass*	*Winter Biomass*	*Mean*	*%*
SARDINIA BAY A				
Donax serra	6,62	0,00	3,31	3,36
Bullia rhodostoma	17,06	166,00	91,53	92,93
Gastrosaccus psammodytes	0,00	2,49	1,25	1,27
Isopoda	4,17	0,63	2,40	2,44
TOTAL	27,85	169,12	98,49	100,00
SARDINIA BAY B				
Bullia rhodostoma	3,68	9,05	6,37	90,48
Gastrosaccus psammodytes	0,00	0,38	0,19	2,69
Isopoda	0,00	0,96	0,48	6,82
TOTAL	3,68	10,39	7,04	99,99
ST. GEORGES STRAND				
Donax serra	74,73	102,76	88,75	81,96
D. sordidus	13,31	5,55	9,43	8,71
Bullia rhodostoma	2,40	9,50	5,95	5,50
Gastrosaccus psammodytes	0,00	1,67	0,84	0,78
Isopoda	1,42	1,31	1,37	1,27
Nephtys sp.	3,90	0,00	1,95	1,80
TOTAL	95,76	102,79	108,28	100,02
MAITLAND RIVER				
Donax serra	7468,32	5580,50	6524,41	98,54
D. sordidus	51,98	27,36	39,67	0,60
Bullia rhodostoma	37,25	40,05	38,65	0,58
B. digitalis	0,00	8,01	4,01	0,06
B. diluta	3,10	0,00	1,55	0,02
B. pura	0,00	18,67	9,34	0,14
Gastrosaccus psammodytes	0,00	0,50	0,25	0,00
Isopoda	4,34	0,40	2,37	0,04
Cerebratulus sp.	0,00	1,55	0,78	0,01
Lumbrineris tetraura	0,00	0,60	0,30	0,00
TOTAL	7564,99	5677,66	6621,33	99,99

entering the sea in close proximity to the sampling site. Similarly, St Georges Strand is close to the mouth of the Swartkops River and may also receive some sewage effluent. The two Sardinia Bay beaches are far from river mouths and have virtually non-existent *Donax* populations. Their macrofauna biomass is due mainly to *Bullia rhodostoma*, the scavenging plough-shell of eastern Cape beaches. *Donax* spp. thus dominate the biomass values (Table 4) of the two beaches near river mouths while *B. rhodostoma* dominates the two beaches far from river mouths (Sardinia Bay A and B), suggesting that in the former cases particulate food and in the latter cases carrion are the most abundant food sources. On these four beaches the three most important macrofaunal organisms were *D. serra*, which averaged 1654 g/1 m transect, *B. rhodostoma* which averaged 36 g/1 m transect and *D. sordidus* which averaged 12 g/1 m transect. No other macrofaunal species averaged more than 2 g/1 m transect.

A noticeable feature of these beaches is the low number of isopods which are generally abundant on sandy beaches (Brown 1973; Hayes 1974). This is a result of the virtual absence of washed-up algae, and organic matter coming from the sea is mainly in the form of

TABLE 5

Macrofauna diversity ($\bar{H}$), species richness (SR) and evenness (J') values for all tide levels on the four beaches.

Beach and Level		$\bar{H}$	*SR*	*J'*
Sardinia Bay A	HW	0,80	0,72	0,80
	MW	1,26	1,11	0,63
	LW	1,30	0,65	0,83
Sardinia Bay B	HW	0,00	0,00	0,00
	MW	0,93	0,91	0,93
	LW	1,46	1,12	0,93
St Georges Strand	HW	0,73	0,38	0,73
	H-MW	0,80	0,26	0,80
	MW	1,06	0,49	0,66
	M-LW	1,89	0,84	0,95
	LW	1,83	1,14	0,80
Maitland River	HW	0,50	0,46	0,50
	H-MW	0,17	0,31	0,10
	MW	0,86	0,71	0,37
	M-LW	1,89	1,48	0,60
	LW	2,36	1,69	0,73

particulate matter, plankton and occasional carrion. *Donax* occupies the niche of filter feeding on particulate matter and plankton, and *Bullia* occupies the niche feeding on stranded plankton and carrion. Mysids (*Gastrosaccus psammodytes*) were always encountered but were never as abundant as they are on Cape beaches (Brown & Talbot 1972), and polychaets (*Nephtys* sp. and *Lumbrineris tetraura*) and nemertean worms (*Cerebratulus* sp.) are rare.

Diversity, species richness and evenness values for the macrofauna are given in Table 5. Although sample sizes were in most cases too low for accurate use of these indices, they do nevertheless indicate some distinct trends. On all beaches diversities increased as expected (Eltringham 1971) from HW to LW, indicating greater stability and more available niches at lower tide levels due to less desiccation, smaller temperature ranges and increased feeding times. Diversity values were, however, low at all tide levels, reflecting the general paucity of macrofaunal species on sandy beaches. Species richness values were also low, but decreased towards LW on the two Sardinia Bay beaches and increased towards LW on Maitland River and St Georges Strand beaches. This decrease towards LW on the former two beaches was due to increasing dominance of *Bullia rhodostoma* there. Evenness values were varied but were particularly low in areas dominated by *Donax serra*. The highest values of these three indices recorded here were 2,36 for diversity ($\overline{H}$); 1,69 for species richness (SR) and 0,95 for evenness (J′) as opposed to maximum values of 4,93; 11,45 and 0,86 respectively for subtidal, estuarine sands in the Hampton Roads area in Virginia (Boesch 1973). This stresses the poorness of these beach faunas and the predominantly physically controlled nature of their unstable habitat (Sanders 1968).

A dendrogram depicting the results of the similarity analysis is shown in Figure 3. At high levels of similarity this yields numerous small groups of tide levels which, because of the general paucity of this fauna, are not considered significant. A 15% level of similarity yields the most logical division of the different beaches tide levels into three main groups as follows:

1. A series of levels characterized by low numbers ($< 30/m^2$) and few species, but no single species very dominant. These levels had no particular environmental factors exclusively in common. All levels at Sardinia Bay beaches A and B and St Georges Strand and Maitland River HW.
2. Three levels characterized by relatively high diversities, moderate numbers ($50\text{-}150/m^2$) and no single species dominating. These are the MW, M-LW and LW levels at Maitland River.
3. Very high numbers ($>250/m^2$) and total dominance by *D. serra* result in very low diversities at the Maitland River H-MW level.

The most noticeable feature of these groups is that they are not based on intertidal heights or degrees of exposure and the dominant factor appears to be available food. All levels belonging to Group 1 are characterized by either little food or little time to feed (at high tide levels). Group 2 levels experience both sufficient food and sufficient feeding time while Group 3 appears to experience less feeding time but excess food. Available food thus appears to limit numbers and affect community composition.

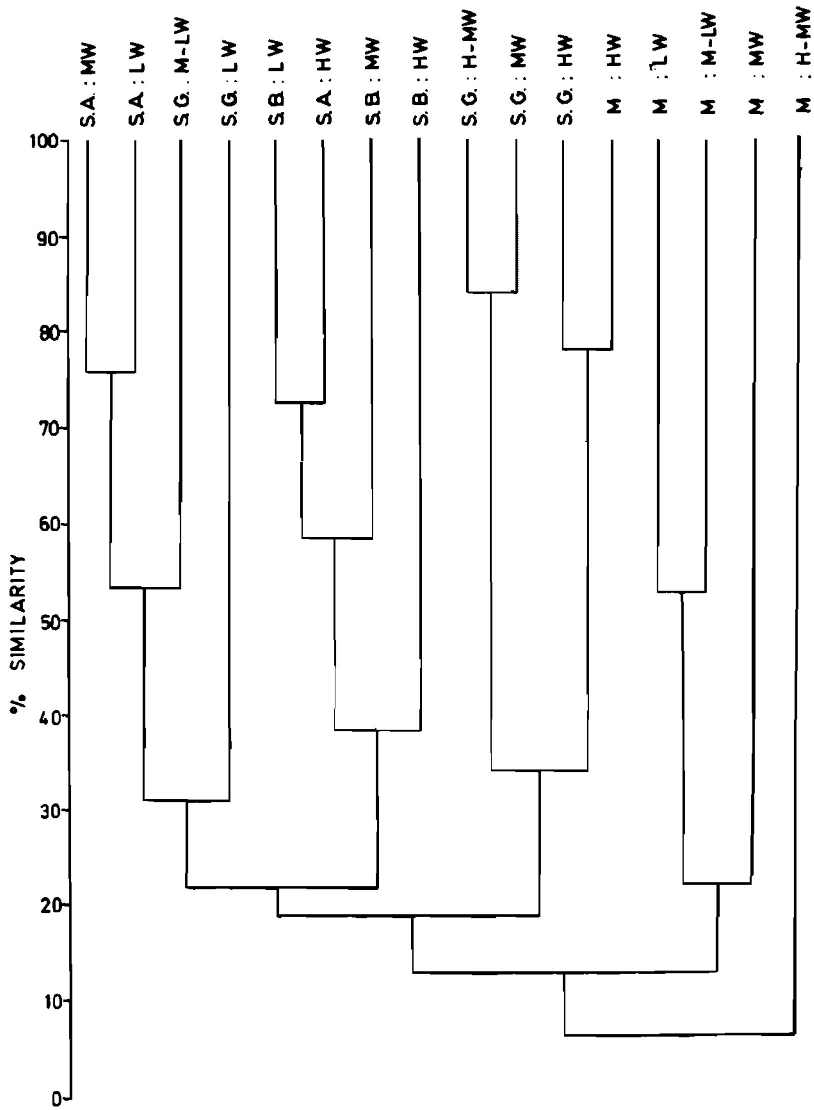

FIGURE 3

Dendrogram showing macro-faunal affinities between tide levels on the four beaches. S.A. = Sardinia Bay A; S.B. = Sardinia Bay B; S.G. = St. Georges Strand; M = Maitland River.

Meiofauna

Meiofauna numbers are given in Tables 6 to 9, their taxonomic composition in Figure 4 and their distribution on each beach in Figure 5. All of these results refer to mean values, and seasonal differences between summer and winter will not be discussed here. None of these tables or figures have been corrected for losses during extraction or for deeper-lying animals. Nematodes are generally the dominant taxon in marine meiofauna (McIntyre 1969) although the proportion of harpacticoid copepods increases in coarser sands on exposed beaches (Rao 1970; Gray & Rieger 1971; McLachlan 1977b). As these four beaches are all

TABLE 6

Mean numbers (summer and winter) of meiofauna recorded on Sardinia Bay beach A. Numbers are per $10cm^2$ surface area or $150cm^3$ sand.

Tide Level and Depth (cm)		*Nematodes*	*Harpacticoids*	*Mystacocarids*	*Oligochaets*	*Others*	*Total*
HW	0–15	220	61,5	2	13,5	11	308,0
	15–30	70,5	133	3,5	5	7,5	219,5
	30–45	59,5	64,5	12	2	2,5	140,5
	45–60	51,5	47,5	13	8	2,5	122,5
	60–75	88	43	8	5	5	149,0
							939,5
MW	0–15	91,5	24	0,5	20,5	5	141,5
	15–30	21,5	4	0,5	3,5	2	31,5
	30–45	15,5	7	0,5	1	0,5	24,5
							197,5
LW	0–15	41,5	7,5	0	4,5	4	57,5
	15–30	29	6,5	0	2	2	39,5
	30–45	16	0	0	1	1	18,0
							115,0
TOTAL		708	401	41	67	41	1258
%		56,3	31,9	3,3	5,3	3,3	100,1

reasonably exposed they would be expected to have high proportions of harpacticoid as well as mystacocarid crustaceans (McLachlan 1977b). If the proportions of these two crustacean groups are added together they dominate three of the beaches, and nematodes dominate Sardinia Bay beach A (Figure 4). Averaging their proportions for the four beaches shows that, overall, crustaceans (48%) are slightly more important than nematodes (44%). In terms of contributions of individual species the crustaceans are, however, considerably more important than the nematodes as they are represented by only about 10 species as opposed to about 30 common nematode species (McLachlan & Furstenberg

TABLE 7

Sardinia Bay beach B. Legend as for Table 6.

Tide Level and Depth (cm)		*Nematodes*	*Harpacticoids*	*Mystacocarids*	*Oligochaets*	*Others*	*Total*
HW	0-15	33,5	30,5	1	5,5	2,5	73,0
	15-30	84	223	4,5	18,5	7	337,0
	30-45	73,5	214	17,5	13,5	4	322,5
	45-60	64,5	90	44	4	1,5	229,0
	60-75	133	116	21	15	3	287,0
							1248,5
MW	0-15	76,5	139	3,5	13	11,5	243,0
	15-30	143	115	33	10,5	24,5	326,0
	30-45	113	44,5	18,5	5,5	4,5	185,5
	45-60	110	15	20	10	4	159,0
							913,5
LW	0-15	158	623,5	6	20,5	5,5	813,5
	15-30	67	390,5	29	15	9,5	506,0
	30-45	58	132	29	9	8	236,0
							1555,5
TOTAL		1115	2134	229	143	89	3710
%		30,1	57,5	6,2	3,9	2,4	100,1

1977). Soft bodied forms were not abundant. Oligochaets never reached high numbers but are nevertheless important because of their relatively large size (Giere 1975). The 'others' category was dominated by turbellarians, followed by annelids and nauplii. High numbers were recorded in many cases and the uncorrected counts often exceeded 1000/10 cm² (Tables 6 to 9).

On the two beaches with shallow water tables and slow drainage (Maitland River and Sardinia Bay A) the meiofauna was concentrated in the upper layers at HW (Figure 5), as was found on a sheltered beach with poor drainage in Algoa Bay (McLachlan 1977b). On

TABLE 8

St Georges Strand. Legend as for Table 6.

Tide Level and Depth (cm)		*Nematodes*	*Harpacticoids*	*Mystacocarids*	*Oligochaets*	*Others*	*Total*
HW	0–15	398,5	3	0,5	3,5	19,5	425,5
	15–30	177,5	117	0,5	6	78	378,5
	30–45	256,5	39,5	0,5	28	11,5	336,0
	45–60	125,5	187,5	17	28,5	18,5	376,5
	60–75	208,5	309,5	25	7,5	31,5	581,5
	75–90	70	39	4	7	1	121,0
							2219,0
MW	0–15	427,5	960	84	27,5	167	1666,0
	15–30	155,5	136,5	48	7,5	23	370,5
	30–45	73	229	38,5	10,5	9,5	360,0
	45–60	46	23	15	20	4	107,0
							2503,5
LW	0–15	170	43,5	1	8,5	17	239,5
	15–30	92,5	28,5	0	24	11,5	156,5
	30–45	25	4	0	8	5	42,0
							438,0
TOTAL		2229	2122	235	190	400	5176
%		43,1	41,0	4,5	3,7	7,7	100,0

the two better drained beaches the meiofaunal communities were concentrated lower on the shore as for a well-drained beach in Algoa Bay (McLachlan 1977b) and in other parts of the world (Wieser 1959; Ganapati & Rao 1962; McIntyre 1968). Maximum densities occurred in the surface layers at MW on St Georges Strand and in the surface layers at LW on Sardinia Bay B. This emphasizes the great importance of drainage on sandy beaches (Steele *et al.* 1970; Brown 1971) and the meiofauna appears to be concentrated at those levels where desiccation is not too severe but oxygen availability not too low, i.e. where a small degree of desiccation does occur (Pennak 1940; Ganapati & Rao 1962; Jansson 1967; McLachlan 1977b; McLachlan *et al.* 1977). Where drainage and desiccation are rapid the meiofauna

TABLE 9

Maitland River beach. Legend as for Table 6.

Tide Level and Depth (cm)		*Nematodes*	*Harpacticoids*	*Mystacocarids*	*Oligochaets*	*Others*	*Total*
HW	0–15	689,5	284	405,5	59,5	68	1506,5
	15–30	518	213	48	51,5	39,5	879,0
	30–45	240,5	203	33	13,5	14,5	504,5
	45–60	213,5	357	19	12	10,5	612,0
	60–75	100	399	16	20	4	539,0
							4031,5
MW	0–15	99	55,5	15,5	14,5	17,5	202,0
	15–30	60	47,5	9,5	4	7,5	128,5
	30–45	40,5	41	4	2,5	8	96,0
	45–60	38	16	5	5	2	66,0
							492,5
LW	0–15	118	46,5	4,5	12,5	30	211,5
	15–30	101,5	59	1,5	7,5	18,5	188,0
	30–45	19	19	1	2,5	4,5	46,0
							445,5
TOTAL		2240	1742	564	209	228	4983
%		45,0	35,0	11,3	4,2	4,6	100,1

may be concentrated where the water table drops to 15-30 cm, and where drainage is slow (i.e. finer sands) meiofauna may be concentrated where the water drops to 50-60 cm during spring low tide. While the distribution of meiofauna on a beach may be mainly due to water content and oxygen availability, meiofaunal densities are probably largely determined by amounts of available food (Ganapati & Rao 1962; Hulings 1974; McLachlan 1977b).

Individual biomass values for dominant taxa are given in Table 10. Turbellarians and nauplii were given an estimated biomass value of 0,5 μg. Using these figures, total meiofauna biomass values were calculated for each beach and tide level. These values, as well as total numbers counted, were then corrected for losses during extraction and losses through not being able to sample the total meiofaunas. Corrected numbers and biomass values together with their correction factors are given in Table 11. These corrected numbers are high (152-7056/10 cm^2) compared to those usually recorded from sandy beaches (50-2000, but up to 10 000/10 cm^2 : McIntyre 1969). The range in biomass value was 0,08-3,36 g/m^2. The highest correction factor (1,86), indicates that at Sardinia Bay B HW, 46% of the meiofauna was missed through extraction losses and not being able to sample deep enough. This is a large proportion and shows that although correction may involve errors, corrected figures are essential for quantitative work.

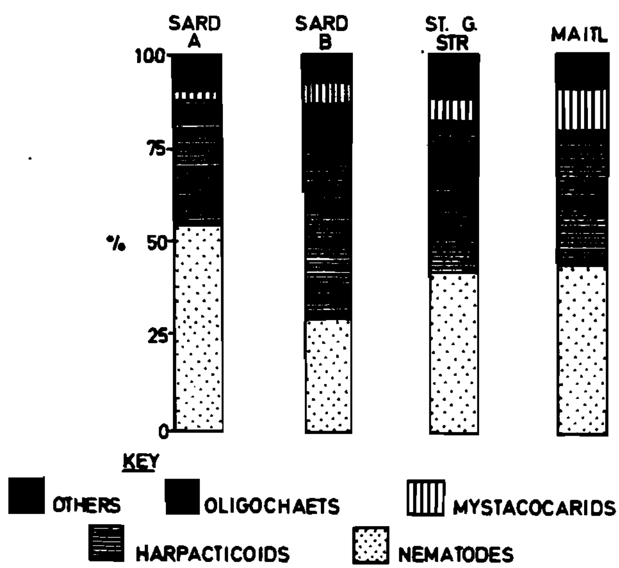

FIGURE 4
Taxonomic composition of the meiofauna on the four beaches.

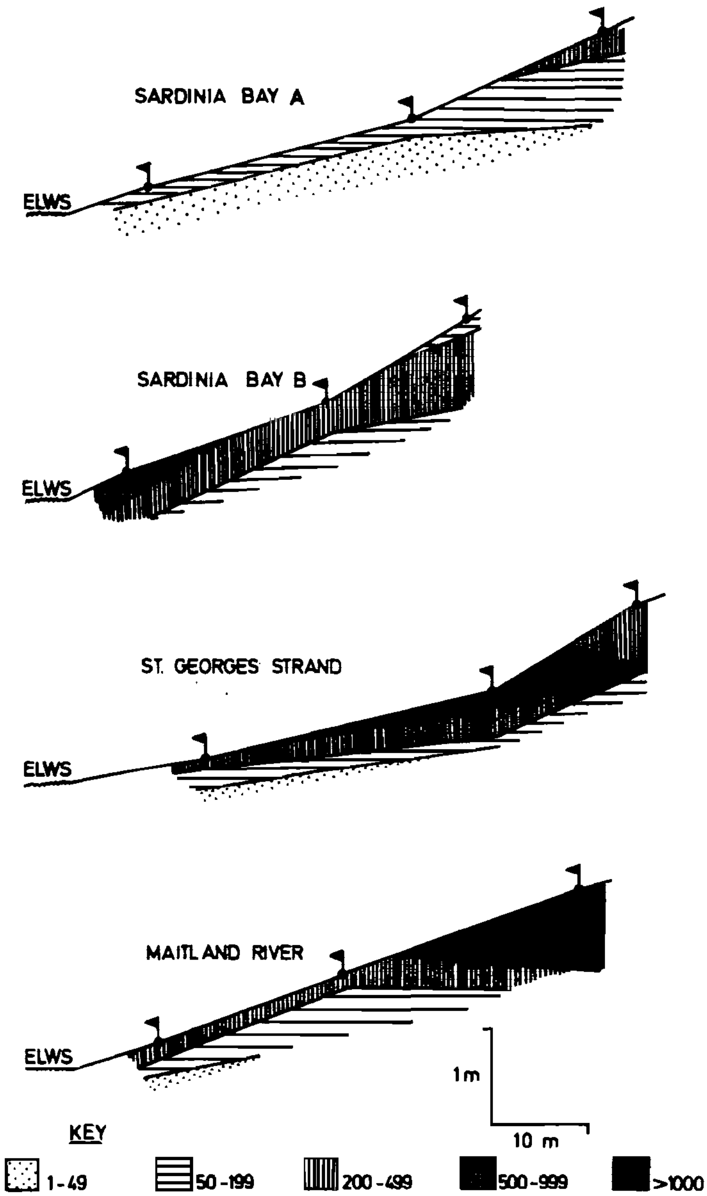

FIGURE 5

Mean distribution patterns of the meiofauna on the four beaches. Density scale is in numbers/150 cm³ sand.

Comparison of macrofauna and meiofauna

The macrofauna and meiofauna of these four beaches are compared on the basis of their biomass values and production estimates for 1 m transects of beach in Table 12. Included for comparison are two other beaches in Algoa Bay (McLachlan 1977b) for which turnovers of 10 were used for meiofauna, 2,5 for Sundays River beach macrofauna and 3,5 for Kings Beach macrofauna. This table shows that the macrofauna exhibits both the highest and lowest biomass value (7,0-6621,3 g/1 m transect) while the meiofauna is more constant (10,5-76,0 g/1 m transect), supporting the idea that small metazoans can usually maintain more stable populations on sandy beaches (McIntyre 1968, 1969; McLachlan 1977b).

TABLE 10

Individual ash-free, dry biomass values for dominant meiofauna taxa.

Taxon	*Individual Mass (μg)*
Nematoda	0,5
Harpacticoida	0,4
Mystacocarida	0,4
Oligochaeta	1,6

TABLE 11

Corrected numbers and biomass values for the meiofauna from all tide levels of the four beaches. Included are the correction factors by which total counted numbers were multiplied to obtain actual numbers present. N = numbers/10cm²; B = biomass in g/m²; CF = correction factor. Division of numbers by the correction factor gives the numbers counted (Tables 6–9).

Beach	*Tide Level*								
	HW			*MW*			*LW*		
	N	*B*	*CF*	*N*	*B*	*CF*	*N*	*B*	*CF*
Sardinia Bay A	1400	0,67	1,49	278	0,17	1,41	152	0,08	1,32
Sardinia Bay B	2321	1,09	1,86	1306	0,64	1,43	2038	0,85	1,31
St Georges Strand	3040	1,37	1,26	3154	1,39	1,26	556	0,32	1,27
Maitland River	7056	3,36	1,75	690	0,38	1,40	566	0,29	1,27

The production estimates indicate that both faunal components are quantitatively important in the flow of energy through these beaches, and on this basis each component dominates three beaches. The average of the percentage contribution to the secondary production on these six beaches is 53% for macrofauna and 47% for meiofauna. Had these estimates of production per transect been extended to a height of more than 2 m above ELWS the meiofaunal contribution would have been greater as macrofauna is virtually absent above this level on all these beaches while meiofauna is abundant right up to the dunes. These production estimates are therefore strictly for the intertidal zone and were they to include the supratidal fringe the meiofauna would increase in relative importance. The meiofauna is nevertheless of about the same quantitative importance as the macrofauna in the intertidal zone and accurate estimation of the flow of energy through, and role of, both these components of beach fauna warrants further study.

CONCLUSIONS

Distinctness of macrofauna and meiofauna communities

The terms macrofauna and meiofauna have in the literature been considered merely arbitrary size-divisions of the metazoan benthos based on practical differences in collection (McIntyre 1964, 1969; Muus 1967; Swedmark in Hulings & Gray 1971). McIntyre (1968) noted, however, that on tropical sandy beaches the meiofauna differs from the macrofauna not only in size but also in the ecological niche it fills. Working on Scottish beaches he later

TABLE 12

Biomass values and production estimates for macrofauna and meiofauna in 1m transects of each beach. B = biomass g/1m transect; P = production in g/1m transect; % = % contribution to the total macro- and meiofaunal production (Kings Beach and Sundays River data from McLachlan (1977b)).

Beach	*Macrofauna* B	*Macrofauna* P	*Macrofauna* %P	*Meiofauna* B	*Meiofauna* P	*Meiofauna* %P	*Total P*
Sardinia Bay A	98,5	246,3	64,1	13,8	138,0	35,9	348,3
Sardinia Bay B	7,0	17,5	4,7	35,4	354,0	95,3	371,5
St Georges Strand	108,3	270,8	33,5	53,7	537,0	66,5	807,8
Maitland River	6621,3	16553,3	95,6	76,0	760,0	4,4	17313,3
Kings Beach	24,9	87,2	45,4	10,5	105,0	54,6	192,2
Sundays River	156,4	391,0	72,3	15,0	150,0	27,7	541,0

(1971) noted that the meiofaunal populations were much more diverse than the macrofauna and were controlled by different factors. The present aim is to expand on McIntyre's ideas and to show in fact that the macrofauna and meiofauna are quite distinct on the beaches studied here. Meiofauna may broadly be separated into burrowing and interstitial forms and Wieser (1959) has proposed that, barring nematodes, an interstitial fauna will only develop in sediments coarser than 200 μm. Interstitial meiofauna has been found in sands of more than 500 μm (McIntyre 1971; Hulings & Gray 1976) but McIntyre & Murison (1973) have proposed that a median grain size of about 230 μm might be the optimum for the development of an interstitial fauna. As particle diameters on the beaches studied here were 200-310 μm, i.e. all close to the proposed optimum value, a rich interstitial life would be expected. In actual fact, virtually all the meiofauna is interstitial, as opposed to burrowing. It is postulated that under such conditions the meiofauna is quite distinct from the macrofauna. The following lines of evidence substantiate this.

Taxonomy. Sixteen macrofaunal species have been recorded (McLachlan 1977b and present study: 6 molluscs, 5 polychaets, 4 crustaceans and 1 nemertean) while there appear to be more than 100 meiofaunal species. The macrofauna is dominated by molluscs (> 90% of numbers) while the meiofauna is dominated by nematodes and harpacticoid and mystacocarid crustaceans.

Size. A plot of number of organisms per m^2 against the size category should yield a pyramid whose base is made up of small forms (Sanders 1960). Such a histogram for these beaches (Figure 6) reveals, however, not a pyramid but two clusters of size classes - (1) meiofauna of

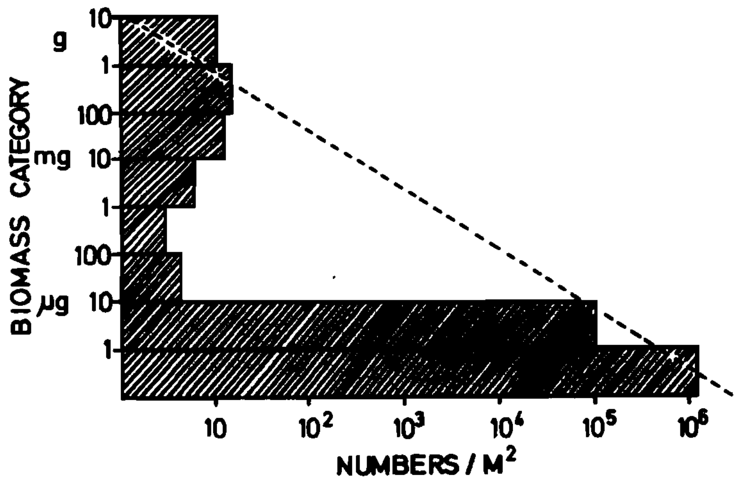

FIGURE 6

Histogram of average numbers of animals of different mass categories on Eastern Cape beaches.

mainly 0,1 - 2,0 μg ash-free dry mass and (2) macrofauna 1 mg - 5 g ash-free dry mass. It must be pointed out that to compile this histogram additional samples were taken using a dredge of 0,5 mm mesh for mysid larvae at lower tide levels. These samples supply the 10 μg to 1 mg categories in the histogram.

Thus, on the basis of size, two distinct metazoan faunas develop on these beaches. Coupled to these size differences are differences in metabolic rates, generation times and turnovers. The absence of forms of intermediate size may be explained as follows. The meiofauna here consists mainly of true interstitial forms which are very uniform in size, while the macrofauna includes only large burrowers, and intermediate sizes are selected against by turbulence and abrasion. Forms a little larger than the meiofauna could not pursue interstitial life as they would be damaged by abrasion of the sand grains, while forms slightly smaller than the macrofauna may be restricted to near-surface layers by oxygen requirements and then easily be washed away by turbulence. This is supported by the fact that the young of many macrofaunal forms (*Donax, Bullia*) often only enter the intertidal zone after first settling or hatching subtidally (Hanekom 1975; personal observations).

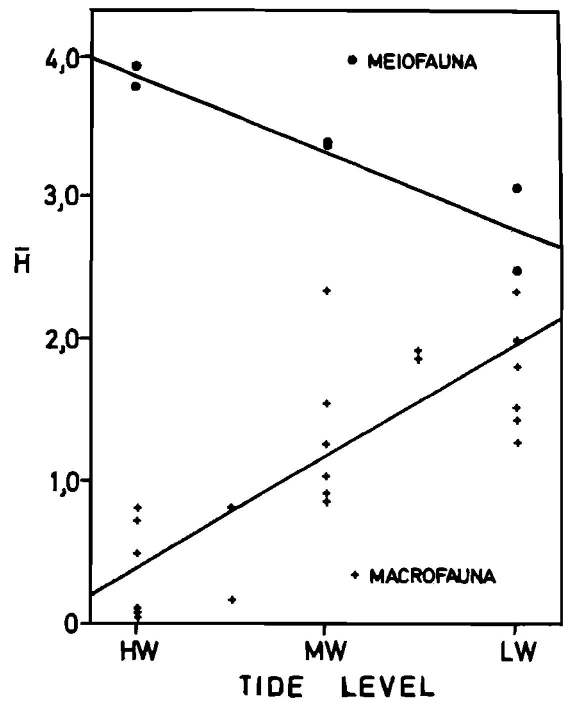

FIGURE 7

Macrofauna and meiofauna species diversities plotted against tide levels and showing regression lines.

Habitat. On the sandy beach the meiofaunal habitat may be considered to be the pore spaces in the sediment, often to considerable depth, while the macrofaunal habitat is basically the flat sand surface. The meiofaunal habitat is a three-dimensional, relatively stable and diverse habitat where the dominant abiotic factors are pore size, water content and degree of oxygenation. The macrofaunal habitat is basically two-dimensional as virtually all the macrofauna is restricted to the sand surface for feeding and respiration. The dominant abiotic factors here are wave action and desiccation. Because of its two-dimensional and largely physically controlled nature the macrofaunal environment is less stable and less diverse than the more three-dimensional environment of the meiofauna.

Community structure. Psammolittoral meiofaunal communities are generally diverse (McIntyre 1971; McIntyre & Murison 1973) while the macrofaunal communities are poor in species (McIntyre 1971; McLachlan 1977b). Meiofaunal diversities have been studied on two beaches (McLachlan & Furstenberg 1977) and macrofaunal diversities on six beaches using the Shannon index (Odum 1971). These values, all converted to $\log_2$, are shown in Figure 7, plotted against tidal levels. The meiofaunal diversity values are based on the nematode and crustacean components only, while macrofaunal values are based on the total fauna. It can clearly be seen that all the meiofaunal values are higher than the macrofaunal values, confirming the idea of their more diverse three-dimensional environment. Further, macrofaunal diversity values decrease from LW to HW on all beaches while meiofaunal diversity values show just the opposite trend. Linear regression lines were obtained for the meiofaunal and macrofaunal diversity values by giving tide levels values of 1-5 (HW-LW). The lines were:

Meiofauna: $Y = 4{,}15 - 0{,}27\ X$ ($p < 0{,}01$; 4d.f.)

Macrofauna: $Y = 0{,}007 + 0{,}37\ X$ ($p < 0{,}001$; 20d.f.)

where Y = Shannon diversity value, and X = tide level value. The habitats occupied by the meiofauna and macrofauna on these beaches are therefore different, and within them different factors control species diversity.

Similarity analysis of the meiofaunal (McLachlan & Furstenberg 1977) and macrofaunal (present study) communities resulted in different divisions of the beaches. Three meiofaunal communities were distinguished, one occurring in sand that dried out during low tide and two occurring in different grades of sand that remained saturated. Three macrofaunal communities were distinguished. These bore little relation to tidal levels and appeared to be more related to quantities of available food. While particle size and desiccation thus appear to be important in determining the types of meiofaunal communities, available food appears to be the most important factor in the case of the macrofauna.

Migrations. The only notable movements that the meiofauna appears to undergo on these beaches are vertical migrations at higher tide levels. These are coupled to the alternate drying and wetting of the sand during the tidal cycle (McLachlan *et al* 1977). These movements are in the order of 12 cm in summer and 6 cm in winter. Many macrofaunal organisms migrate horizontally with the tides (*Donax sordidus, Bullia rhodostoma*) or simply bury themselves (*Donax serra, Bullia rhodostoma*) as part of their tidal cycle of activity. Others even swim into the water (*Eurydice* (Alheit & Naylor 1976)).

Reproduction. Most of the macrofauna, and particularly *Donax* and *Bullia*, reproduces seasonally while the meiofauna appears to have continuous reproduction.

In view of these differences it is concluded that the macrofauna and meiofauna on these beaches are entirely separate faunal components and not merely practical separations of a spectrum or pyramid of benthos. It must be stressed that these conclusions apply specifically to the beaches studied here, though they may hold for any environment where the substrate is coarse enough for virtually all the meiofauna to be interstitial, i.e. sands above Wieser's (1959) 200 μm limit.

Importance of the meiofauna

The importance of the meiofauna on these beaches may be assessed from both a quantitative and a functional point of view. Because of the small individual size of the species, the meiofauna never attains a high biomass value and is therefore only of relative quantitative importance in areas where a macrofauna is not well developed. Sandy beaches are usually such places.

Comparison on the basis of numbers favours the meiofauna, with an average ratio in the order of $10^5 : 1$. Biomass comparison favours the macrofauna and an average ratio would be 5 : 1 in its favour. The most reliable comparison, based on production, shows that on average (unweighted) the meiofauna and macrofauna are approximately of equal importance on these beaches. It is noticeable, however, that on the one beach that does support a rich macrofauna (MR), the meiofauna is of negligible quantitative importance.

As regards the functional importance of the meiofauna on these beaches, little is known. The macrofaunal animals are either scavengers or filter feeders, and feed mainly on carrion, plankton and particulate matter brought in by the waves. The meiofaunal animals probably feed mainly on particulate and soluble organic matter *via* bacteria attached to sand grains (McIntyre & Murison 1973). The only important exchange of energy between these two components could be the possibility of filter feeders feeding on meiofauna stirred up by wave action. To test the feasability of this, several hundred litres of sea water were collected in the shallows at a number of beaches and passed through a 37 μm screen. The meiofauna was stained in rose bengal and counted and, from a knowledge of its mass, its contribution to the total ash-free dry mass of the filtered material was determined. On average the meiofauna made up 0,03% of the ashable material. This indicates that, even were a large proportion of this material not available to filter feeders, the meiofauna could be discounted as a food source for the macrofauna. McIntyre (1969, 1971) and McIntyre & Murison (1973) came to the same conclusion, though in finer sediments where a greater spectrum of animal sizes is represented the meiofauna may be grazed on by the macrofauna (Elmgren 1976).

The meiofaunas on these beaches therefore appear to be at the top of a separate food web comprising particulate and soluble organic matter and bacteria in the sand (McIntyre &

Murison 1973). The only importance of this system to its environment appears to be in the recycling of nutrients (McIntyre 1969; Elmgren 1976). Beaches are supposed to filter enormous volumes of sea water and rough estimates indicate that each metre-wide transect may filter five to ten million litres per year. Pearse *et al* (1942) called beaches 'great digestive and incubating systems', and suggested that they return to the sea the nutrients derived from breakdown of organic matter trapped in the sand. Meiofauna is thought to accelerate the rate of this nutrient cycling by keeping bacterial populations in active growth by grazing and stirring (Elmgren 1976). Hayes (1974), however, found nutrient recycling of negligible importance on some Californian beaches while Hale (1975) found it to be extremely important in sandy estuarine sediments. Further work is needed to quantify this in different environments.

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