STUDIES ON THE PSAMMOLITTORAL MEIOFAUNA OF ALGOA BAY, SOUTH AFRICA

II. THE DISTRIBUTION, COMPOSITION AND BIOMASS OF THE MEIOFAUNA AND MACROFAUNA

A. MCLACHLAN
Zoology Department, University of Port Elizabeth

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ABSTRACT

Two beaches in Algoa Bay, South Africa, have been found to support a relatively rich and varied meiofauna. Highest numbers were recorded at HW on the sheltered beach (2 250/10 cm^2) and the lowest numbers at LW on the same beach (60/10 cm^2). On the exposed beach numbers were more uniform but were highest between MW and LW. Distribution of the meiofauna on the sheltered beach was limited mainly by the amounts of available oxygen in the interstitial water while on the exposed beach amounts of available food, and to a lesser extent oxygen, were limiting. The meiofauna of the sheltered beach was dominated by nematodes and that of the exposed beach by Crustacea (harpacticoid copepods and mystacocarids). Meiofauna biomass values were highest in winter and lowest in summer. Macrofauna was richer on the exposed beach, mainly due to the sand mussel, *Donax serra*. Production estimates based on standing crop indicated that the meiofauna may account for 55 per cent and 28 per cent of the total secondary production on the sheltered and exposed beaches respectively.

INTRODUCTION

There are few published accounts of surveys of beaches which include both the meiofauna and the macrofauna (McIntyre 1968; Nagabhushanam & Rao 1969) and these are not strictly quantitative. A comparison is, however, essential if the ecological importance of the meiofauna in an ecosystem is to be estimated. Numerical comparison of the meiofauna and macrofauna would favour the meiofauna while a comparison based on biomass would favour the macrofauna. The ideal ecological comparison should therefore be based on production or energy flow. As this is often very difficult to estimate directly, production estimates based on biomass are probably the most meaningful when comparing meiofauna and macrofauna. Bearing this in mind a survey of the psammolittoral meiofauna of Algoa Bay was undertaken.

The basic questions this survey attempted to answer were the following: (1) What is the distribution pattern of the psammolittoral meiofauna of Algoa Bay and what factors are responsible for this pattern? (2) Does this pattern have any pronounced seasonal variation? (3) What are the main components of the meiofauna? (4) How does the distribution and composition of the macrofauna relate to, or correlate with, that of the meiofauna? (5) What is the relative importance of the meiofauna and macrofauna with respect to numbers, biomass and production?

In order to answer these questions, all tide levels on both the sheltered Kings Beach and the exposed Sundays River Beach (McLachlan 1977) were quantitatively surveyed over a 13-month period.

METHODS

Meiofauna surveys

Surveying meiofauna involves two processes, the accuracy of which should be calculated. These are (1) taking the samples and (2) extracting the meiofauna from the samples. The accuracy of the methods used in these surveys was tested before sampling as follows.

Between the HW and MW levels on Kings Beach a 10 m line was drawn parallel to the shore. Every metre along this line a 30 cm vertical core was taken with a hand-operated stainless-steel corer (McLachlan 1977). The meiofauna was extracted from each core, stained overnight by addition of 2–3 ml 0,1 per cent rose-bengal stain and preserved in 5 per cent formalin. The meiofauna was then counted using a low-power stereomicroscope. The result was a mean meiofauna count of 1 174 animals per core with a standard deviation (SD) of 89 and a coefficient of variation (CV) of 7,6 per cent. (Gray 1971) and Hulings & Gray (1971) state that 3–4 cm is the optimal corer diameter and that 4–8 samples are sufficient for most surveys. The corer used here had an internal diameter of 3,57 cm (i.e. a cross sectional area of 10 cm^2). The CV on four samples taken with this corer would be 18,96 per cent which may be approximated to 20 per cent for this programme. This was considered to be sufficiently accurate despite the patchiness of psammolittoral meiofauna (Pennak 1940; Hulings & Gray 1971; personal observations) and taking into account that it is not the aim of this study to investigate differences in distribution or numbers between small sections of beach but rather to trace broad patterns.

Extraction was done using an Oostenbrink (1960) extractor modified by Dr J. P. Furstenberg of the Zoology Department, University of Port Elizabeth. This extractor has a mean efficiency of 80 per cent for the common meiofaunal taxa, *e.g.* nematodes and crustaceans (Furstenberg pers. comm.). Samples were washed through a 1 mm screen into the extractor and, after extraction, the animals were trapped on a 0,075 mm screen over a 0,045 mm screen. Earlier tests had shown that use of the 0,045 mm screen increased the total counts by a mean of 38 per cent (six tests). Further, examination of the filtrate showed that less than 5 per cent of the meiofauna passed through the 0,045 mm screen and that these were only small and larval nematodes and flatworms.

For the purpose of this study meiofauna is that part of the fauna passing undamaged through a 1 mm screen but being trapped by a 0,045 mm screen. The collecting screen (0,045 mm in this case) has a noticeable influence on the total counts as McIntyre (1964) found that 60 per cent of the total nematodes passed a 0,076 mm screen.

The meiofauna of Kings Beach and Sundays River was sampled every three months for 13 months starting in January 1974. Inspection of sea temperature data from the Port Elizabeth harbour (McLachlan 1977) had revealed the highest temperatures in January and the lowest in July and August. Sampling times were therefore arranged to coincide with these 'temperature seasons' in the sea. Both Kings Beach and Sundays River were sampled at the HW, MW and LW tide levels to 90 cm, 60 cm and 45 cm (McLachlan 1977) at each three-monthly time of sampling. Summer samples were repeated in January 1975 in order to have some seasonal overlap.

At each tide level four series of cores, 30 × 10 cm^2, were taken 1 m apart along a line parallel to the shore using the method of cutting steps (Hulings & Gray 1971). Two 15 cm cores from each 15 cm depth range were combined and sealed in glass bottles for later analysis.

Cores were returned to the laboratory within three hours and all were extracted within 24 hours of collection. Extraction, staining and counting were done as described above. The number of specimens belonging to each taxon, *e.g.* nematodes, harpacticoids, mystacocarids, etc. were counted separately. Specific identification of the meiofauna will be dealt with in Part III of this series.

In order to determine the percentage of the meiofauna living below the depth ranges sampled at each tide level, the counts were extrapolated graphically and the deeper lying meiofauna estimated from the area beneath the curves. Counts and biomass could thus be corrected to allow for the animals lost during extraction (20 per cent) as well as those living too deep to be sampled. The 0–4 per cent of the meiofauna passing through the collecting sieves was ignored.

Meiofauna biomass

Calculation of individual, ash-free, dry biomass for meiofauna posed problems. An estimation of the biomass was, however, essential for a meaningful comparison with the macrofauna. For dominant groups, such as nematodes and harpacticoids, where large numbers could be obtained, the following procedure was adopted. A large number of animals (20–40) was counted onto a cover slip. They were quickly dipped into distilled water during the process to remove excess salt. The cover slip was then oven-dried at 55°C for 14 hours, placed in a desiccator till cool and weighed on a Sartorius micro-balance to 10^{-6} g. The slide was ashed at 450°C for four hours, cooled in a desiccator and weighed. Numerous control slides were treated in a similar manner. The ashed mass of each taxon was obtained from the difference between experimental and control slides. A mean individual ash-free biomass was then calculated for each taxon.

Macrofauna surveys

The macrofauna of Kings Beach and Sundays River was sampled during April and October 1974 at the same tide levels as the meiofauna. As most macrofauna species have relatively long life cycles and as little variation would be expected in their populations, two surveys were considered sufficient for estimation of the standing crop. Autumn and spring were chosen so as to miss any peaks in spawning, larval settlement or mortality that might occur in summer or winter.

At each tide level four areas of 0,25 m^2 were excavated to a depth of 30 cm and the sand washed through a 2 mm screen. Tests with a 1 mm screen held under the 2 mm screen had shown that none of the macrofauna was of a size range that could pass through the larger screen but be retained by the finer one. In this manner an area of 1 m^2 was sampled at each tide level. The macrofauna was taken back to the laboratory, all species identified and the total numbers counted.

Macrofauna biomass

The shells of molluscs were removed and the soft tissue, together with the other animals collected at each tide level, was oven-dried at 105°C for 24 hours. After cooling in a desiccator and weighing, the samples were ashed at 550°C for four hours. Thereafter they were again cooled in a desiccator and reweighed. The difference between these two masses was the ash-free dry biomass of the macrofauna.

The mollusc shells were treated with dilute hydrochloric acid until effervescence ceased. The solution was filtered through glass-fibre paper and the paper plus residue dried and ashed. Clean filter paper blanks, washed with hydrochloric acid acted as controls. The ash-free dry mass of the organic matter in the shells was obtained from the difference between experimental and control papers. Summing these results with the biomass of the soft tissue gave the total, ash-free, dry biomass of the macrofauna.

RESULTS

Meiofauna surveys

The results of the meiofauna surveys have been presented in the form of contour maps of the numerical distribution of animals, as done by Renaud-Debyser (1963) (Figures 1–5 for Kings Beach and Figures 6–10 for Sundays River). Included in each figure are contour maps of the total numbers of meiofauna, the numbers of dominant taxa (nematodes, harpacticoids and mystacocarids) and finally the total numbers of all the other taxa combined. These other taxa included acarines, turbellarians, gastrotrichs, ostracods, oligochaets, polychaets, tardigrades and occasional members of the temporary meiofauna (McIntyre 1969) such as crustacean nauplii and calanoid copepods.

Figure 11 shows the relative percentages of the different taxa making up the meiofauna of these two beaches during each period of sampling, calculated from the combined counts of the three tide levels of each beach. The Kings Beach meiofauna consisted of a mean of 59 per cent nematodes, 17 per cent harpacticoid copepods, 9 per cent mystacocarids and 15 per cent other taxa which were dominated by oligochaets (10 per cent). The Sundays River meiofauna consisted of only 31 per cent nematodes but 42 per cent harpacticoids and 17 per cent mystacocarids. The remaining 10 per cent was again dominated by oligochaets (6 per cent).

Figure 11 shows some wide fluctuations in the relative proportions of the different taxa. The most notable fluctuation on Kings Beach was the very high proportion of 'others' on 7.1.74. This was due to an aggregation of oligochaets at HW, and is not considered a normal fluctuation. On Sundays River the three important taxa, nematodes, harpacticoids and mystacocarids, all showed wide fluctuations, but these had no regular pattern.

Animals were encountered at all depths sampled and they penetrated below the water tables. On both beaches they appeared to penetrate well below 1 m into the sand at HW, which is very deep for meiofauna, but not unknown (Renaud-Debyser 1963). On Kings Beach,

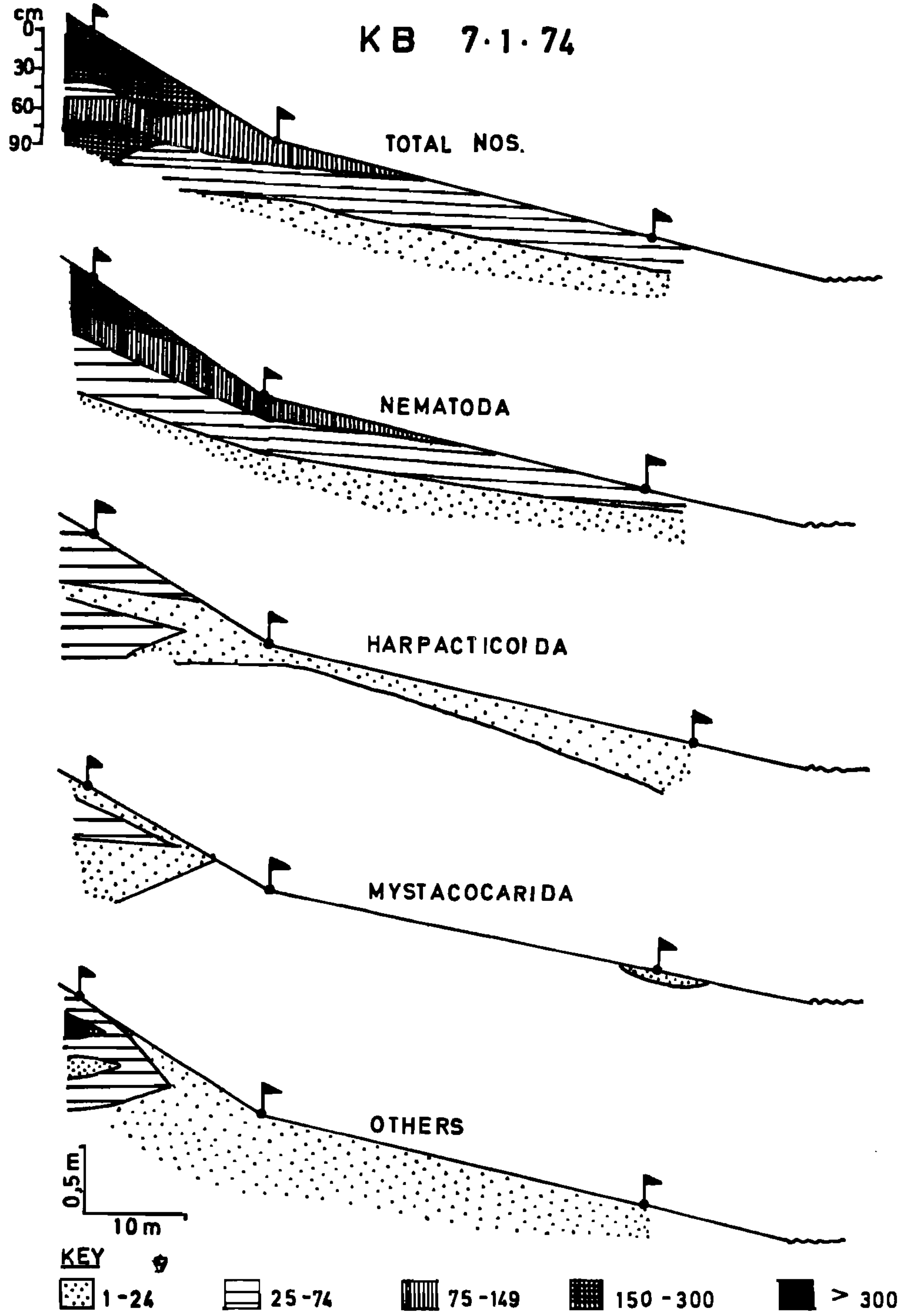

FIGURE 1

Kings Beach, 7.1.74. Meiofauna distribution during spring low tide. Flags indicate low, mid and high tide levels and the key indicates animal numbers per 150 cm³ of sand.

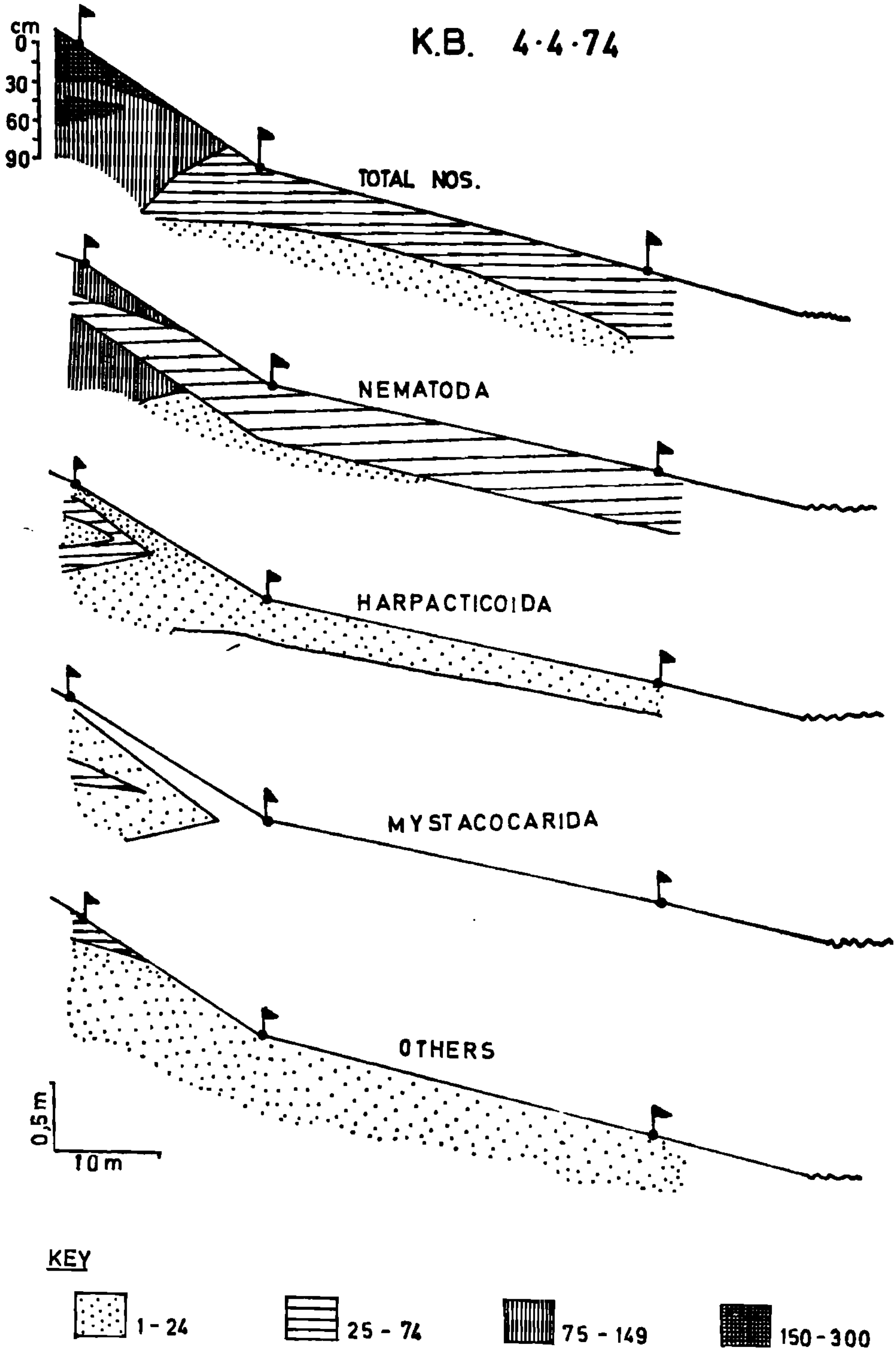

FIGURE 2
Kings Beach, 4.4.74. Legend as for Figure 1.

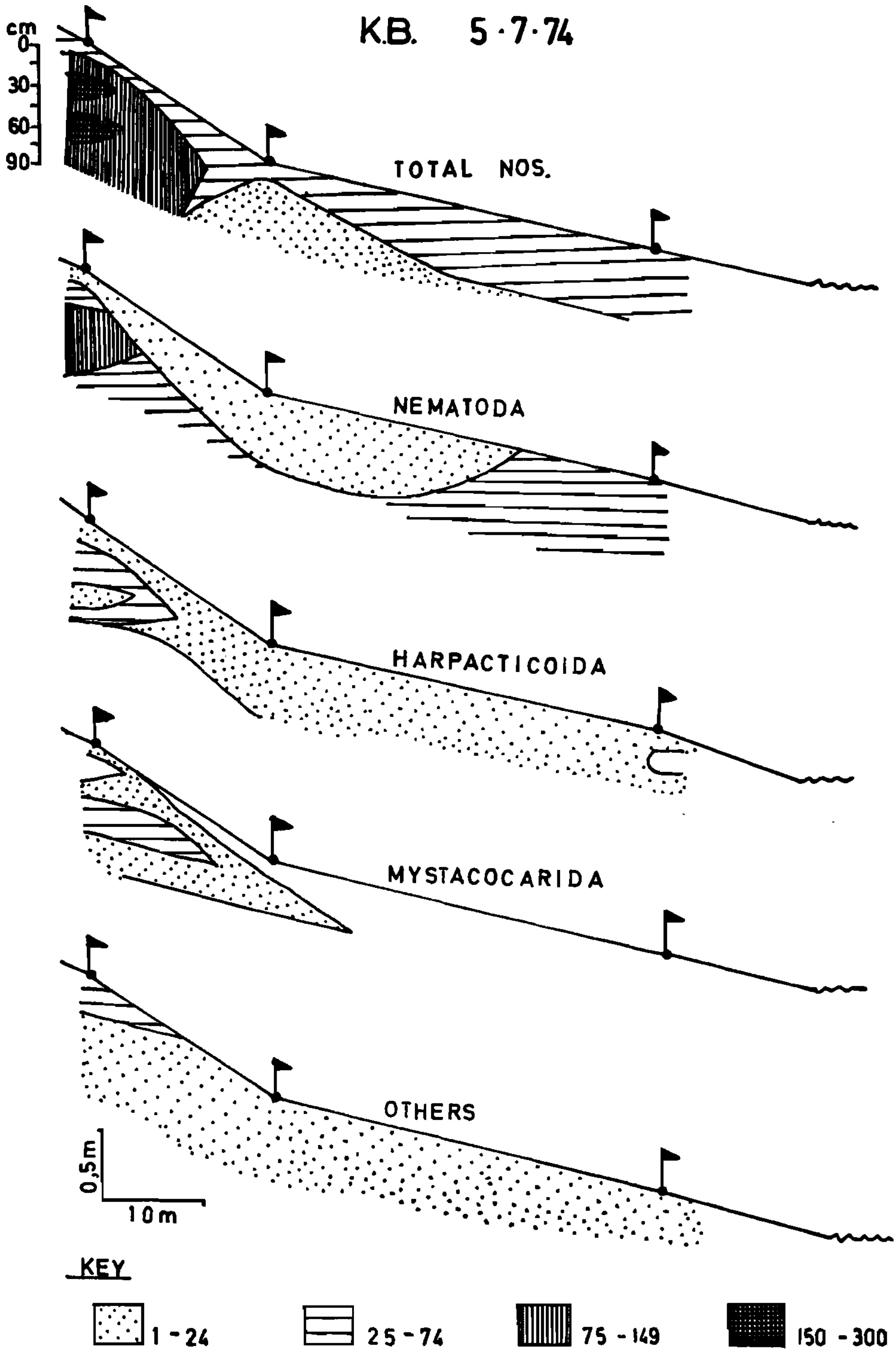

FIGURE 3
Kings Beach, 5.7.74. Legend as for Figure 1.

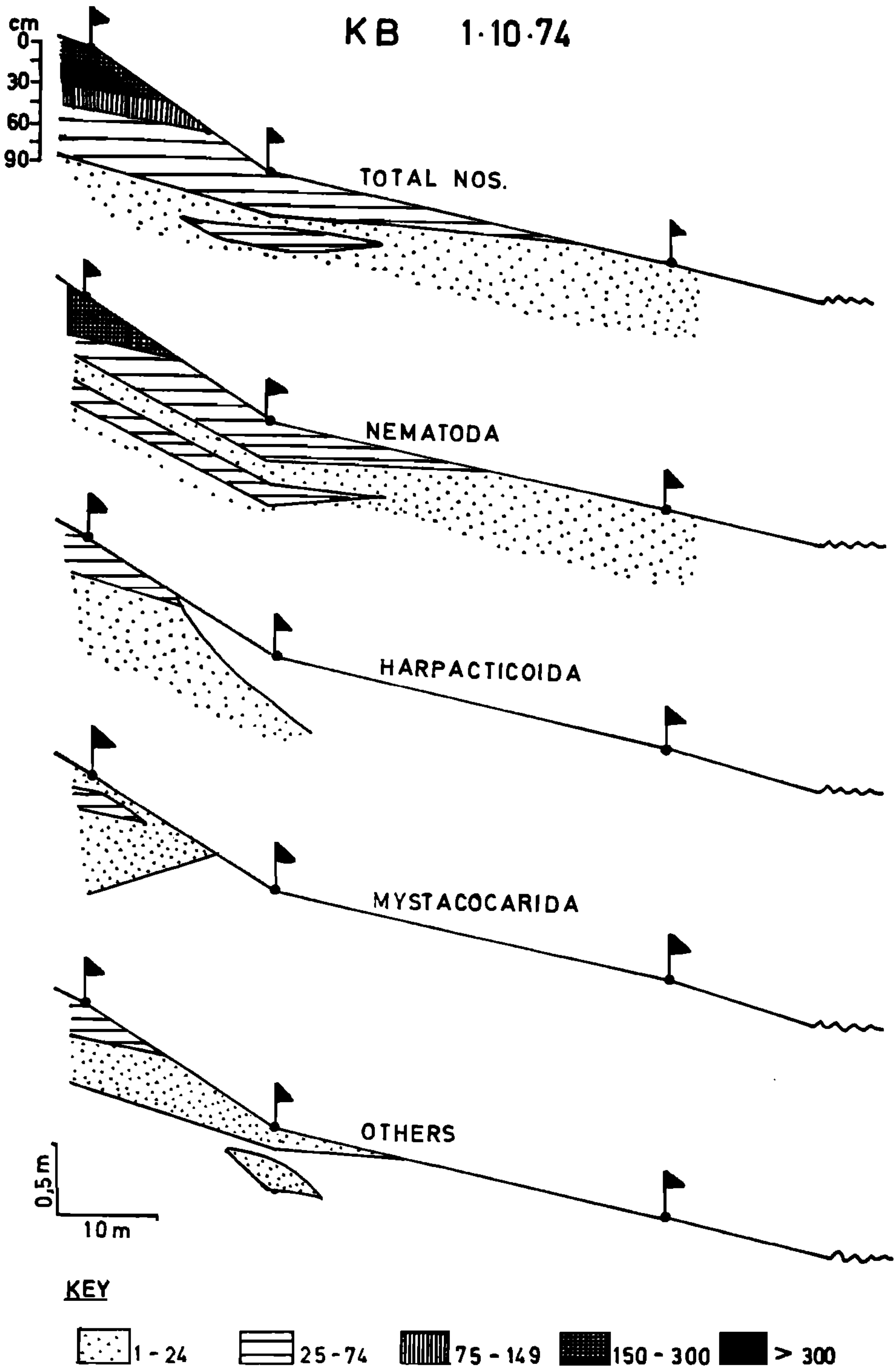

FIGURE 4
Kings Beach, 1.10.74. Legend as for Figure 1.

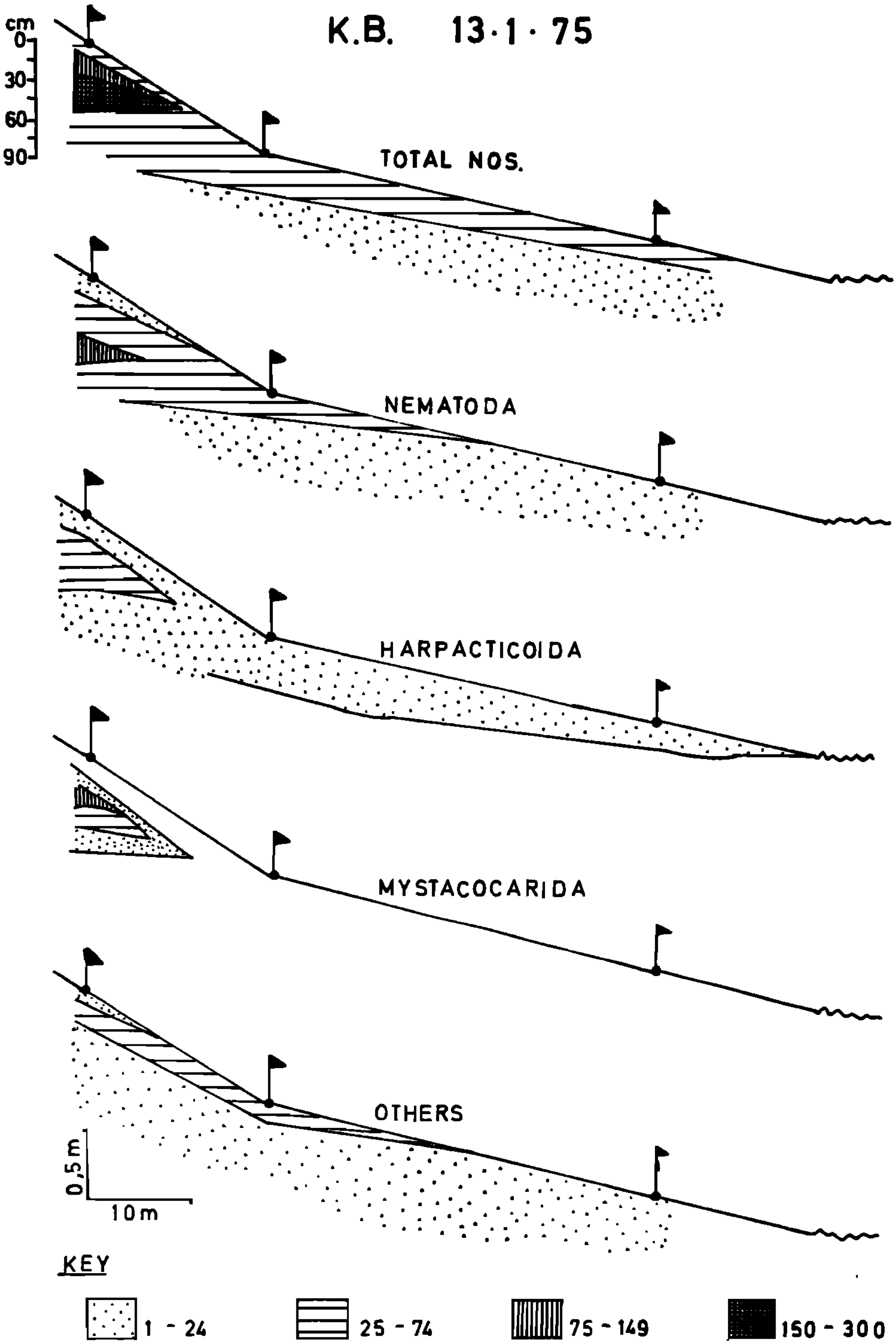

FIGURE 5
Kings Beach, 13.1.75. Legend as for Figure 1.

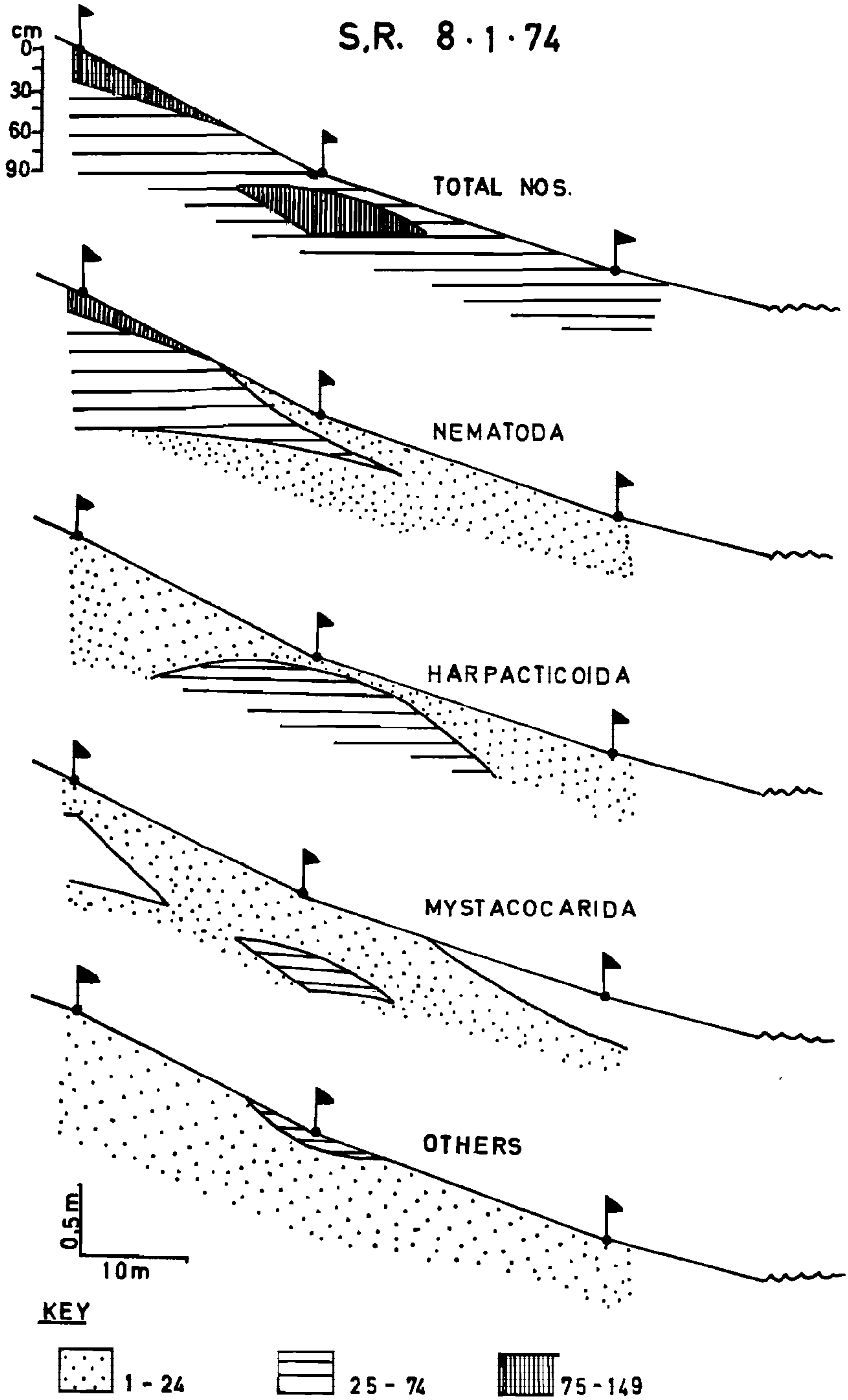

FIGURE 6
Sundays River, 8.1.74. Legend as for Figure 1.

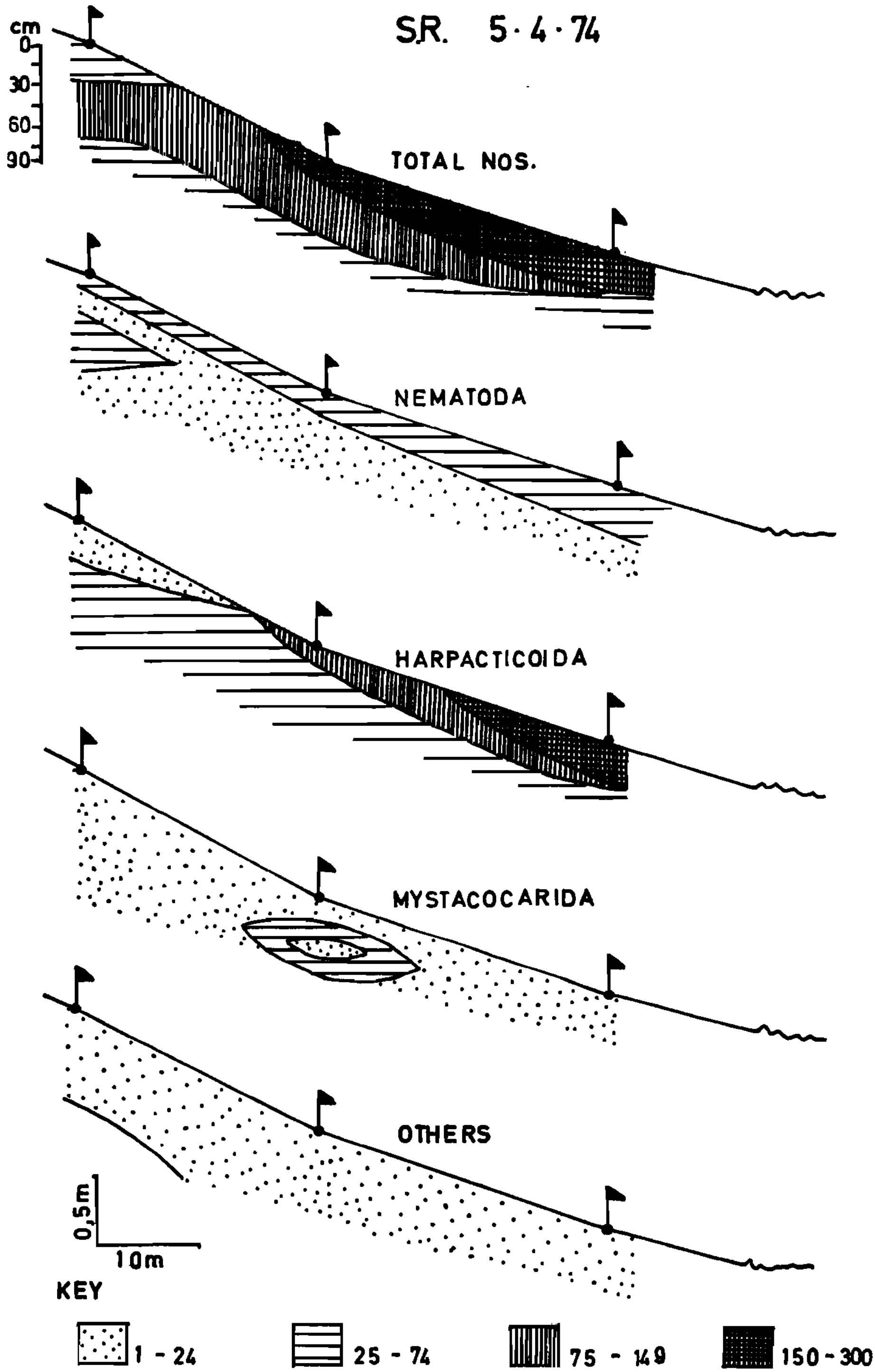

FIGURE 7
Sundays River, 5.4.74. Legend as for Figure 1.

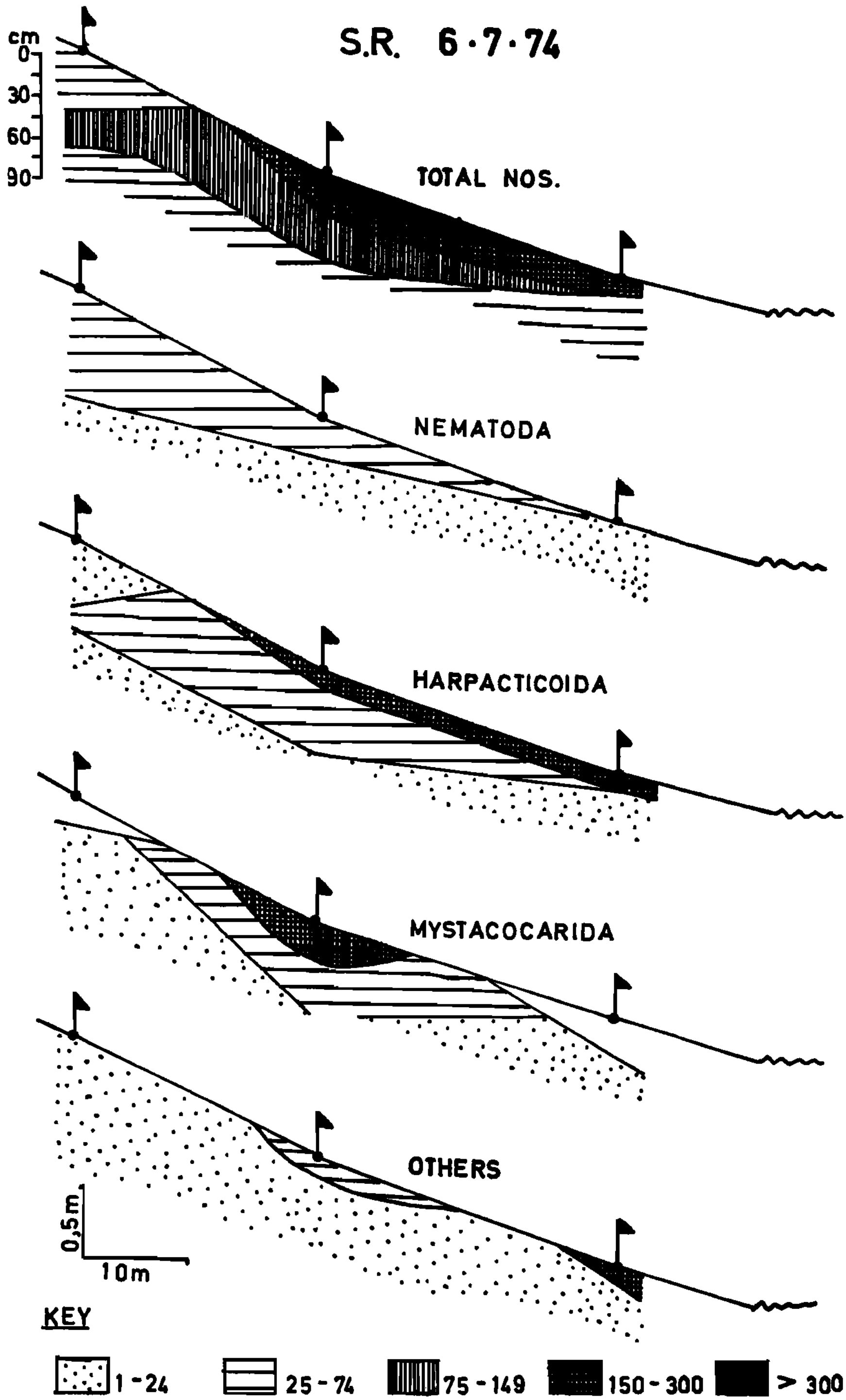

FIGURE 8
Sundays River, 6.7.74. Legend as for Figure 1.

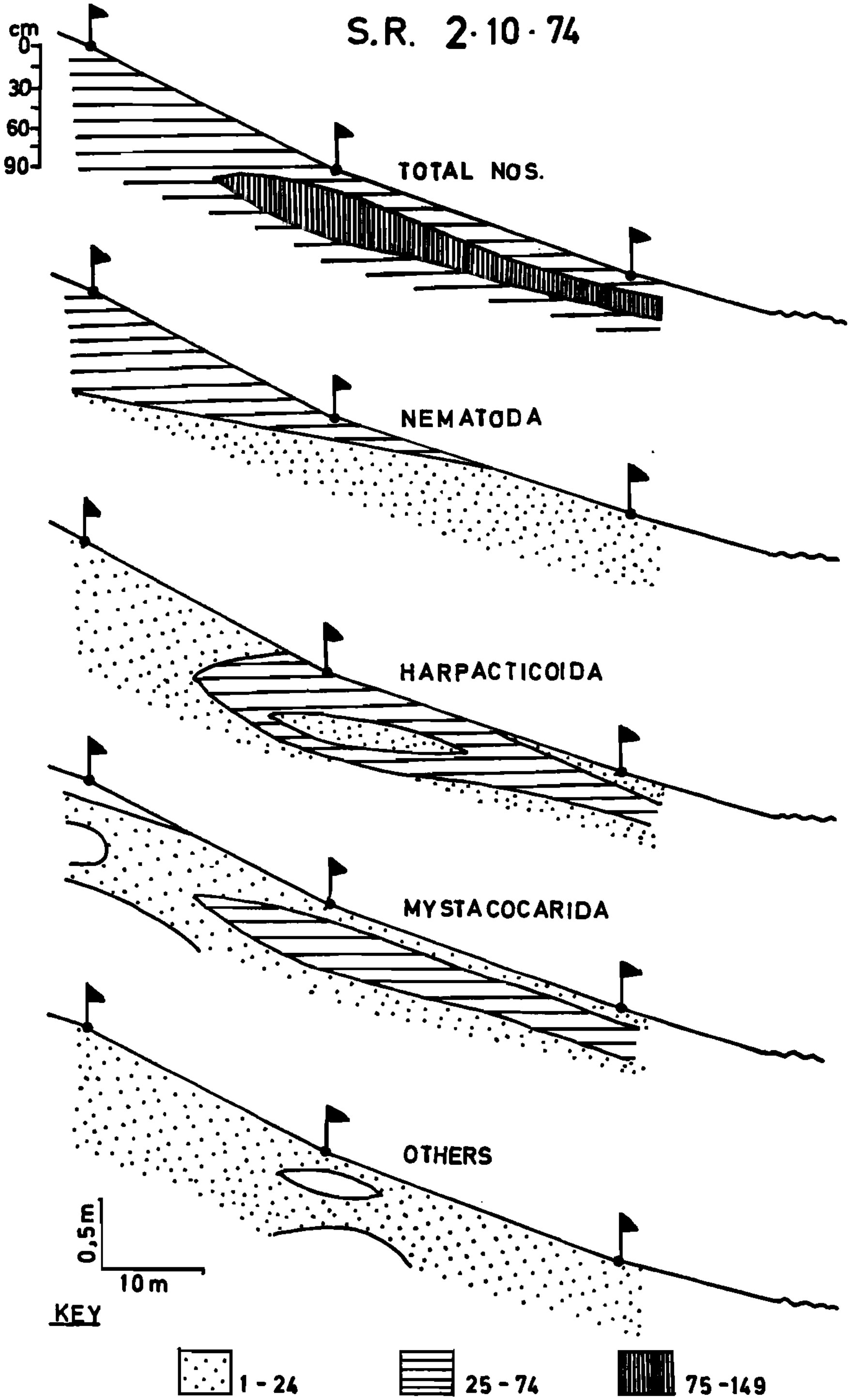

FIGURE 9
Sundays River, 2.10.74. Legend as for Figure 1.

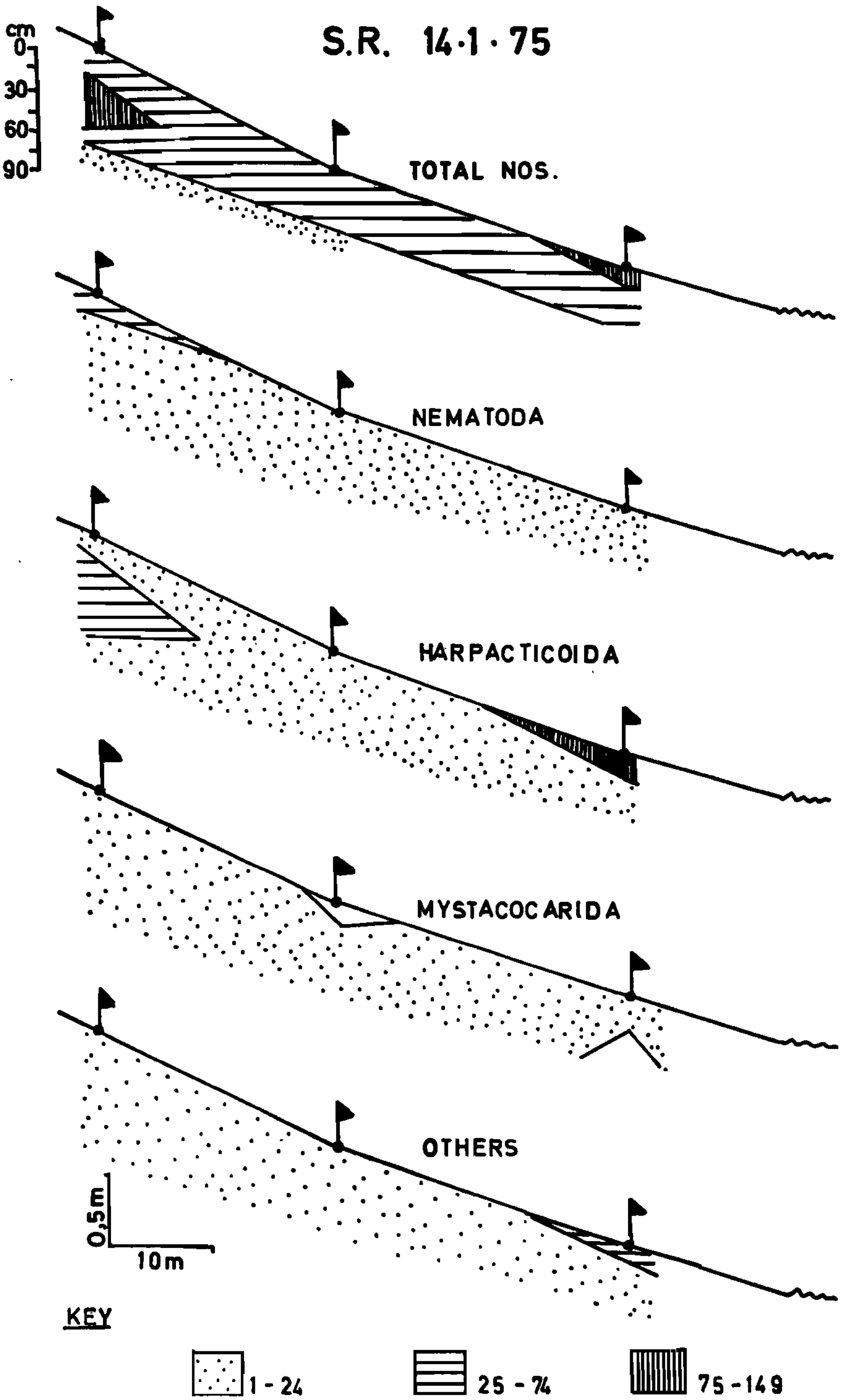

FIGURE 10
Sundays River, 14.1.75. Legend as for Figure 1.

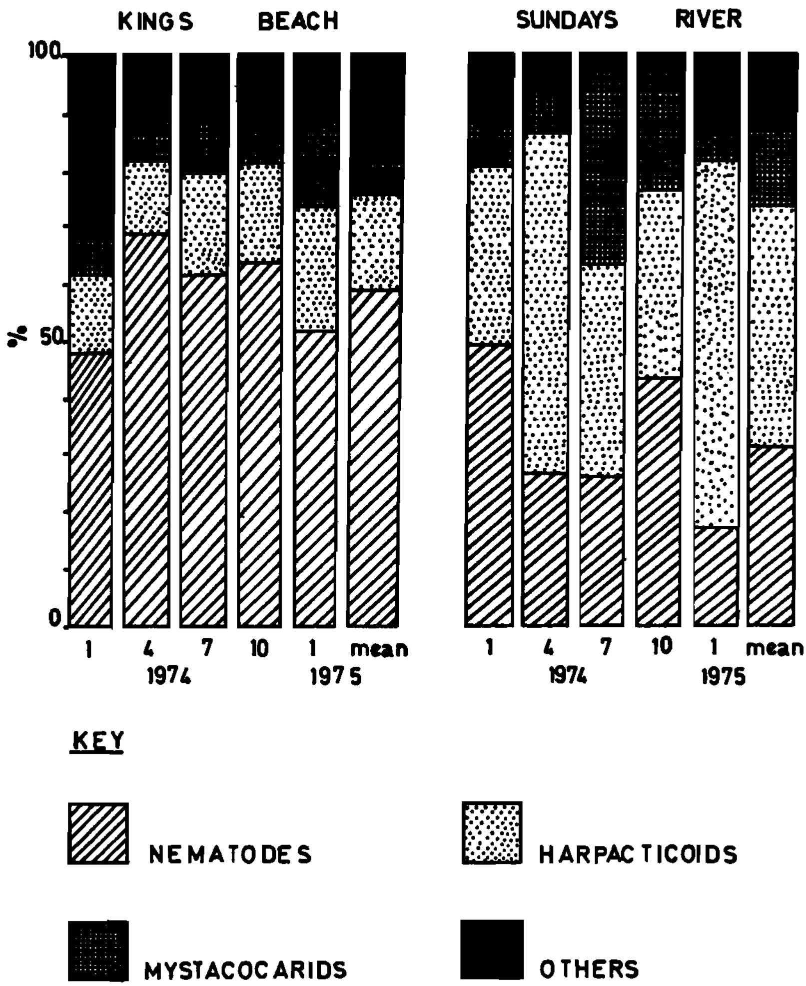

FIGURE 11

Percentages of different taxa making up the meiofauna of Kings Beach and Sundays River. Numbers below each column refer to months during 1974 and 1975.

animals tended to concentrate around HW and decrease in numbers towards LW. The different taxa appeared to occupy characteristic tide levels and depths in the sand which showed some fluctuation with the seasons. At Sundays River the meiofauna was concentrated between MW and LW, but decreased only slightly towards HW. Some seasonal movements were again apparent. Inspection of Figures 1–10 and comparison with the environmental factors analysed in McLachlan (1977) suggested that available oxygen was the dominant limiting factor on Kings Beach, while both oxygen and food (estimated in the form of chlorophyll *a*) and perhaps to a lesser extent desiccation, were the dominant factors at Sundays River. In order to quantify the effects of these factors on the numerical distribution of the meiofauna the following statistical analyses were carried out. A linear regression line was calculated for mean meiofauna numbers and percentage oxygen saturation on Kings Beach and a multiple regression line (Snedecor 1956) for mean meiofauna numbers, percentage oxygen saturation and chlorophyll *a* (taken as representing available food) at Sundays River.

The regression line for Kings Beach was

$$Y = 47{,}5 + 2{,}33X$$

where Y is the mean meiofauna number per 150 cm^3 sand, and X is the percentage oxygen saturation. This regression was found to be highly significant ($r = 0{,}84$; $p < 0{,}01$). If the 0–15 cm level at HW is left out, however, the regression becomes even more significant ($r = 0{,}86$ for $Y = 56{,}4 + 2{,}56X$). It may thus be concluded that 71 per cent (*i.e.* r^2 expressed as a percentage) of the meiofauna distribution on Kings Beach can be explained by the availability of oxygen but that desiccation or lack of food in the surface layer at HW can also be an important factor.

The multiple regression equation for Sundays River was

$$Y = 4{,}84 + 0{,}338X_1 + 11{,}312X_2$$

where Y is the mean meiofauna number per 150 cm^3 sand, X_1 is the percentage oxygen saturation and X_2 is the mg chlorophyll *a* per kg dry sand multiplied by 10^2. This regression was found to be significant ($p < 0{,}05$). It may therefore be concluded that both oxygen and food (chlorophyll *a*) are limiting factors at Sundays River and that food is the more important of the two. Desiccation, which is generally directly related to oxygen availability, may be of some importance at upper HW levels. As chlorophyll *a* at Sundays River was below the limit of sensitivity of the method used it is not considered feasible to estimate its exact critical levels.

Meiofauna biomass

TABLE 1

Mean, individual, ash-free, dry mass of meiofauna taxa from Kings Beach (KB) and Sundays River (SR). All masses in μg.

Taxon	*Locality*	*Mean*	*Range*
Nematoda	KB	0,5	0,2–1,4
Nematoda	SR	0,3	0,1–0,5
Harpacticoida	KB + SR	0,4	0,3–0,5
Mystacocarida	KB + SR	0,4	0,3–0,5
Oligochaeta	KB	1,6	1,1–2,0

The mean, individual, ash-free, dry biomass for different meiofauna taxa is listed in Table 1. The results have been taken to the nearest 0,1 μg and include a mean and range of values. Taxa not appearing in the table were too rare to weigh and have arbitrarily been given a biomass of 0,5 μg (*e.g.* tardigrades, nauplii, ostracods and polychaets). As all of the minor taxa, except oligochaets, make up very little of the meiofauna numbers, approximation of their biomass is considered permissible. As there was a noticeable size difference between Kings Beach and Sundays River nematodes their biomass was estimated separately.

Using the biomass values in Table 1, the meiofauna biomass per square metre has been calculated for all tide levels and seasons on Kings Beach and Sundays River (Table 2). These results have not been corrected for losses during extraction or for animals living below the depths sampled.

TABLE 2

Uncorrected, ash-free, dry biomass values of the Kings Beach (KB) and Sundays River (SR) meiofauna. Upper dates refer to Kings Beach and lower dates to Sundays River. All values in g/m^2. The total biomass values are for the sum of the three tidal levels and not for the whole beach.

	DATE					
Station	7.1.74/ 8.1.74.	4.4.74/ 5.4.74.	5.7.74/ 6.7.74.	1.10.74/ 2.10.74.	13.1.75/ 14.1.75.	*Means* ± SD
KB HW	1,03	0,54	0,79	0,48	0,40	0,65±0,26
KB MW	0,10	0,07	0,05	0,08	0,03	0,07±0,03
KB LW	0,05	0,08	0,07	0,02	0,04	0,05±0,02
Total	1,18	0,69	0,91	0,58	0,47	0,77±0,29
SR HW	0,11	0,16	0,14	0,08	0,12	0,12±0,03
SR MW	0,16	0,16	0,42	0,14	0,05	0,19±0,14
SR LW	0,04	0,22	0,33	0,07	0,15	0,16±0,12
Total	0,31	0,54	0,89	0,29	0,32	0,47±0,25

It can be seen from Table 2 that while the biomass at the different tide levels is fairly uniform at Sundays River, it is very high at HW and low at LW on Kings Beach.

The seasonal fluctuation in the meiofauna biomass is shown graphically in Figure 12 and the fluctuation in numbers of the dominant taxa is shown for comparison in Figures 13 and 14. The pattern on Sundays River Beach appears fairly distinct with the highest biomass in winter and the lowest in summer. The fluctuation in numbers was slightly more complex, harpacticoids reaching a peak in autumn (April) and having lowest numbers in spring. Mystacocarids reached a peak in winter and were least in summer. Nematodes tended to decrease steadily in numbers throughout the sampling period.

On Kings Beach the pattern was not so clear. Very high biomass values were recorded in the first summer and then numbers tailed off towards the second summer with a small peak

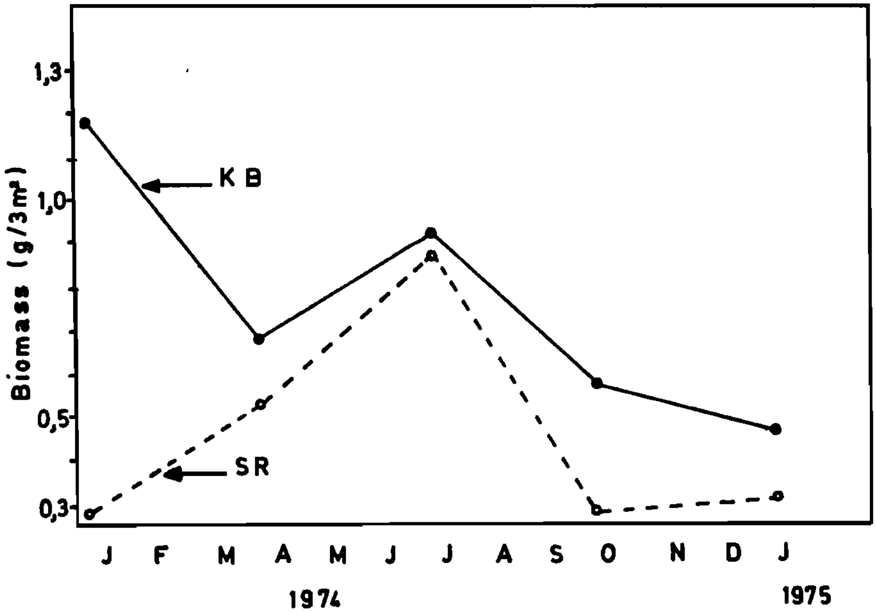

FIGURE 12

Meiofauna biomass totals for the three tide levels on Kings Beach and Sundays River over a 13-month period. The biomass is the uncorrected, ash-free, dry weight.

in winter. The very high biomass of the first summer was largely due to a temporary high aggregation of oligochaets (Figure 11: 'others'), which, because of their relatively high biomass (Table 1) dominated the total biomass. A more reliable picture can be obtained from the curves of numbers in Figure 13. Here it can be seen that nematodes, as on Sundays River Beach, tended to drop steadily in numbers during the sampling period. Harpacticoids and mystacocarids, however, both had more constant numbers with a slight decrease in winter.

Macrofauna surveys

The species recorded during the macrofauna surveys are listed in Table 3.

This macrofauna is typical for these beaches and most of the species were also recorded by Brown (1971) on beaches of the Cape Peninsula. Nagabushanam & Rao (1969) even found *Glycera*, *Donax* and *Bullia* on exposed Indian beaches. The most important and largest of these animals is *Donax serra* which occupies a distinct band near MW on exposed Cape beaches. This band is moderately developed at Sundays River but absent on Kings Beach, which is too sheltered for this species (Hanekom 1975). *D. serra* is thus the main component of the macrofauna at Sundays River. The smaller *D. sordidus* occurs mainly near LW and, unlike *D. serra*, appears to migrate up and down the beach with the tides (Hanekom personal com-

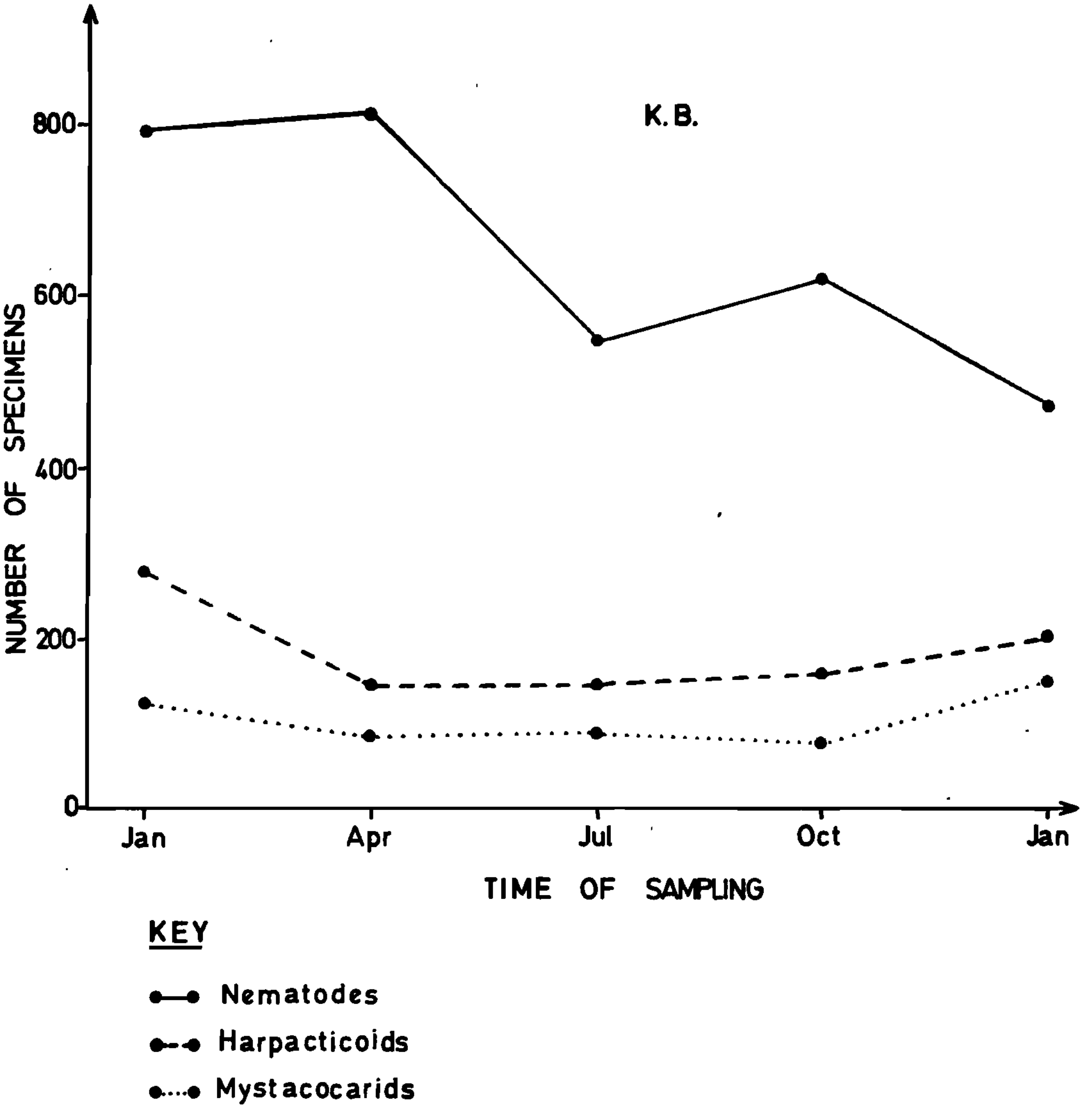

FIGURE 13

Numbers of the dominant taxa summed for 10 cm² at each of the three tide levels on Kings Beach.

munication). The most important component of the macrofauna on Kings Beach is the 'plough shell' *Bullia* which occurs mainly near LW. On both beaches the macrofauna becomes poorer in species as the shore is ascended. This is a fairly typical pattern (Eltringham 1971).

TABLE 3

Species collected during the macrofauna surveys of Kings Beach and Sundays River.

LEVEL	*KINGS BEACH*	*SUNDAYS RIVER*
HW	Crustacea *Eurydice longicornis* (Studer)	Crustacea *Eurydice longicornis* *Pontogeloides latipes* Barnard Insecta Unidentified larva
MW	Polychaeta *Nephtys* sp. *Glycera convoluta* Keferstein *Arabella iricolor* (Mont.) Crustacea *Eurydice longicornis* *Gastrosaccus psammodytes* Tattersall Mollusca *Bullia rhodostoma* Reeve	Polychaeta *Glycera convoluta* *Scolelepis squamata* (Müller) Crustacea *Eurydice longicornis* *Pontogeloides latipes* Mollusca *Donax serra* Röding *Donax sordidus*
LW	Polychaeta *Nephtys* sp. *Glycera convoluta* Crustacea *Gastrosaccus psammodytes* Mollusca *Donax sordidus* Hanley *Bullia digitalis* Meuschen *Bullia rhodostoma*	Polychaeta *Nephtys* sp. Crustacea *Gastrosaccus psammodytes* *Emerita austroafricana* Schmitt Mollusca *Donax sordidus* *Bullia rhodostoma*

Macrofauna biomass values

The ash-free, dry biomass of the macrofauna is given in Table 4. High values at MW at Sundays River are due to the *Donax serra* band.

It is evident from Table 4 that the exposed beach (Sundays River) has a much higher standing crop of macrofauna than the sheltered beach (Kings Beach).

Comparison of macrofauna and meiofauna

As the method used for sampling the macrofauna did not miss any animals, no correction to the macrofauna biomass is necessary. The meiofauna biomass does, however, need to be

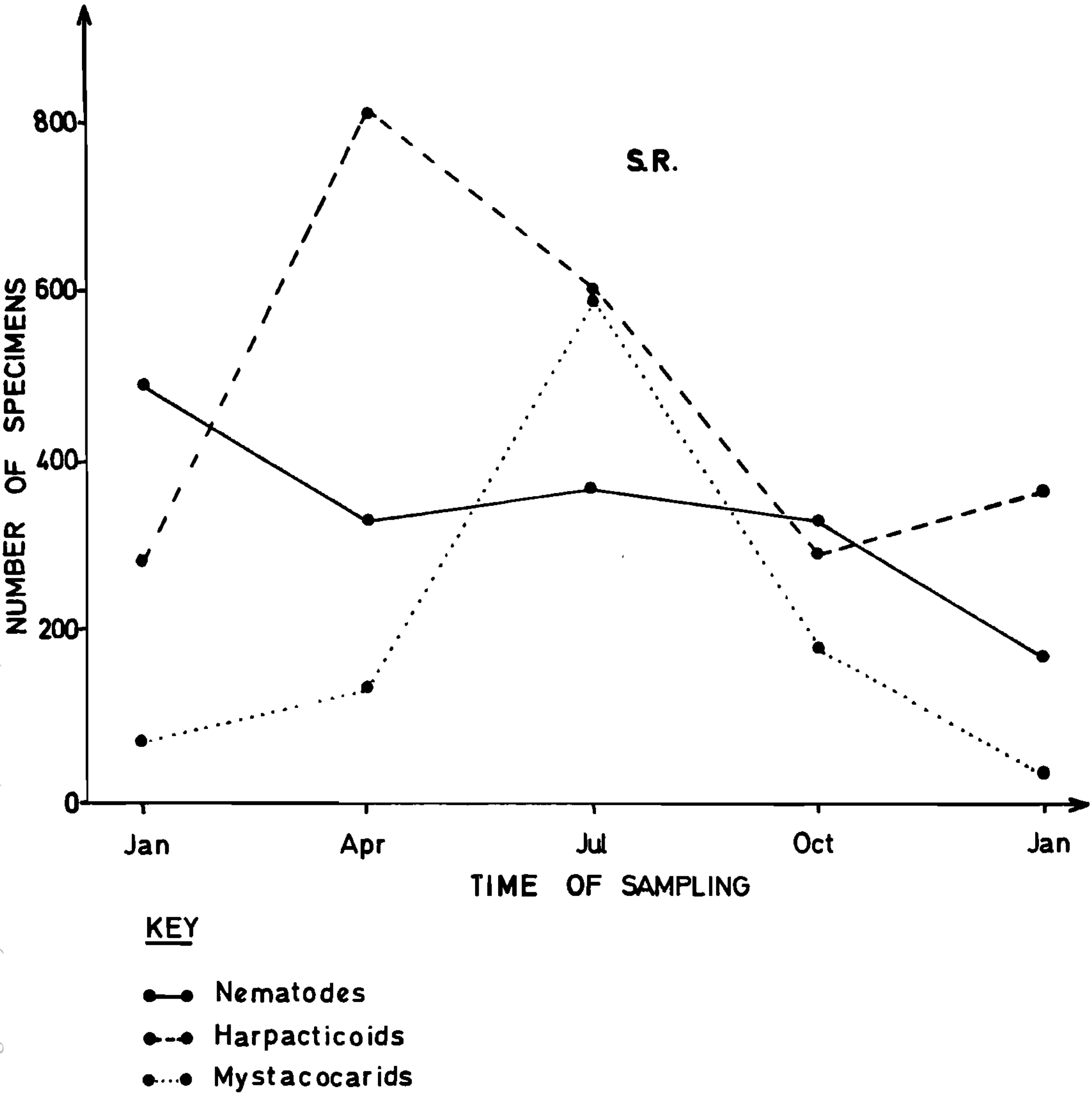

FIGURE 14

Numbers of the dominant taxa summed for 10 cm² at each of the three tide levels on Sundays River Beach.

corrected for losses owing to (1) animals living too deep to be sampled and (2) the 20 per cent lost during extraction. In Table 5 the corrected mean meiofauna biomass and numbers as well as mean macrofauna biomass and numbers are listed for comparison. Also listed is the percentage of the meiofauna at each tide level on both beaches that was estimated to live too deep to be sampled.

TABLE 4

Ash-free, dry biomass of the Kings Beach and Sundays River macrofauna in g/m². Upper dates refer to Kings Beach and lower dates to Sundays River.

Station	Date 2.4.74/3.4.74.	Date 1.10.74/2.10.74.	Mean
KB HW	—	0,02	0,01
KB MW	0,36	0,14	0,25
KB LW	0,71	0,98	0,85
		Total	1,11
SR HW	0,15	0,07	0,11
SR MW	7,83	2,35	5,09
SR LW	1,34	1,03	1,19
		Total	6,39

TABLE 5

Comparison between numbers and biomass of meiofauna and macrofauna of Kings Beach and Sundays River. All biomass values are in ash-free, dry mass (g) per m². Totals represent the totals of values from the three tide levels. Number (corrected) refers to the total number of animals per m² and minimum and maximum counts reflect the range in numbers recorded during different sampling seasons.

	MEAN BIOMASS			MEAN NUMBERS (/m²)						
Station	*Meiofauna not sampled %*	*Meiofauna corrected g/m²*	*Macrofauna g/m²*	*Meiofauna /10⁵ Min.*	*Max.*	*Mean*	*Macrofauna Min.*	*Max.*	*Mean*	*Macro./Meio.*
KB HW	7	0,87	0,01	10,6	22,5	15,4	0	2	1	1/1 540 000
KB MW	1	0,09	0,25	1,0	2,5	1,6	3	8	6	1/26 670
KB LW	19	0,07	0,85	0,6	2,2	1,5	5	7	6	1/25 000
TOTAL	8	1,03	1,11			18,5	—	—	13	1/142 310
SR HW	17	0,18	0,11	4,1	6,6	5,3	2	15	9	1/58 890
SR MW	15	0,27	5,09	1,7	14,7	6,8	2	21	12	1/56 670
SR LW	25	0,25	1,19	1,4	8,0	4,1	12	33	23	1/17 830
TOTAL	20	0,70	6,39			16,2	—	—	44	1/36 820

While macrofauna/meiofauna comparisons on the basis of numbers favour the meiofauna and on the basis of biomass favour the macrofauna, comparisons on the basis of production estimates would have the most ecological significance. Further, because so little is known of meiofauna production, it is considered worthwhile at this point to speculate on production values. McIntyre (1964) suggested that a factor of 10 to convert standing crop to production is probably a conservative figure for meiofauna. For macrofauna he used a conversion factor of two for species living longer than one year and five for short-lived species. Taking into account the relative proportions of long- and short-lived species on Kings Beach and Sundays River, conversion factors of 3,5 and 2,5 are suggested for these two beaches respectively.

Extrapolating the biomass data in Table 5 to cover not just 1 m^2 at each tide level, but a strip 1 m wide from LWS to an intertidal height of 2 m would allow calculation of the production of such an intertidal unit (Hanekom 1975). The production figures so derived (in ash-free, dry mass per intertidal unit per year) are:

	Kings Beach	*Sundays River*
Macrobenthic production	87 g/unit/yr.	391 g/unit/yr.
Meiobenthic production	105 g/unit/yr.	150 g/unit/yr.

The meiofauna thus makes up 55 and 28 per cent of the total secondary production on Kings Beach and Sundays River respectively. Also worthy of note here is the fact that the total intertidal meiofauna biomass at Sundays River (15,0 g/unit) is greater than that on Kings Beach (10,5 g/unit). Although Kings Beach has very high meiofauna numbers at HW, these drop rapidly towards MW and LW. The Sundays River meiofauna numbers are not as high as Kings Beach HW but are more uniform and this consistency, together with a wider intertidal area, yields an overall higher biomass per intertidal unit.

DISCUSSION

From Figures 1–11 it is evident that the two beaches differ markedly in the composition of their meiofauna and mainly in the relative proportion of nematodes and crustaceans (harpacticoids and mystacocarids). Nematodes dominate all tide levels on Kings Beach, while crustaceans dominate the LW and MW levels at Sundays River and nematodes only the HW level. Even the Kings Beach nematode proportion is low in comparison with proportions found by other workers. In most cases nematodes make up 60–80 per cent of the total numbers in the meiofauna (Rees 1940; McIntyre 1964, 1968, 1969; Tietjen 1966; Panikkar & Rajan 1970) and harpacticoids are generally the second most important taxon (McIntyre 1969). Rao (1970), however, found that nematodes made up only 3 per cent of the interstitial fauna on the sandy beaches of some Indian islands. If the mean of these two beaches is taken as an indication of the Algoa Bay mean, the psammolittoral meiofauna of Algoa Bay may be said to consist of 45 per cent nematodes, 30 per cent harpacticoids, 13 per cent mystacocarids and 12 per cent others (8 per cent oligochaets). The relatively high crustacean numbers recorded on these beaches must reflect somewhat different conditions and the fact that the more exposed beach had the higher proportion of crustaceans suggests that this could be related to exposure and/or substrate properties. Gray & Rieger (1971) found that harpacticoids dominated the upper tide levels on an exposed beach while nematodes dominated a more sheltered beach which also had a richer meiofauna. In this connection it is worthy of note that the sands of Kings Beach (Md = 207 μm) are only just coarser than the 200 μm limit of Wieser (1959), which is supposed to be a barrier separating most burrowers from the interstitial sliders.

The meiofauna numbers encountered during this study were 60–2 250/10 cm^2 on Kings Beach and 140–1470/10 cm^2 at Sundays River. Kings Beach thus includes both the highest (at HW) and lowest (at LW) numbers, while densities at Sundays River are much more uniform. Others workers have recorded numbers between 11 and 11 820/10 cm^2 although most values for sandy beaches lie between 50 and 1 500/10 cm^2 (McIntyre 1969). The upper Kings Beach values may therefore be considered high while the remainder are moderate.

The distribution of the different meiofauna taxa on these beaches (Figures 1–10) was by no means uniform and each taxon tended to occupy a characteristic tide level and depth in the sand. On Kings Beach the highest numbers occurred in the top 60 cm at HW and numbers dropped rapidly towards mid and low water and deeper in the substrate. Nematodes reached their highest densities near the surface as did the harpacticoids. Mystacocarids, however, were generally concentrated between the 30 and 60 cm depths at HW and the minor groups were evenly scattered but increased somewhat at HW.

The distribution of meiofauna at Sundays River was noticeably compressed downshore in comparison with Kings Beach. The meiofauna here was concentrated between MW and LW but decreased only slightly towards HW. Ganapati & Rao (1962) and McIntyre (1968) also found maximum numbers at the MW level on more exposed beaches where the particle size was very similar to that of Sundays River. Wieser (1959) came to similar conclusions and Pennak (1940) also found meiofauna distribution compressed downshore on steeper lacustrine beaches. This downshore compression therefore appears to be a normal pattern of meiofauna distribution on exposed beaches.

The different taxa were not confined to quite such characteristic levels at Sundays River as on Kings Beach, and distribution was on the whole more uniform. Nematodes occurred everywhere but tended to be most common in the surface 30 cm towards HW. Harpacticoids also occurred throughout the beach but were most abundant in the upper 30–45 cm between the LW and MW levels. Mystacocarids also exhibited wide distribution but were most abundant at MW 15–60 cm depth. Seasonal variations will be discussed after an examination of the factors responsible for these basic distribution patterns.

The basic pattern emerging from the above is that the meiofauna is concentrated around HW on Kings Beach and around MW at Sundays River. It has been shown that the numerical distribution of the meiofauna on Kings Beach can be explained in terms of the availability of oxygen and at Sundays River by the limiting amounts of available food and oxygen. Kings Beach with its fine sands and poor drainage has lower oxygen values than Sundays River (McLachlan 1977). Food is, however, plentiful here and the chlorophyll *a* values recorded on Kings Beach were more than ten times those recorded at Sundays River. Available oxygen is therefore the main factor limiting meiofauna numbers on Kings Beach. The zone corresponding to 60–100 per cent oxygen saturation on Kings Beach, HW 0–60 cm, is also the zone with the richest meiofauna. At the deeper levels at MW and LW, where oxygen saturation drops below 30 per cent, meiofauna numbers are very low. Jansson (1968) also related the distribution of some species to the availability of oxygen.

It must be emphasized, however, that available oxygen is not the only important factor on Kings Beach and the number/oxygen regression was found to increase in significance (from r = 0,84 to r = 0,86) if the 0–15 cm level at HW were left out of the calculations. This suggests that food may have some influence here, as low chlorophyll *a* values were recorded at the 0–15 cm level (McLachlan 1977: Table 3). Desiccation may, however, also be a factor of importance here.

At Sundays River, oxygen values are higher than on Kings Beach but available food (measured as chlorophyll *a*) is very low and is the main limiting factor (McLachlan 1977: Figure 4 and Table 3). Taking all the data into account it would appear that food is the dominant limiting factor at HW and MW levels but that at LW oxygen also becomes limiting. Effects of desiccation are difficult to estimate because up to approximately 90 per cent water-saturation of the sand, desiccation and oxygen saturation are directly related. It would, however, appear that desiccation may have some significance near the surface at HW.

Panikkar & Rajan (1970) found no clear correlation between meiofauna distribution and chlorophyll values in the sand. Hulings (1974), however, considered food supply a primary factor in the seasonality of Lebanese sand beach meiofauna. As available food has not been monitored seasonally in this study its influence can not be assessed here. Ganapati & Rao (1962) proposed that food, temperature, moisture and substrate texture were the main factors affecting meiofauna distribution and numbers. While in this study substrate does not appear to directly affect the meiofauna numbers, it may well affect the taxonomic composition of the meiofauna which differs so markedly on these two beaches. Substrate does, however, affect numbers indirectly by its effects on drainage and thus on interstitial oxygen.

Gray & Rieger (1971) have considered beach stability as playing an important role in controlling meiofauna biomass values. If this were the case Kings Beach should have a higher biomass than Sundays River. However, while the Kings Beach HW biomass is high, the beach as a whole has a lower total meiofauna biomass than Sundays River. The high biomass at Kings Beach HW has been shown to be a result of sufficient available oxygen in the presence of excess available food. Further, at Sundays River, available food has been shown to be the main limiting factor. If therefore does not appear that beach stability has any great direct influence on the meiofauna biomass of these two beaches.

Salinity is relatively constant in the interstitial environment (McLachlan 1977: Table 4) and it is unlikely that this could have any great influence on the meiofauna. Other workers have found the meiofauna to be extremely tolerant of lowered salinities (McIntyre 1969) and it is unlikely that even heavy rain, which hardly affects interstitial salinities, could have any effect. Salinities would rise fairly slowly due to evaporation and do not appear to affect the meiofauna. Effects of rain on the meiofauna will be discussed again in Part III of this series.

The temperature range experienced on these beaches (McLachlan 1977), is very mild. Various workers have found the meiofauna capable of tolerating extreme temperature ranges (McIntyre 1969) and temperature is thus unlikely to have any limiting influence.

Some seasonal fluctuations in the meiofauna are evident from Figures 1–11. Fluctuations in the relative proportions of different taxa did not show any regular pattern and appear to be partly due to sampling error. Some seasonal patterns in the distribution of certain taxa are, however, apparent. On Kings Beach nematodes moved vertically downwards during winter (Figure 3) to occupy deeper levels in the substrate. This was most pronounced at MW. Harpacticoids also appeared to exhibit a downward movement during winter and spring (Figures 3, 4) at the MW and LW levels. The mystacocarids tended to lie a little shallower at HW during summer and spring than during winter and autumn (Figures 1–5).

At Sundays River nematodes showed a downshore movement during winter (Figure 8) and harpacticoids showed a distinct movement upwards in the substrate and downshore to between the MW and LW levels from summer through to winter (Figures 6–8). They dispersed again towards the next summer (Figures 9, 10). Mystacocarids also showed a movement towards the surface at MW during winter (Figure 8).

Conclusions on seasonal movements are made difficult by the fact that the movements were generally downwards in winter on Kings Beach and upwards in winter at Sundays River. Renaud-Debyser (1963) found a general downward movement of the meiofauna during winter. Harris (1972) also found a downward movement of harpacticoids during winter. The small movements observed on Kings Beach would thus appear to fit in with this pattern while the more pronounced movements at Sundays River are just the opposite. The upward movements in winter at Sundays River coincide with the increase in meiofauna numbers found then. Whether this upward movement in winter is thus due to an increase in crustacean numbers or to an actual upward movement of those living deeper down is difficult to estimate. It would, however, appear that there was both an increase in numbers and an upward movement during winter at Sundays River at MW and LW.

It is interesting that on average the Kings Beach nematodes are nearly twice as heavy as those from Sundays River (Table 1). As far as seasonal trends are concerned other workers (Ganapati & Rao 1962; Renaud-Debyser 1963) have generally found highest numbers of meiofauna in summer and lowest in winter. Kings Beach appears to have followed this pattern while Sundays River showed the opposite trend as far as harpacticoids and mystacocarids are concerned. The mild temperature range and absence of frost in Algoa Bay may explain why numbers showed no drastic drop in winter, but why they should have increased on Sundays River Beach is uncertain. It may have been due to increase in available food, but as this was not monitored seasonally no definite conclusions can be drawn. The steady decrease in nematode numbers on both beaches during the sampling period can not be explained and the large degree of the changes suggests that they are not due only to sampling error.

The macrofauna was found to be richer in both biomass and number of species on the exposed Sundays River beach, where high biomass values were due to the presence of *Donax serra*. Kings Beach on the other hand had a low macrofauna biomass. As far as numbers were concerned the macrofauna/meiofauna ratios were low. Ratios for Kings Beach lay between 1/25 000 and 1/1 540 000 while Sundays River ratios lay between 1/17 830 and 1/58 890. Other workers have recorded ratios between 1/0,09 and 1/42 458. It may therefore be concluded that Kings Beach has a rich meiofauna but a rather depleted macrofauna while Sundays River Beach has a moderate macrofauna and a rich meiofauna. The macrofauna generally dominates the total benthic biomass (Mare 1942) although the meiofauna/macrofauna ratio has been found to be highest on sandy beaches (McIntyre 1968; Nagabushanam & Rao 1969), suggesting that the meiofauna can best establish permanent populations there.

As stated earlier, however, comparisons on the basis of biomass favour the macrofauna just as numerical comparisons favour the meiofauna and comparisons of ecological significance should be based on production values. These were estimated and it was concluded that the meiofauna was responsible for 55 per cent and 28 per cent of the total secondary production on Kings Beach and Sundays River respectively. These are high proportions and serve to underline the great importance of psammolittoral meiofauna. In view of this it is obviously imperative that any study of energy flow on a soft-bottomed ecosystem should include the meiofauna as one of the major components.

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