STUDIES ON THE PSAMMOLITTORAL MEIOFAUNA OF ALGOA BAY III. A QUANTITATIVE ANALYSIS OF THE NEMATODE AND CRUSTACEAN COMMUNITIES

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ABSTRACT

The meiofauna communities at three tide levels on a sheltered and an exposed beach have been analysed and compared. Twenty-nine nematode, eight harpacticoid and two mystacocarid species and species groups have been used. A similarity analysis indicated three distinct communities, one occurring in sand that dries out during low tide, one occurring in fine sand that remains saturated during low tide and one occurring in coarser sand that remains saturated during low tide. Diversities decreased from high to low tide levels on both beaches regardless of meiofauna numbers. The distribution of nematode feeding types is discussed.

INTRODUCTION

McLachlan (1977b) found that nematodes and crustaceans formed the bulk of the meiofauna on the two beaches studied, where nematodes dominated the sheltered beach and crustaceans the exposed beach. Nematodes have generally been found to dominate meiofauna communities with harpacticoids the second most numerous group (McIntyre 1969; Harris 1972a). Despite this, very few community studies have been done on psammolittoral nematodes (King 1962) or crustaceans (Barnett 1968; Harris 1972b). The main reason for this is probably the taxonomic difficulty experienced in working on a fauna with many undescribed species.

The aim of this work was to evaluate the similarity between, and the diversity of, the meiofauna communities of different tide levels and beaches and to attempt to relate this to the prevailing abiotic and biotic factors.

METHODS

Approximately 50 per cent of the nematodes and 30–40 per cent of the harpacticoids collected in the sampling programme described by MacLachlan (1977b) were mounted in 5 per cent formalin in sea water on semi-permanent wax-ring slides and identified. In the case of mystacocarids only 25 per cent of the specimens were identified. This was considered sufficient as only two species of the latter group had been found. Eight species of harpacticoids were recognized. Unidentifiable larvae and species where less than five specimens were encountered during the whole sampling programme were not identified and have therefore not been included in the following analysis. As these species made up less than 5 per cent of the total fauna their omission should have a negligible influence on the similarity analysis and calculations of diversity.

The number of each species at each station was calculated as the mean from the values for the five seasons of sampling (McLachlan 1977b). For this purpose each beach was divided into four areas: HW 0–45 cm deep; HW 45–90 cm deep; MW 0–60 cm deep and LW 0–45 cm deep. Each area was taken to represent a column of sand 45 cm × 10 cm^2 except MW which represented a column of sand 60 cm × 10 cm^2.

The faunal association between the different beach areas was calculated on the basis of the percentage similarity between them, where

$$\% \text{ similarity} = \Sigma \ \% \text{ abundance of each species common to both areas (Ward 1973)}$$

These values were then used in a cluster analysis to construct dendograms using the 'group average' method (Mountford 1962). This was done separately for the nematodes and the crustaceans as well as for both groups together.

Further, indices of concentration of dominance (c) and general diversity ($\overline{H}$) were calculated for each area using the formulae

$$c = \Sigma \left(\frac{ni}{N}\right)^2$$ where n_i represents the number of specimens of species i and N the total number of all species.

and

$$\overline{H} = -\Sigma \left(\frac{ni}{N}\right) \log \left(\frac{ni}{N}\right)$$ where $\overline{H}$ is the Shannon index of general diversity (Odum 1971).

Using the buccal structure criteria of King (1962) the nematodes were grouped into four feeding types: (1) predators, with powerful buccal armature; they either swallow their prey whole or pierce it and suck the liquid, (2) epigrowth feeders with small, often hollow, teeth; they scrape food off surfaces or pierce cells and suck the contents, (3) non-selective deposit feeders which have a large, unarmed buccal cavity and which suck up their food and (4) selective deposit feeders which have small, unarmed buccal cavities and which feed on smaller food than non-selective deposit feeders. The proportions of the different feeding types were calculated for each beach area.

RESULTS

Twenty-nine nematode, eight harpacticoid and two mystacocarid species or species groups were recognized. Except for the mystacocarids, identifications were taken to family or genus level only. This was considered sufficient for the analysis as further identification would have been extremely difficult and there were probably many new species. The numbers of the different species recorded in the four areas on both the sheltered Kings Beach and the exposed Sundays River Beach are shown in Table 1. These are the mean numbers per 10 cm^2 taken over five seasons.

From the values in Table 1 the dendograms in Figure 1 have been computed. These show

TABLE 1
Mean numbers of nematodes and crustaceans recorded in the four areas on Kings Beach and Sundays River beach from January 1974 to January 1975. Depth in cm.

Species	Kings Beach (Numbers/10 cm²)				Sundays River			
	HW 0–45	*HW* 45–90	*MW* 0–60	*LW* 0–45	*HW* 0–45	*HW* 45–90	*MW* 0–60	*LW* 0–45
NEMATODA								
Axonolaimus, sp. A	36,6	17,9	0,8	0,2	4,5	5,4	0,7	0,2
Axonolaimus, sp. B	22,4	4,5	0,8	0	3,1	3,5	5,8	3,2
Oncholaimidae, sp. A	41,6	21,7	0,8	2,0	0,4	0,2	0,7	0,5
Oncholaimidae, sp. B	0,3	2,1	0,4	0,2	0	0	3,5	1,5
Cyatholaimus sp.	5,2	4,0	0,3	0	15,1	19,3	8,1	0,2
Longicyatholaimus sp.	26,2	19,1	11,6	0	0	0	0,2	0
Choniolaimus sp.	0,3	0,4	33,6	17,0	0	0,4	0,2	0,2
Dasynemellidae, sp. A.	3,3	4,9	12,0	20,6	0	0	0	0,3
Promonhystera sp.	3,6	3,4	24,2	24,0	0	0,4	0,2	0,2
Theristus spp.	6,8	5,9	6,2	8,2	12,7	1,3	0,9	4,0
Enoplidae, sp. A	9,0	2,3	1,6	0	0,5	0,2	0,6	0,8
Enoplus sp.	4,6	2,6	0	0,6	9,0	1,2	0,2	0
Oxystominidae, sp. A	17,5	18,5	0,6	1,2	0,5	1,5	5,5	2,0
Microlaimus sp. A	13,1	6,8	0,4	0,4	0,4	0	13,1	1,4
Rhynchonema sp.	4,9	7,5	0,3	0,4	4,5	4,5	10,5	2,3
Choniolaimidae, sp. A	1,1	1,5	0	0	2,1	0,9	0	0
Monhysteridae, spp.	4,1	4,9	0	0,6	10,7	10,5	8,5	12,3
Microlaimus sp. B	18,3	15,7	0,4	0,4	2,0	2,1	1,5	0
Microlaimus sp. C	5,2	0,2	4,6	5,8	2,0	3,4	1,1	0,8
Monoposthiidae, sp. A	6,8	10,7	0	0	5,6	0,8	3,4	0,7
Mesacanthion sp. A	1,4	1,9	0,3	0	0,4	0,2	0,6	0,1
Siphonolaimidae, spp.	12,8	15,1	6,2	1,6	0	0,1	0,6	0,4
Enoplolaimus sp.	2,2	1,5	0	0	0,4	1,9	0,8	0,2
Oxystominidae, sp. B	0,8	1,1	0,3	0	0,1	0,2	1,1	0
Mesacanthion sp. B	1,1	0,4	5,8	0,6	0,4	0,2	0	0,3
Dasynemella sp.	0	0	0,3	0,4	0,5	2,0	0,1	0
Chromadoridae, sp. A	10,4	0,4	9,4	2,0	0	0,2	0	0
Desmoscolex sp.	0,3	0	0	0	0,1	0,6	0	0
Oncholaimidae, sp. C	1,6	0,2	0,6	0,8	0,5	17,5	5,5	1,6
HARPACTICOIDA								
Arenopontia sp.	105,2	61,8	1,6	1,2	25,2	42,8	107,0	9,6
Leptomesochra sp.	0	0	0	0	0	1,8	12,6	2,8
Praeleptomesochra sp.	0	0	0	0	0	0	0,4	3,6
Ameiridae, sp. A	0	0	0	0	0	0	6,6	0,4
Hastigerella sp. A	10,8	2,4	0,2	0	14,8	27,8	58,4	5,4
Hastigerella sp. B	0,8	0,6	0	0	1,0	2,2	4,2	0,2
Psammastacus sp.	0	0	0	0,6	0	0,2	4,2	112,8
Leptastacus sp.	0	0,2	0	0	6,6	6,4	14,8	3,0
MYSTACOCARIDA								
Derocheilocaris delamarei Hessler, 1972	0	0	0	0,2	0,6	0	101,2	11,6
Derocheilocaris algoensis McLachlan & Grindley, 1974	52,0	51,2	0,2	0	2,2	18,4	67,0	1,6
Mean Total Nos/10 cm²	430,3	291,4	123,5	89,0	125,9	178,1	449,8	184,2

the faunal associations between the eight beach areas, first on the basis of the nematode fauna only, then on the basis of the crustacean fauna only and finally on the basis of the combined faunas. The dendogram based on nematodes only shows relatively high affinities between all beach areas except the Kings Beach LW and MW areas which show less than 20 per cent association with the other areas. On the basis of their crustacean fauna all the areas become more similar with the exception of the Sundays River LW area which shows only 20 per cent association with the other areas. The dendogram based on the total fauna separates both the above-mentioned areas at the 25 per cent level. In this way the two beaches can be divided into three areas of distinct meiofaunal communities:

(1) King Beach LW and MW;
(2) Sundays River LW; and
(3) all the other areas

The characteristics of these faunas will be discussed later.

Figure 2 shows the values of c and $\overline{H}$ and the mean total meiofaunal number per 10 cm^2 on Kings Beach and Sundays River Beach. On both beaches dominance (c) increased and diversity ($\overline{H}$) decreased from HW towards LW. On Kings Beach numbers dropped rapidly from HW to LW, following a similar pattern to the diversity, but on Sundays River Beach numbers increased to a maximum at MW and then decreased again towards LW, *i.e.* on Sundays River Beach diversity was not dependent on numbers.

Figure 3 shows the proportions of the different nematode feeding types for each beach area and for each beach as a whole. Predators and selective deposit feeders remained low throughout and all areas were dominated by epigrowth feeders and non-selective deposit feeders. On both beaches the percentage of non-selective deposit feeders increased from HW to LW while epigrowth feeders showed the opposite trend.

DISCUSSION

Although nematodes dominated these beaches in number of species (and in total numbers on Kings Beach), individual species never reached such high numbers as some of the crustacean species. No single nematode species averaged more than 3,5 per cent of the total meiofaunal number on both beaches while several crustaceans averaged more than 5 per cent. The harpacticoid, *Arenopontia* sp. was the dominant meiofaunal animal on both beaches, accounting for 15 per cent and 16 per cent of the numbers on Kings Beach and Sundays River Beach respectively. Similarly the mystacocarid, *Derocheilocaris algoensis* accounted for 8 per cent and 9 per cent of the numbers on the two beaches, the harpacticoid, *Hastigerella* sp. A, for 2 per cent and 9 per cent, the harpacticoid, *Psammastacus* sp., for 0 per cent and 10 per cent and the mystacocarid *D. delmarei*, 0 per cent and 10 per cent.

It should thus be borne in mind that although nematodes may dominate most meiofaunal communities, individual species may not be so important. On the beaches studied here crustaceans would seem better candidates for population studies.

The dendograms show some interesting patterns and two general conclusions emerge. Firstly, it can be seen in Figure 1 that dendograms based on nematodes only or harpacticoids

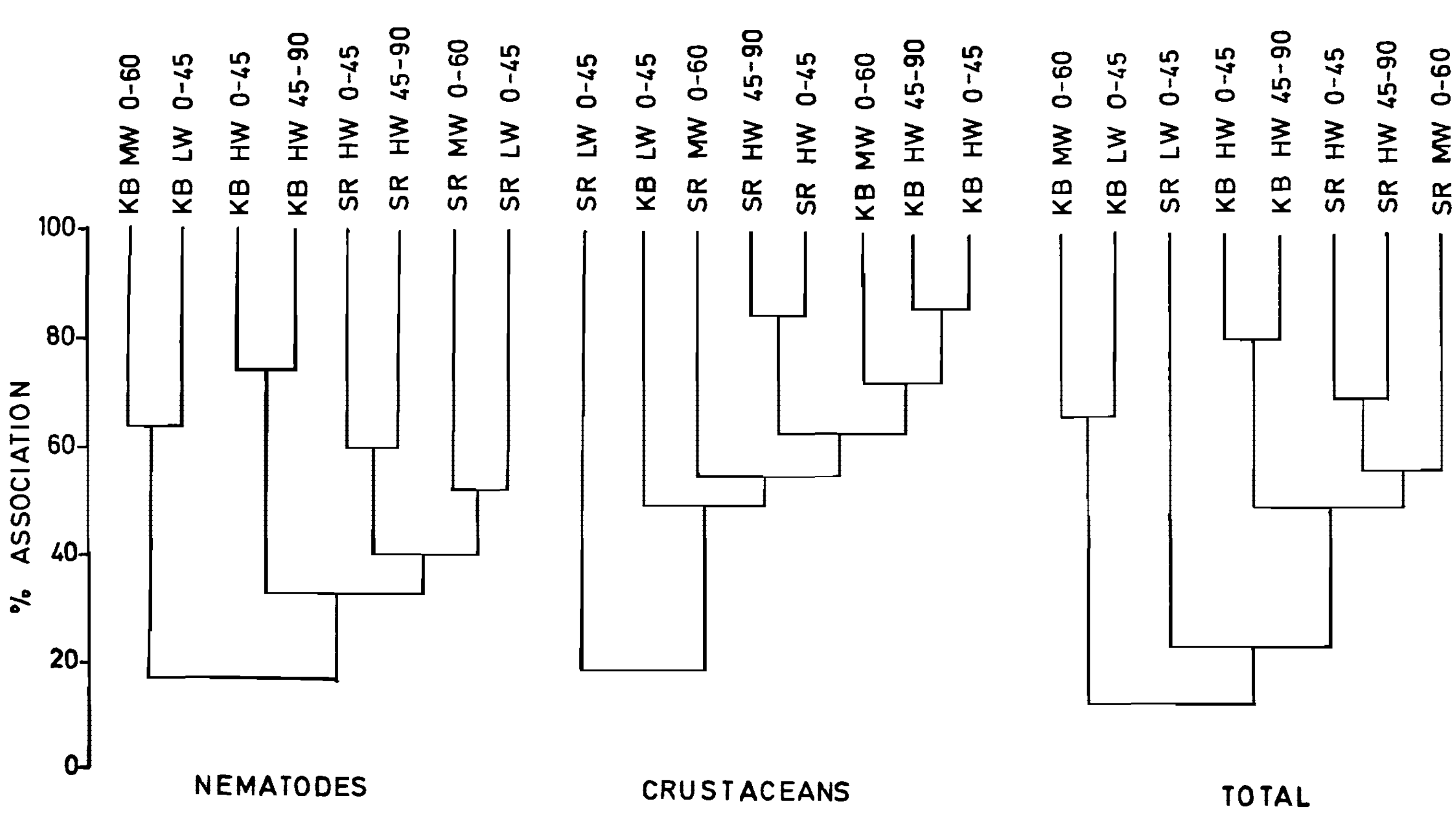

FIGURE 1

Dendograms grouping the Kings Beach and Sundays River beach areas on the basis of faunal similarities. This is done on the basis of nematodes only, then crustaceans only and finally for the combined nematode and crustacean faunas.

only gave different results, suggesting that environmental factors influence these different taxa differently. Secondly it may be concluded that on the basis of the combined nematode and crustacean fauna these two beaches may be divided into three faunal areas with the following characteristics:

(1) Kings Beach LW and MW; characterized by fine, saturated sand, relatively large amounts of available food and low oxygen values (McLachlan, 1977a) and dominated by the nematodes, *Promonhystera* sp., *Choniolaimus* sp. and Dasynemellidae. Total numbers and diversity were relatively low and dominance relatively high (Figure 2). Crustaceans were scarce.

(2) Sundays River Beach LW; characterized by relatively coarse, saturated sand with little available food and moderate oxygen values (McLachlan, 1977a). This fauna was dominated by the large harpacticoid, *Psammastacus* sp., although the mystacocarid, *D. delamarei*, and monhysterid nematodes were also fairly common. Numbers and diversity were very low, dominance very high (Figure 2). The relatively large size of *Psammastacus* may in some way be an adaptation to the coarse sand found in this area.

(3) All the other areas, namely, Kings Beach HW and Sundays River Beach HW and MW; characterized by some desiccation during low tide and consequently relatively high interstitial oxygen values (McLachlan, 1977a). Sand particle size and available food were variable. Dominant species were the harpacticoid, *Arenopontia* sp., and the mystacocarid, *D. algoensis*. Although no species was dominant, nematodes were common throughout these areas. Diversity was high, dominance low and numbers variable (Figure 2).

Interpretation of a dendogram is arbitrary as regards the percentage association above which faunas are considered homogeneous. King (1962), studying psammolittoral nematodes, used a value of 25 per cent and Ward (1973) studying sublittoral nematodes, used 27 per cent. All areas here considered homogeneous exhibited at least 50 per cent association and those three considered distinct less than 25 per cent. The boundaries of the three faunal areas proposed thus appear to be fairly distinct.

From the dendograms it can be seen that on both beaches the two HW areas were very similar. This suggests that subdivision of the HW stations into two areas was artificial and that samples from different depths at HW were not as distinct as those coming from different tide levels. In both cases the line separating the faunas lay between the saturated and desiccated parts of the beaches during low tide. Thus Kings Beach HW and Sundays River HW and MW, all of which experience desiccation, form one faunal area, while Kings Beach MW and LW which remain saturated during low tide and have fine sand form another, and Sundays River LW which also remains saturated but has medium sand forms the third. It therefore appears that (1) desiccation due to drainage and (2) particle size are the dominant factors influencing the species composition of these psammolittoral meiofaunas. Available food (measured as chlorophyll *a:* (McLachlan 1977a, 1977b)), which varied widely between Kings Beach and Sundays River, appears to influence numbers but not faunal composition. If desiccation was the dominant factor it might be expected that Sundays River MW would show a greater faunal association with Kings Beach HW than with Sundays River HW as it experiences the same degree of desiccation as the former (McLachlan 1977a). Inspection of the dendograms reveals that this was not the case, however, and Sundays River MW was

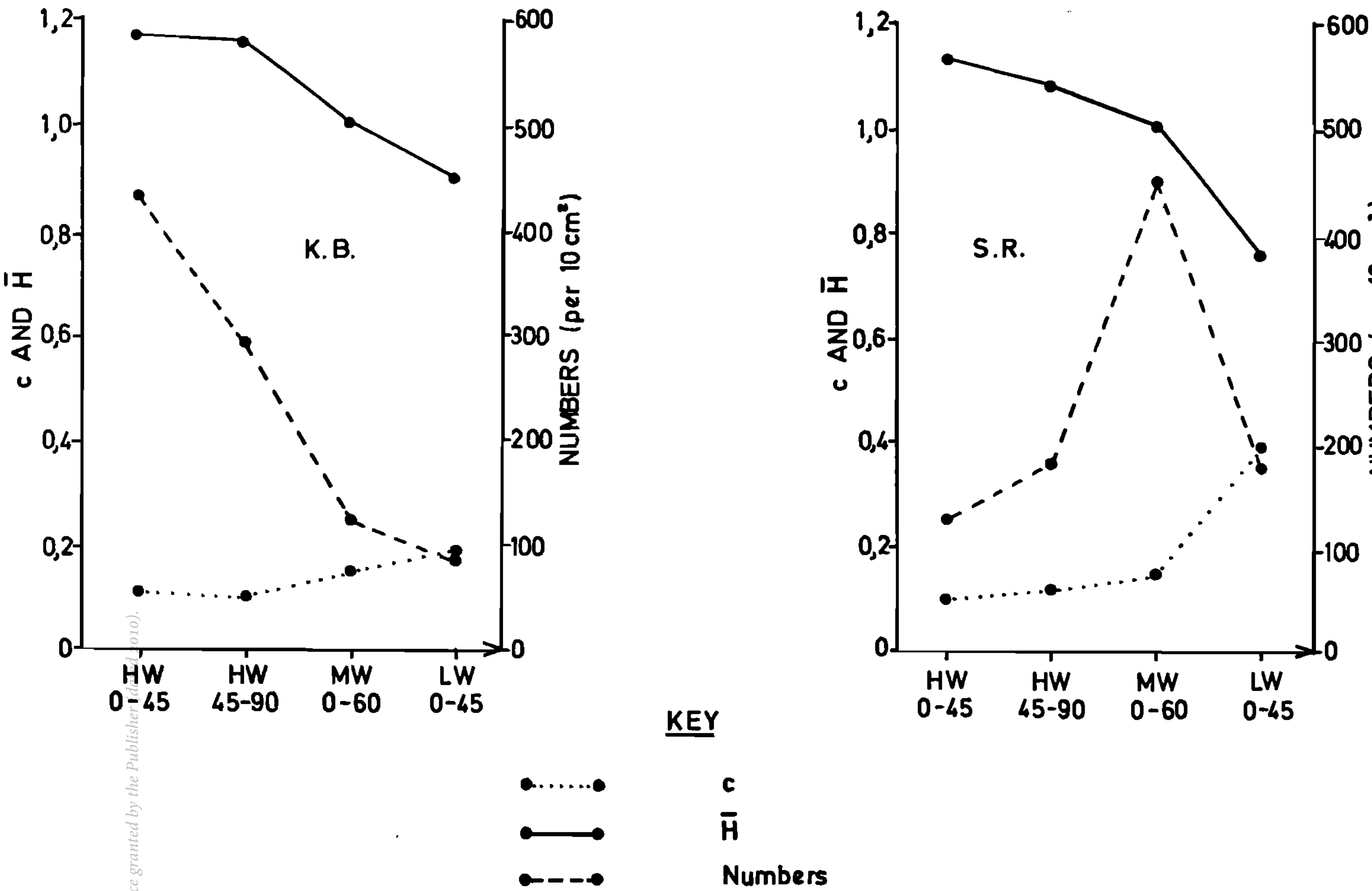

FIGURE 2

Diversity (H̄) and dominance (c) values and mean meiofaunal numbers recorded from the differentareas on Kings Beach (left) and Sundays River beach (right).

most closely associated with the Sundays River HW areas. This supports the view that substrate particle size, and possibly other factors, also influence the species composition of the meiofauna.

Figure 2 indicates diversity ($\bar{H}$) decreasing and dominance (c) increasing from HW to LW on both beaches. According to Sanders' (1968) 'stability-time hypothesis', number of species (i.e. diversity) decreases along a physiological stress gradient as the environment becomes more physically, as opposed to biologically, controlled. Increased physiological stress is due to increased physical fluctuation or increasingly unfavourable physical conditions. It may therefore be concluded that the interstitial environment becomes increasingly physically controlled, or abiotic, from HW to LW on the beaches studied here. This implies that there are fewer niches and thus greater dominance by a few species at LW. (It is interesting that as far as the macrofauna is concerned the opposite is generally the case with a greater number of species and individuals at LW than at HW (McLachlan 1977b). Macrofauna and meiofauna communities therefore appear to be influenced by different factors and may thus be considered distinct and not arbitrary subdivisions of the benthos of these beaches). The factors responsible for the more unfavourable conditions towards LW are uncertain but the decreasing oxygen levels must be important. Movement and abrasion of the sand particles at lower tide levels may also be a factor making this part of the shore more 'abiotic'.

As far as nematodes were concerned, Kings Beach HW had the most diverse and Kings Beach LW the least diverse fauna. Kings Beach HW must therefore represent optimum conditions and provide most niches for nematodes. This is probably due to a combination of large amounts of available food, well-oxygenated interstices and optimum pore sizes (McLachlan 1977a).

Sundays River MW had the most diverse crustacean fauna and Kings Beach LW and MW the least diverse. The relatively coarse sand and well-oxygenated interstices at Sundays River MW appear to be responsible for the optimum conditions there. Pennak (1940), studying the tideless beaches of lakes, found harpacticoids to be concentrated in areas where the sand was neither too dry nor too wet and Jansson (1968) found harpacticoids to be the group most sensitive to desiccation and low oxygen levels. As thorough oxygenation only occurs through desiccation, harpacticoids (and probably also mystacocarids) would be expected to be most abundant where oxygen is abundant but desiccation not too severe. The degree of desiccation experienced at Sundays River MW must therefore be optimal for harpacticoids and this effect seems to be further enhanced by the coarseness of the sand. Kings Beach HW experienced the same degree of desiccation as Sundays River MW (McLachlan 1977a) and also had a high number of crustaceans but, probably due to the finer sand, had a lower crustacean diversity (Table 1).

On the whole, diversity and dominance values (Figure 2) were similar for all levels of both beaches except Sundays River LW, which had a fauna with very high dominance. On Kings Beach diversity and numbers followed the same pattern while on Sundays River Beach diversity appeared to be independent of numbers. Here diversity decreased from HW to LW but numbers were maximum at MW. As has been mentioned, the low diversity at Sundays River LW was due to dominance by the harpacticoid, *Psammastacus* sp. This was a large species which appeared to be specially adapted to the coarse sand found at this station.

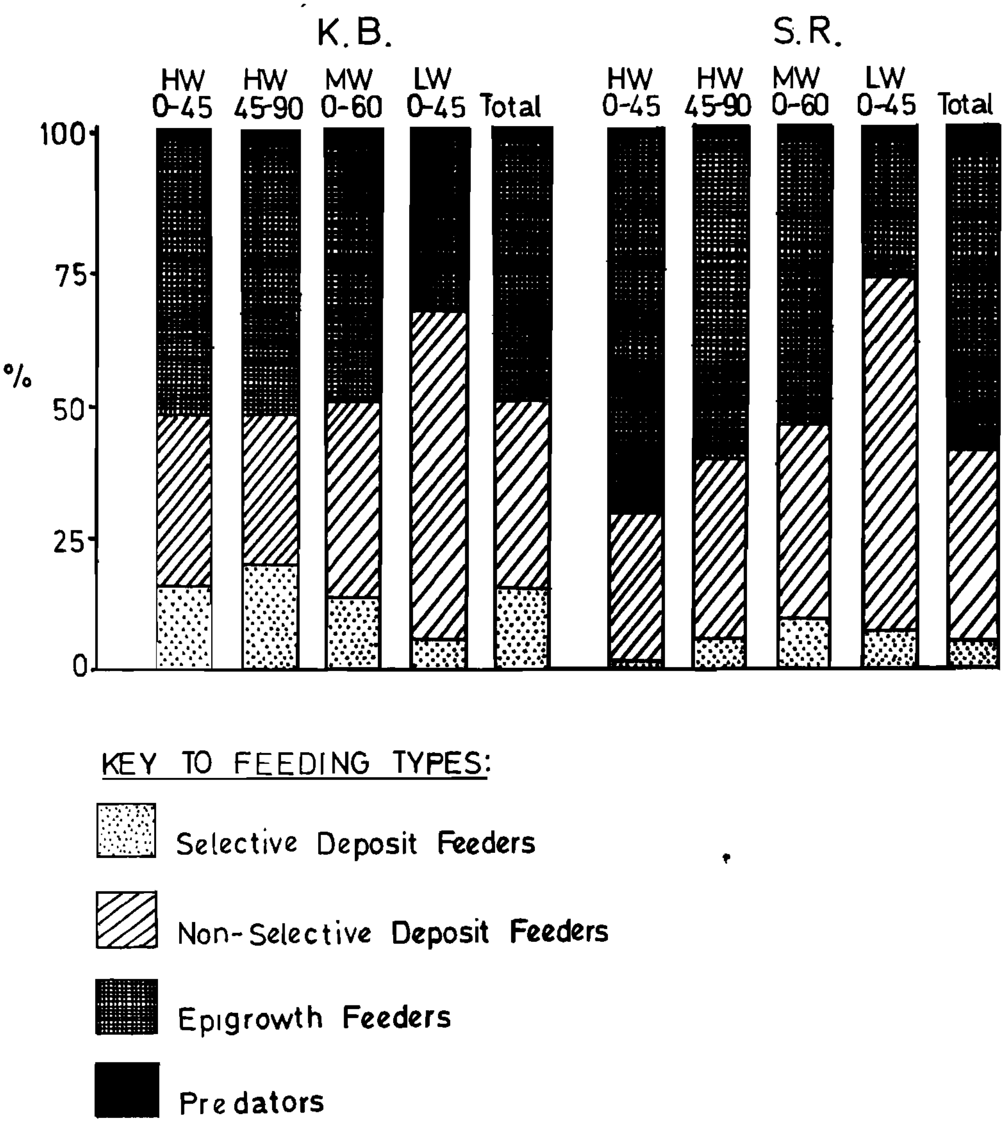

FIGURE 3

Relative proportions of different nematode feeding types at different beach areas on Kings Beach and at Sundays River.

The beaches exhibited the same trend as far as nematode feeding types were concerned (Figure 3). There was an increase in non-selective deposit feeders and a decrease in epigrowth feeders from HW to LW. Both beaches were, however, dominated by epigrowth feeders, followed by non-selective deposit feeders. Selective deposit feeders made up approximately 16 per cent and 6 per cent of the nematodes at Kings Beach and Sundays River respectively and predators constituted 4 per cent on both beaches. Sundays River had a greater proportion of epigrowth feeders while Kings Beach had more deposit feeders. The greater proportion of deposit-feeding nematodes on Kings Beach is most probably related to less wave action and thus more deposited detritus.

King (1962) found an increase in deposit feeders below LW where there was less wave action and also found most deposit feeders on a more sheltered beach. This would therefore appear to be a general pattern. King (1962) also found epigrowth feeders to dominate the upper tide levels on an exposed beach and related this to the smaller amounts of deposited detritus at higher tide levels. Although organic matter in the sand was not determined in this study (for reasons explained in McLachlan 1977a) it would appear that the same explanation holds for both beaches here. Tietjen (1966) also found deposit feeders more numerous in areas with greater amounts of organic matter. Finally, as found by King (1962), there appears to be no correlation between feeding types and particle size distribution at the different beach areas.

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