

MIGRATIONS OF SANDY BEACH MEIOFAUNA

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ABSTRACT

The meiofauna at higher tide levels on a sheltered beach has been found to undergo vertical migrations correlated with the alternate drying and wetting of the sand during the tidal cycle. This movement may be modified by temperature differences between summer and winter and day and night. No major horizontal up/downshore movement of the meiofauna has been found during the tidal cycle and it appears that rain also has little effect on the meiofauna.

INTRODUCTION

In a recent study of the psammolittoral meiofauna of Algoa Bay, South Africa (McLachlan 1975), the question was asked whether the distribution patterns of the meiofauna, as sampled during low tide, exhibit any diurnal variations, particularly in relation to the tidal cycle.

Little detailed work has been done on migrations of meiofauna. Renaud-Debyser (1963) did some work on the colonization of submerged cores by meiofauna and Boaden (1963) studied the reactions of an archiannelid to various factors. Bush (1966) found a downward movement of meiofauna after heavy rain, and various authors, reviewed by McIntyre (1969), have studied the effects of temperature, grain size and oxygen on meiofauna movements. Boaden (1968) suggested migrations related to tidal movements, with most animals leaving the surface area when the wave surges crossed their habitat. His samples, however, only covered the surface 5 cm of sand over a period of five hours.

There are three basic directions in which meiofauna populations can move. These may be defined as (a) vertically, (b) 'horizontally' upshore and/or downshore and (c) horizontally alongshore. Only the first two of these components are of interest here as alongshore movements would not result in an animal entering areas of notably different conditions and it is highly unlikely that such movements would be anything but random on a uniform beach. Further, the method employed in this study of taking a series of samples parallel to the shore at each tide level would have eliminated any patchiness or variation in the alongshore distribution. Hence an investigation into the vertical and horizontal movement of the meiofauna in relation to daily changes in physical conditions was carried out.

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STUDY SITE

Kings Beach is a relatively sheltered beach of fine sand (median particle diameter 200-220 μm) which supports high numbers of meiofauna in the upper tide levels. The intertidal distance is approximately 50 m and the intertidal height about 2 m. The upper tidal levels experience moderate desiccation during low tide and the water saturation of the sand near the surface can drop to below 50% on hot days. Due to the reasonably fine sand and low permeabilities, oxygen saturation of the interstitial water drops fairly rapidly below the surface and falls below 30% deeper in the substrate and towards LW. The annual temperature ranges from about 5 to over 30°C on the sand surface at HW and from 13 to 25°C in the sea (McLachlan 1975).

METHODS

Vertical migration

The effects of tides and diurnal temperature fluctuations on vertical migrations were ascertained by systematic sampling over a complete tidal cycle. A site between MW and HW, which supported large numbers of animals and experienced maximal temperature changes and desiccation during low tide, was studied. Samples were taken three days after highest spring tide (3 December 1974) when low water was at 12h10 and high tide at 18h30. Two rods were hammered into the sand 20 m apart on a line parallel to the shore between the MW and HW levels. A rope with marks every metre was spanned between the rods 1 m above the sand. At 10h00 10 cores, each 2 m apart, were taken under the rope with a hand-operated corer of internal dimensions 25 cm x 5,7 cm². This was repeated every two hours for 14 hours. Each series of cores was taken 25 cm away from the previous series, in this manner eight cores being taken along every 2 m over 14 hours. By waiting for a downsurge of the waves it was possible to take these cores even during high tide. Each core was cut into 12 x 2 cm segments and the last cm discarded. The 10 core segments from each 2 cm vertical height at each time of sampling were pooled and sealed in glass jars which were taken back to the laboratory every few hours. Thus for every 2 cm depth range the total area covered was 57 cm², i.e. 114 cc of sand. These samples were extracted, stained and counted as in McLachlan (1975). Specimens belonging to the dominant taxa were counted separately.

Every hour during this experiment, and continuing till 08h00 the next morning, the following factors were measured in the experimental area: the sand temperature just beneath the surface and at a depth of 30 cm, and the depth of the water-table. The temperature of the sea water was also measured in the shallows (about 0,5 m deep). For the duration of sampling cloud-cover was slight with a moderate wind.

Six months later (June 1975) sampling was repeated at three hour intervals over a 24h period. Cores were divided into eight 3 cm-sections. Low tide was at 10h45 and the weather was cool with a moderate wind. On the evening of 11 June an unusual northerly wind blew small amounts of sewage onto the beach.

Horizontal migration

Experiments to determine horizontal movement were conducted five days after the previous experiment and three days before spring tide (December 1974). Low tide was at 08h05 and high tide at 14h10.

Movement was monitored over a five-hour period on the rising tide (08h30-13h30) and a further five-hour period on the outgoing tide (15h00-20h00). A note was made of the times when water reached and left the experimental site.

Sand was collected from the experimental area, washed three times in fresh water and dried at 110°C for 15 hours. Experimental tubes 15 cm x 10 cm² were filled with the 'sterile' sand and set up as in Figure 1 after moistening with sea water until equivalent to the surrounding beach.

The tubes were removed from the beach after five hours and three 2 cm-segments were removed from each end of the cores. Segments from corresponding depths were pooled. Samples were analysed as before.

RESULTS

Vertical migration

Figures 2 and 3 show the beach profile and the physical factors respectively.

A rapid drop in surface sand temperature (Figure 3) together with a rapid rise in the water table was noticeable when the tide had reached the experimental site at 15h00. The drop of

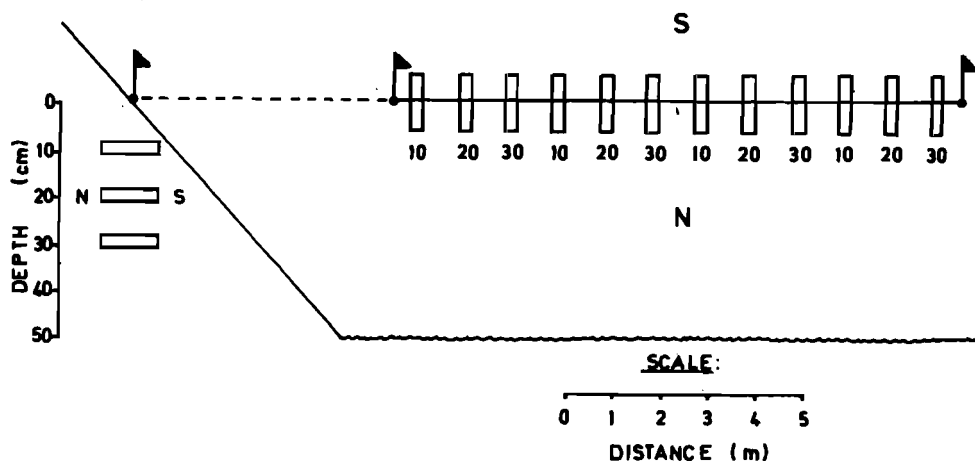


FIGURE 1

Plan of the horizontal migration experiment showing positions of the buried cores. The N (downshore) and S (upshore) ends of the cores are indicated as well as their vertical positions in the sand and the order in which they were placed.

the water table and rise in surface sand temperature after the tide had receded was slow since the sun had set and air temperatures were lower. The water table dropped to 65 cm below the surface during the day but only to 58 cm at night, presumably due to reduced evaporation. Diurnal surface temperatures varied between 33°C and 18°C while temperatures at a depth of 30 cm varied between 22°C and 20°C. Figures 4-7 show the depth distribution of the meiofauna over 14 hours. At this site meiofauna is fairly abundant down to about 60 cm depth but is concentrated at 10-30 cm (McLachlan 1975). The cores taken here thus sampled the upper half of the meiofauna populations and included the most densely populated depths. The high numbers near the surface at 18h00 (Figure 4 : 8 hours) were due to striking an atypical aggregation of turbellarians and can therefore be disregarded as being unrepresentative.

Figures 4-7 show a steady downward movement till 14h00 (4 hours in figures) and then a continued upward movement. In order to enable a more direct comparison with the tidal cycle the data in Figures 4-7 have been replotted against time and superimposed on a tidal curve in Figure 8. For nematodes and harpacticoids (the dominant taxa) the depth in the sand has been plotted above which a constant total number of animals occurred. For nematodes it was calculated from Figure 5 how far down each column one had to go to get a total of 300 animals. This represents about 25% of the total nematode population which is concentrated at 0-30 cm depth (McLachlan 1975). These depths were then plotted in Figure 8. Totals of 200 were used for harpacticoids. This is about 40% of the total harpacticoid

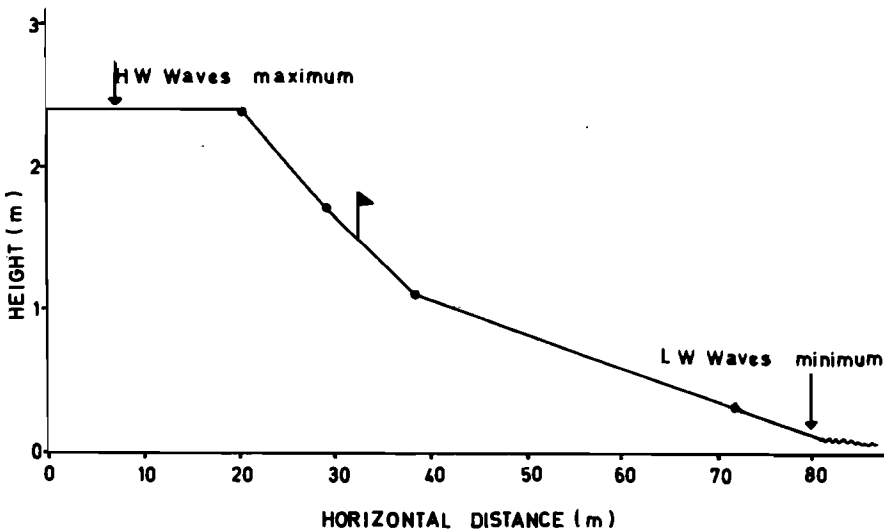


FIGURE 2

Kings Beach profile showing the vertical migration experimental level as well as the highest and lowest points reached by the waves on upsurge at high tide and downsurge at low tide.

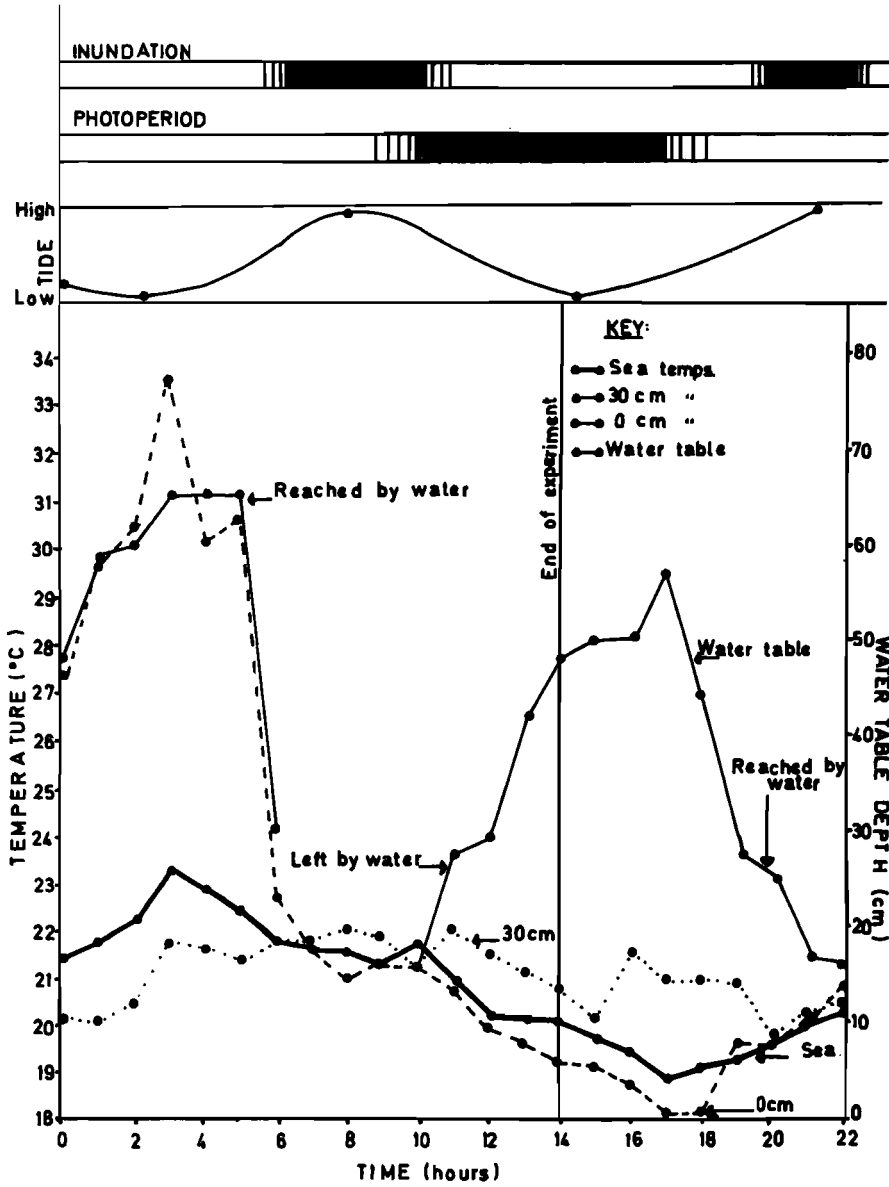


FIGURE 3

Summary of variation in physical factors monitored during the first (summer) vertical migration experiment. The vertical line at 14 hours represents the end of the experiment and 0 hours represents 10h00 on 3.12.74. Note is also made of the times when the tide reached and left the experimental area.

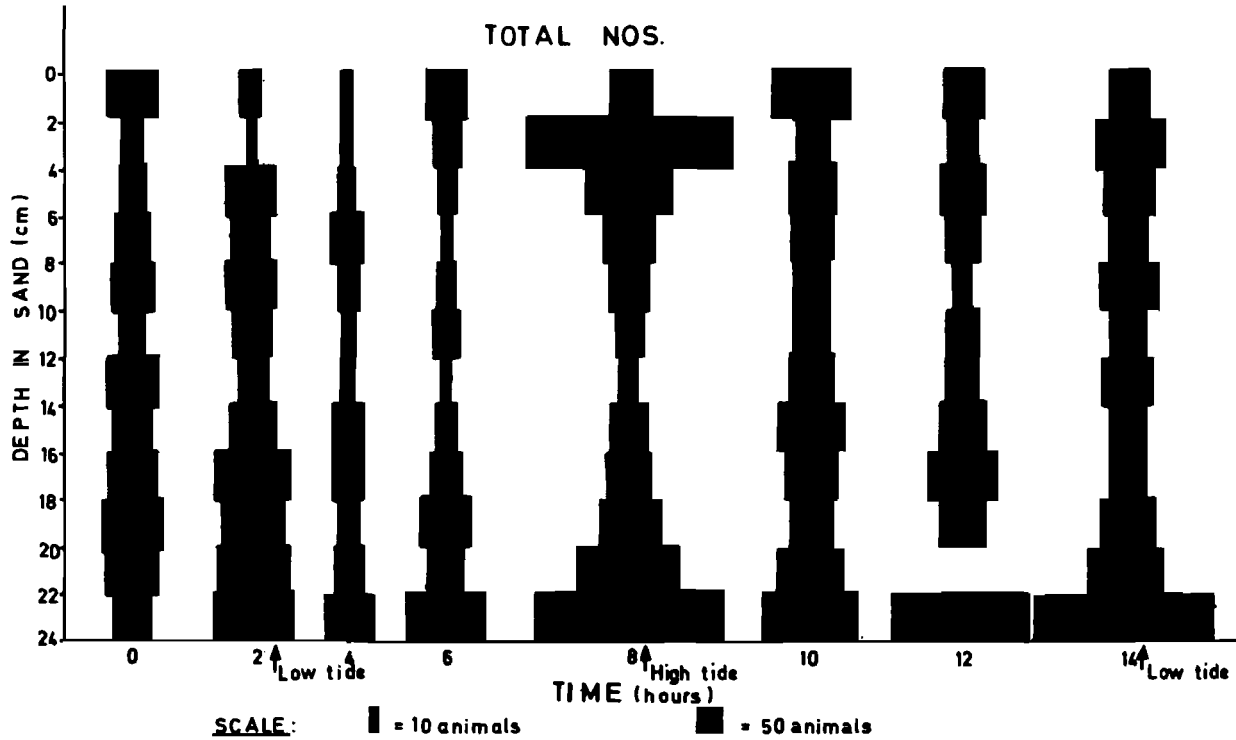


FIGURE 4
Vertical distribution of meiofauna per 57 cm² in the top 24 cm of sand during the 14-hour vertical migration experiment.

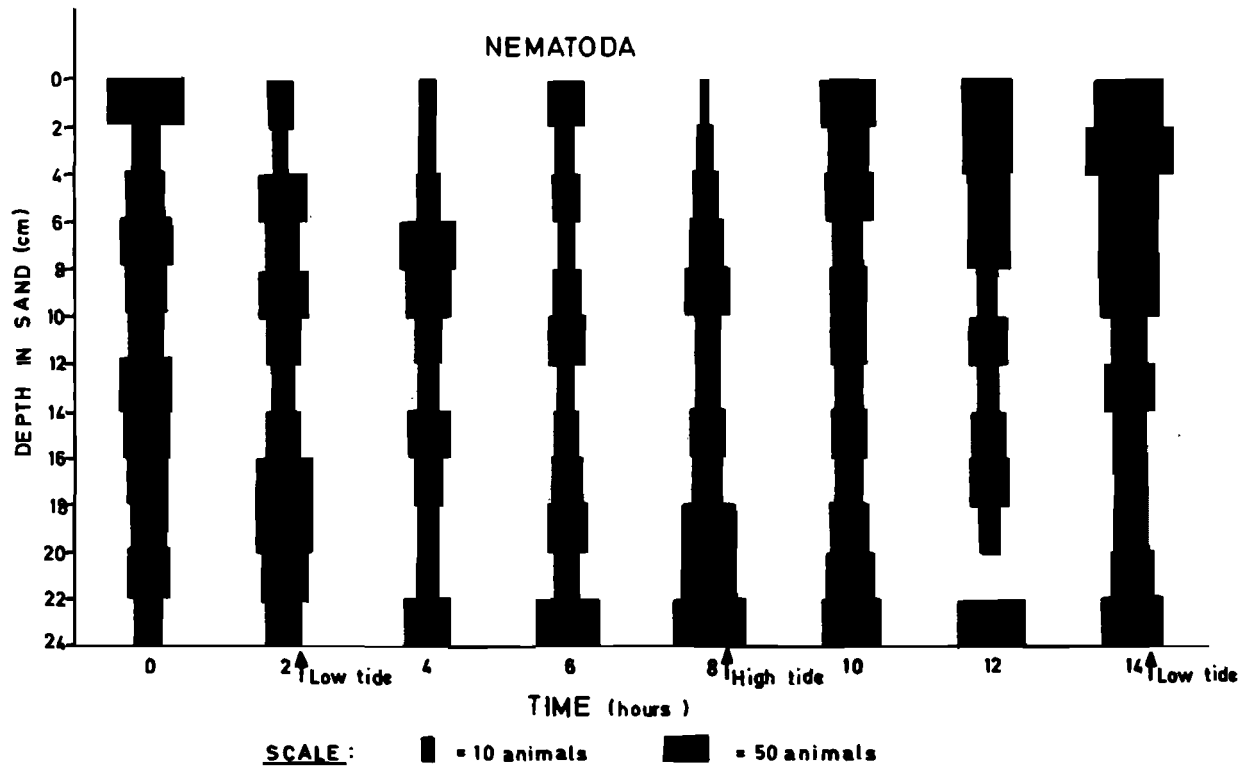


FIGURE 5
Vertical distribution of nematodes per 57 cm² during the 14-hour vertical migration experiment.

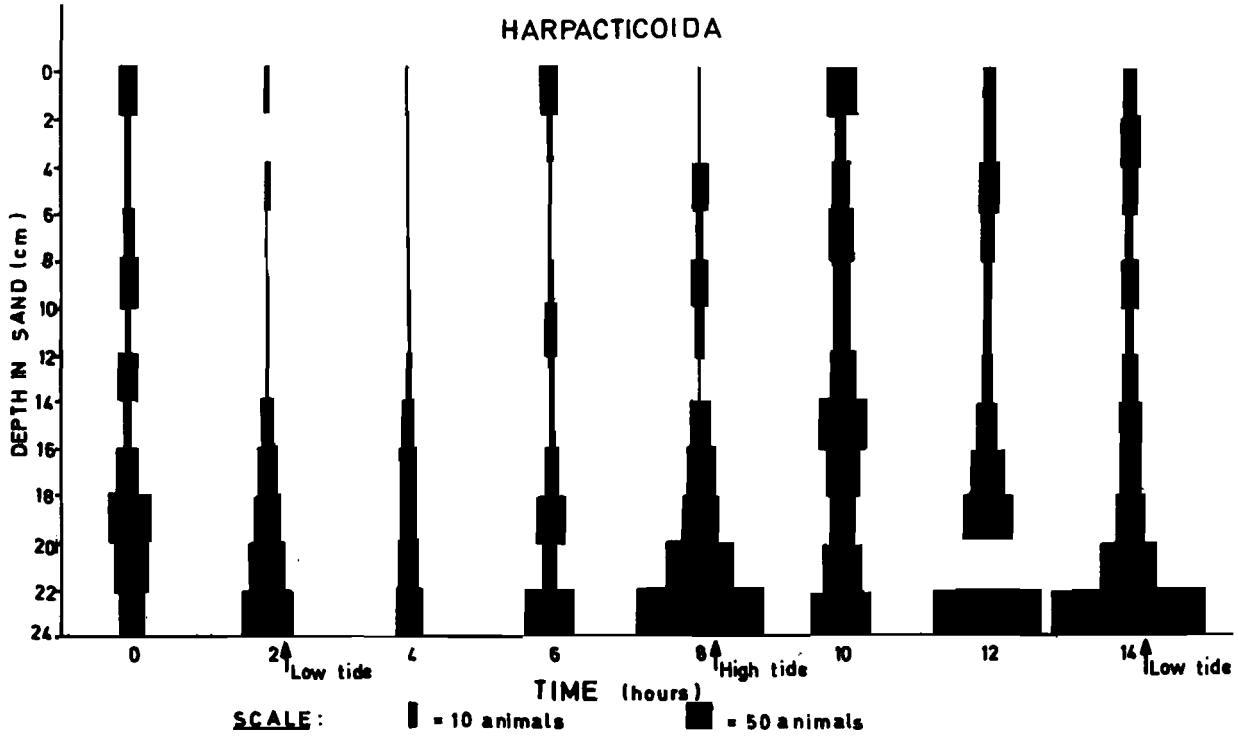


FIGURE 6
Vertical distribution of harpacticoid copepods per 57 cm² during the 14-hour vertical migration experiment.

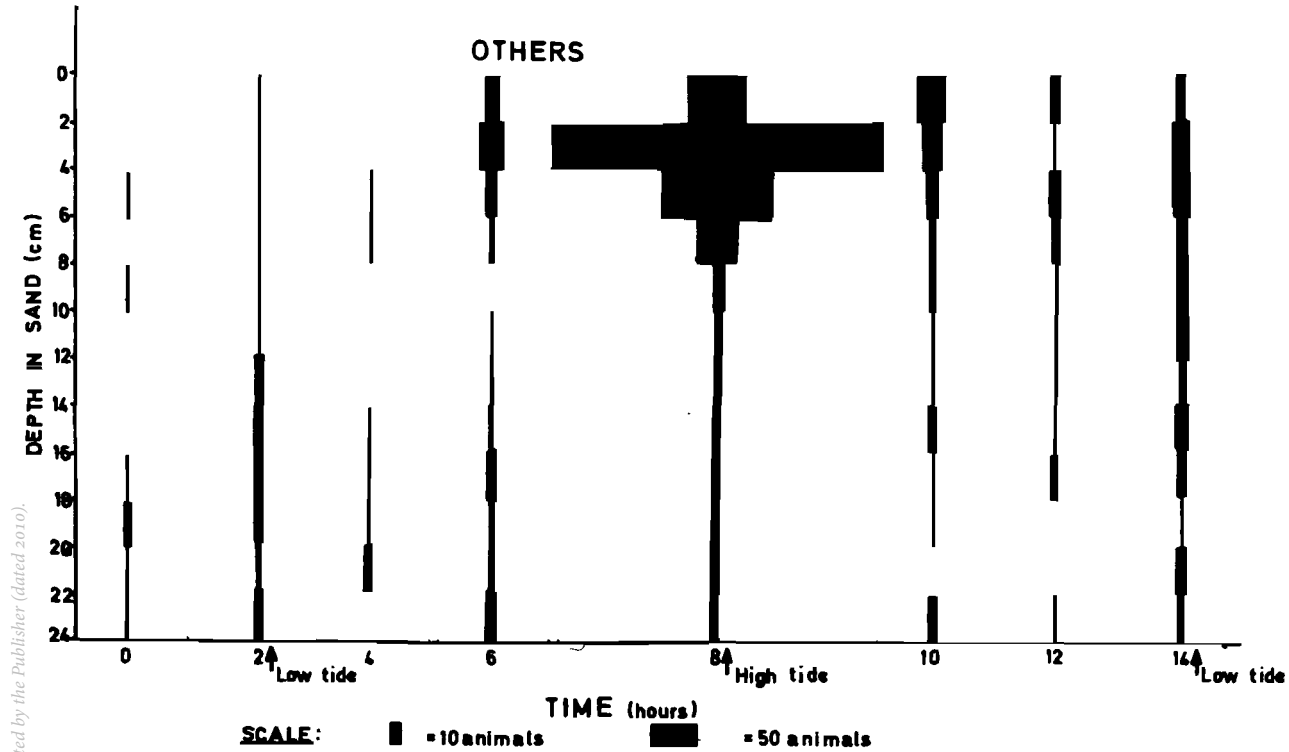


FIGURE 7
Vertical distribution of minor taxa per 57 cm² during the 14-hour vertical migration experiment.

population, which is concentrated at 15-30 cm (McLachlan 1975). These numbers were selected as being the maximum numbers that could be obtained in each case without going below 24 cm, which was the maximum depth sampled. These depths were not plotted for total numbers as a very irregular distribution of the minor taxa had been found (Figure 7). Nematodes and harpacticoids, however, made up the bulk of the meiofauna and have generally been found to have fairly uniform distributions on this beach.

The vertical migration of nematodes and harpacticoids shows a close correlation with tidal fluctuation. There is, however, a noticeable lag between tidal extremes and the maximum and minimum depths of the animals.

Regressions of depth distribution of harpacticoids and nematodes against tidal index (1 = high tide and 10 = low tide) were plotted assuming a migration lag of 1, 2 and 3 hours for harpacticoids and 3, 4 and 5 hours for nematodes.

For harpacticoids regression lines for 1, 2 and 3 hour lags gave correlation coefficients of 0,86; 0,97 and 0,85 respectively. The coefficient for 2 hours being the highest ($p < 0,001$) suggests that harpacticoid migrations lag 2 hours behind the tidal cycle. The equation for this was

$$Y = 11,0 + 1,2 X$$

where Y is the depth in cm above which 200 harpacticoids occur and X is the value of the tidal index 2 hours before the harpacticoids reach this depth.

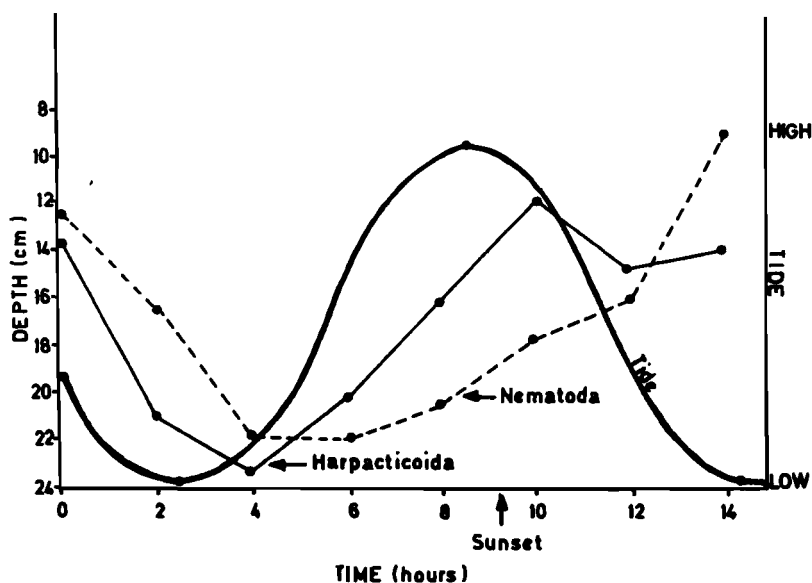


FIGURE 8

Depth distribution of meiofauna superimposed on a graph of the tidal cycle. Values plotted for the meiofauna show the depths in the substrate above which 300 nematodes and 200 harpacticoids occurred per 57 cm²

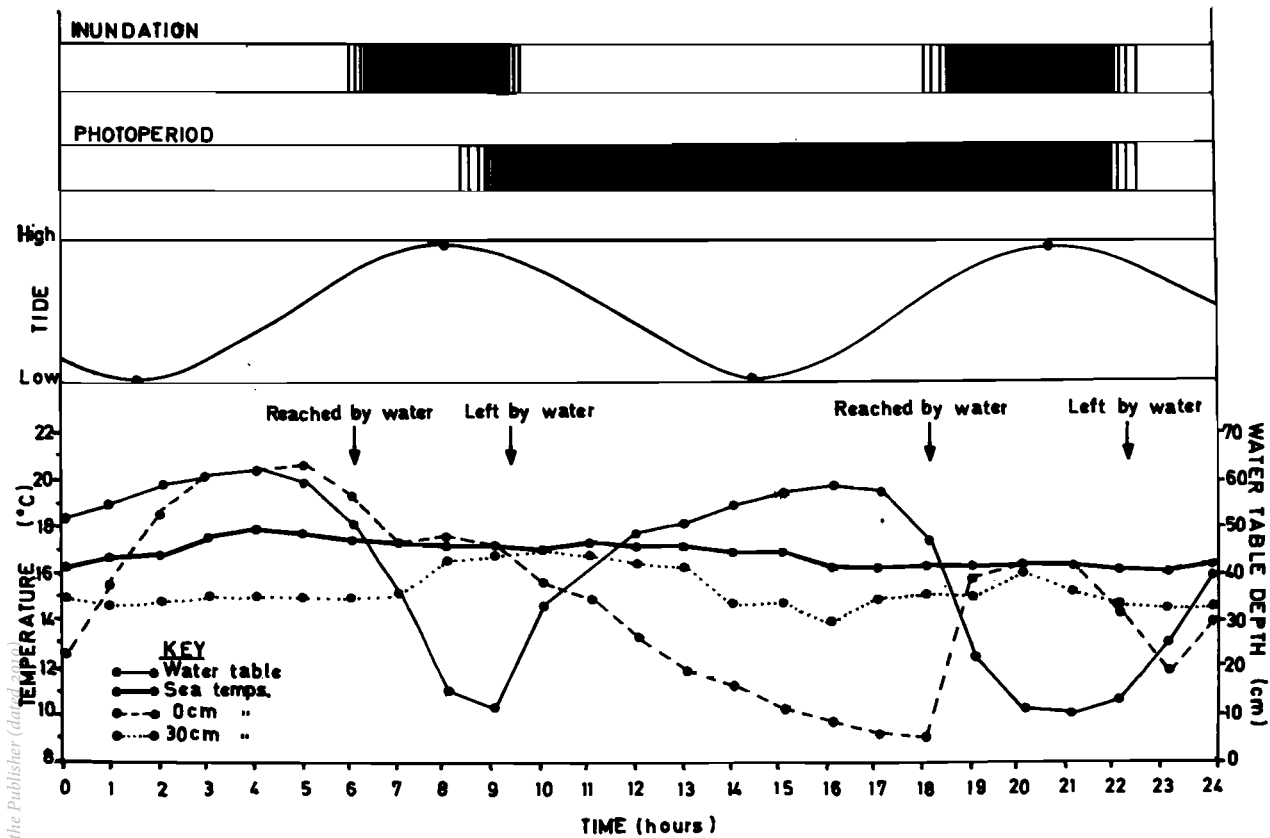


FIGURE 9

Summary of all the physical variables monitored during the second (winter) vertical migration experiment on Kings Beach.

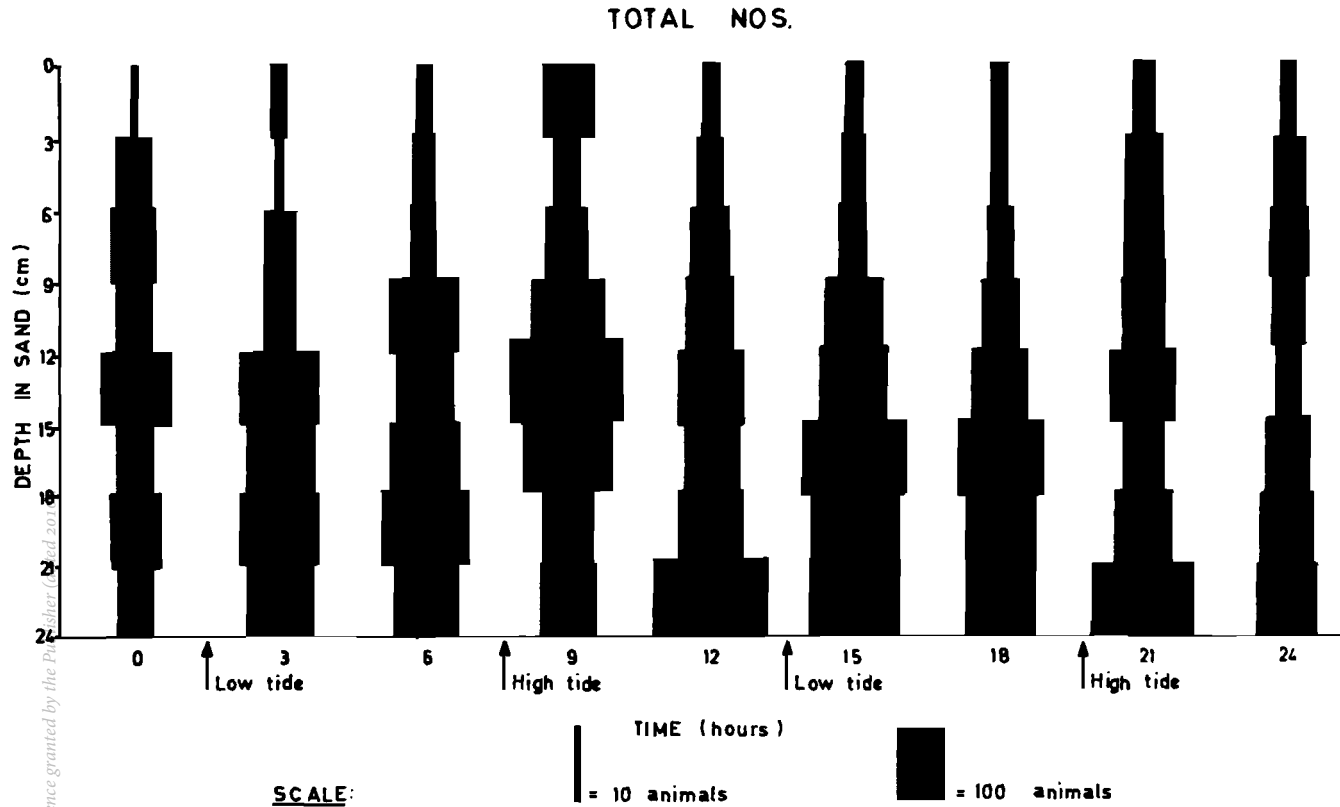


FIGURE 10
Vertical distribution of meiofauna per 57 cm² in the top 24 cm of sand during the 24-hour winter vertical migration experiment.

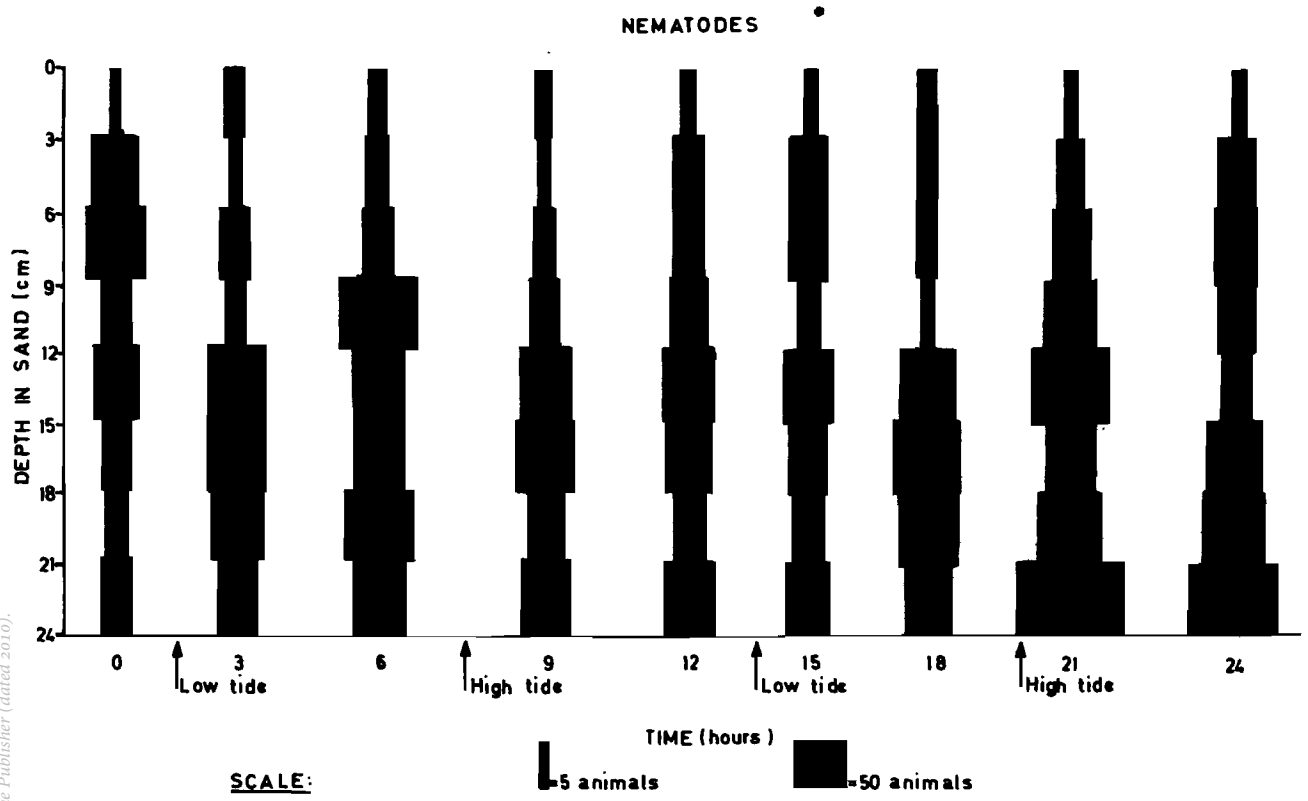


FIGURE 11
Vertical distribution of the nematodes per 57 cm² during the winter vertical migration experiment.

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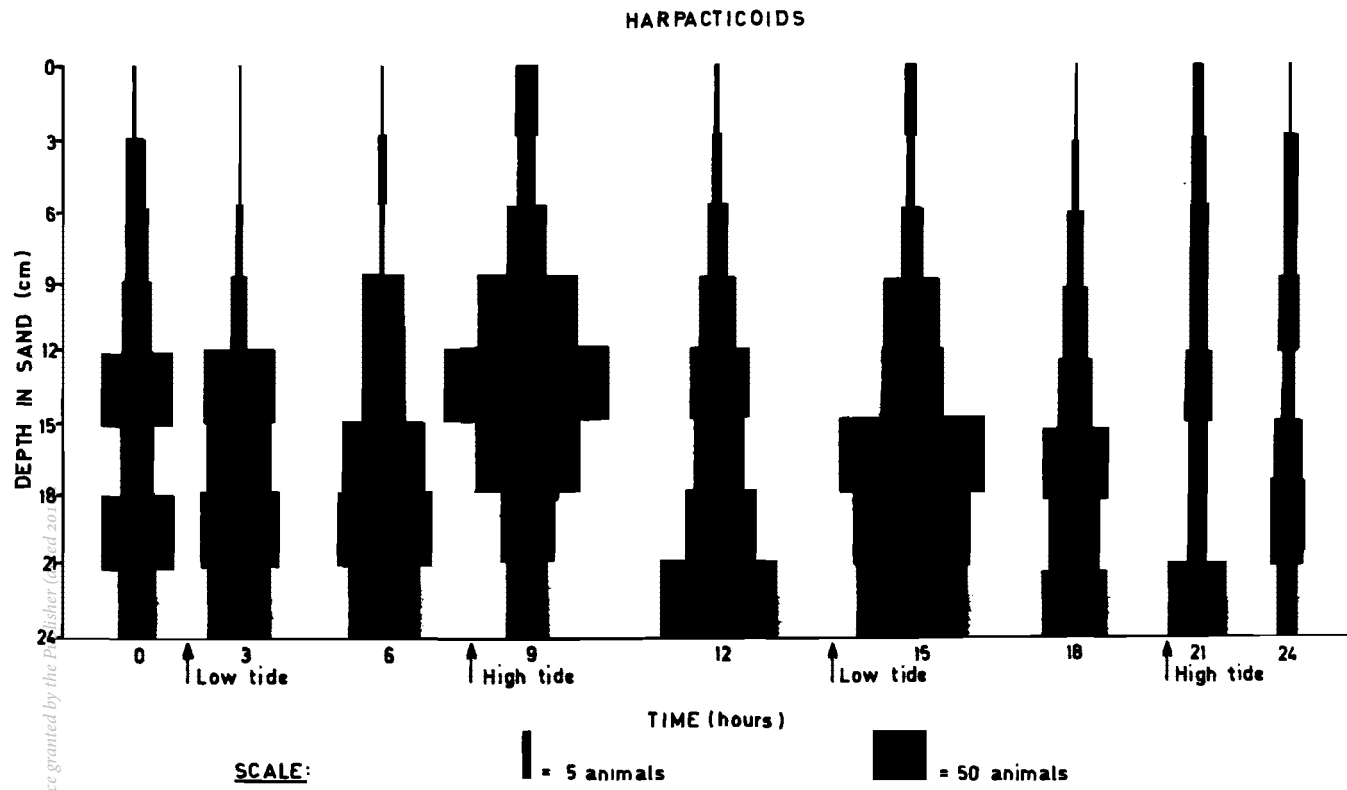


FIGURE 12
Vertical distribution of the harpacticoids per 57 cm² during the winter vertical migration experiment.

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For nematodes regression lines for 3, 4 and 5 hours gave correlation coefficients of 0,82; 0,91 and 0,80 respectively. The coefficient for 4 hours was the most significant ($p < 0,01$) suggesting a 4 hour lag between the tidal cycle and nematode movements. The equation for this was

$$Y = 13,7 + 0,9 X$$

where Y is the depth in cm above which 300 nematodes occur and X is the value of the tidal index 4 hours before nematodes reach this depth.

Figures 9-14 show the results of the winter migration study. The physical parameters (Figure 9) were essentially the same but temperatures were lower and darkness longer than in summer.

The depth distributions of the animals in the sand are illustrated in Figures 10-13. Vertical movement of nematodes and harpacticoids is shown in Figure 14. The depths above which 100 and 200 specimens of each of these taxa occurred per 57 cm² surface have

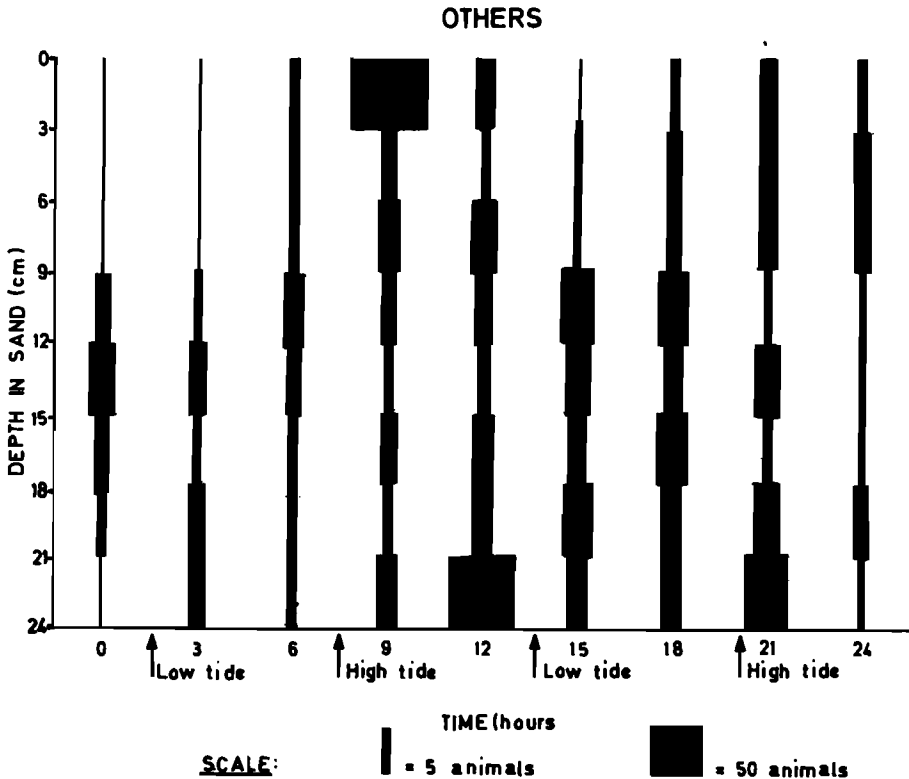


FIGURE 13

Vertical distribution of the minor taxa per 57 cm² during the winter vertical migration experiment.

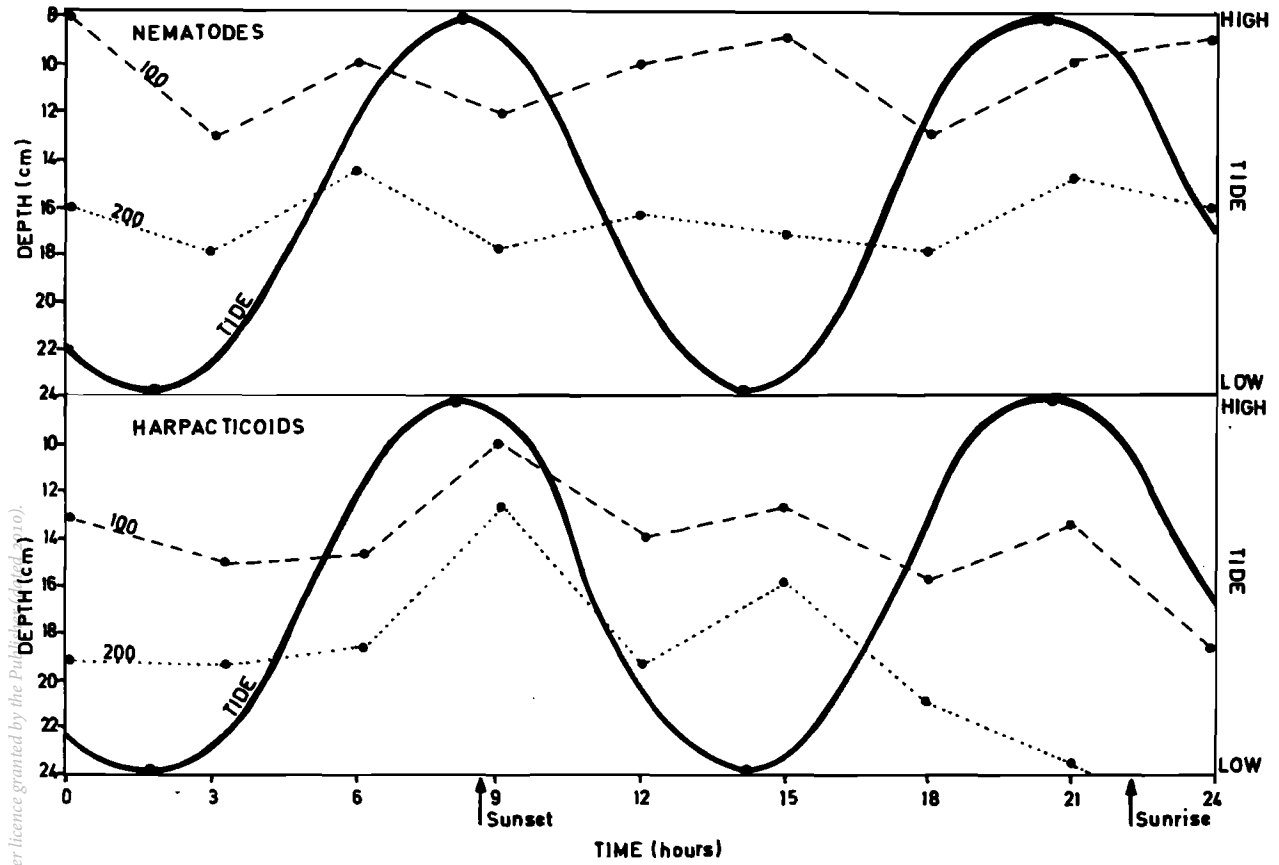


FIGURE 14
Vertical distribution of nematodes and harpacticoids superimposed on curves of the tidal cycle during the winter vertical migration experiment. Values for the nematodes and harpacticoids show the depths in the sand above which 100 and 200 animals occurred per 57 cm².

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been superimposed on a tidal curve as in Figure 8. As slightly fewer animals were encountered than in summer, depths for 300 animals could not be used. It was also attempted to obtain regression equations for the winter experiments. However, the only section of the curves that gave significant correlations were for harpacticoids from 0-12 hours. For the top 100 harpacticoids correlation coefficients for 1; 2 and 3 hour lags were 0,83; 0,81 and 0,54. It may thus be concluded that during daylight hours in winter harpacticoid migrations lag 1 hour behind the tide. The regression equation for this was $Y = 10,3 + 0,54 X$ ($r = 0,83$ $p < 0,10$) where Y is the depth in cm above which 100 harpacticoids occur and X is the value of the tidal index 1 hour before the harpacticoids reach that depth.

Similarly for 200 harpacticoids correlation coefficients for 1; 2 and 3 hour lags were 0,87; 0,59 and 0,20 respectively. This again indicates a 1 hour lag with the equation being $Y = 13,3 + 0,78 X$ ($r = 87$; $p < 0,10$) where Y is the depth in cm above which 200 harpacticoids occur in the sand and X is the value of the tidal curve 1 hour before they reached that depth.

Summer and winter movements of harpacticoids were therefore the same though the extent of vertical migration was less in winter (Figures 8, 14). When darkness coincided with low tide there was a slight rise in animal numbers near the surface. The fact that the harpacticoid population occupied deeper levels at the second low tide may be partly attributed to sewage pollution mentioned earlier. The winter lag between migration and tidal cycle is of the order of one hour.

Nematode migration is not as well marked (Figure 14) though the worms appear to have been unaffected by the sewage pollution.

Horizontal migration

The results of the horizontal migration experiment are presented in Figure 15. The experimental area was inundated for 3hr 20min. on the rising tide and 2hr 30min. on the falling tide.

More animals entered the cores on the falling tide than on the rising tide, though approximately equal numbers of animals entered both ends of the cores. The numbers of animals sampled were, however, too low to arrive at any firm conclusions, though there appears to be no distinct or directional horizontal movement.

DISCUSSION

The results of the summer vertical migration experiment clearly indicated a correlation between the tidal cycle and the depth distribution of the meiofauna. This was best illustrated in Figure 8 where there was a vertical movement covering more than 10 cm. This movement was downwards on the outgoing tide and upwards on the incoming tide. The harpacticoids were consistent with a lag of approximately two hours behind both the low and high tides. After dark, however, their downward movement on the outgoing tide appeared to have ceased and they levelled off (12-14 hours in Figure 8). Nematodes exhibited a four hour lag

behind the low tide and at least a six hour lag behind the high tide. This greater lag of the nematodes and levelling off of the harpacticoids after dark would appear to be due to the cooler conditions at night. This tendency, together with the correlation between the tidal and migration cycles suggests that this migration of the nematodes and harpacticoids is related to desiccation of the sand.

The absence of downward movement of the meiofauna after high tide at night was substantiated in the winter experiment (Figure 14). Here the meiofauna rose on each incoming tide and dropped on the outgoing tide during the day, but either levelled off (nematodes) or dropped slightly and then rose again (harpacticoids) on the outgoing tide during the night. Further, the extent of the vertical movements was less in the winter experiment than in the summer experiment. This appears to be related to the lower temperatures, and therefore less desiccation, in winter than in summer. Decreased desicca-

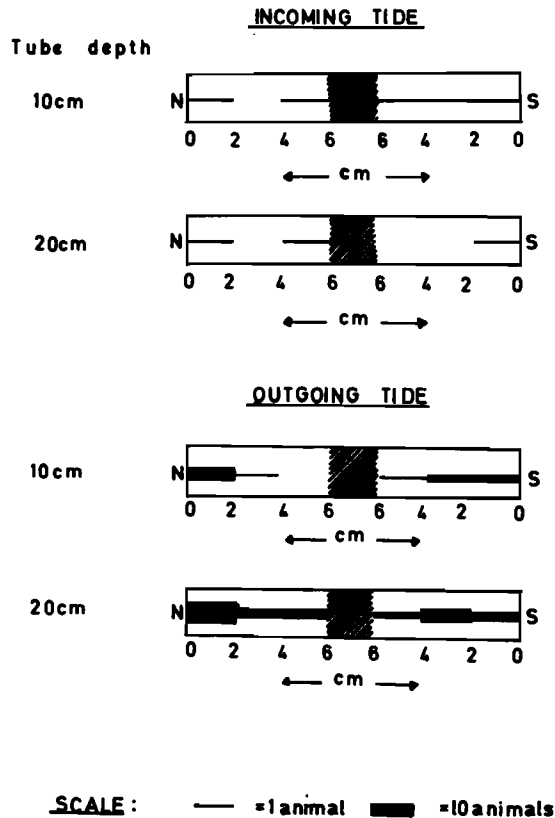


FIGURE 15

Distribution of meiofauna in sterilized sand cores burried for five hours on an incoming and an outgoing tide. The shaded area in each core represents the central 3 cm which was not studied. N denotes the downshore end.

tion owing to lowered temperatures also appears to be the explanation for the lack of downward movement during low tide at night. The role of desiccation is especially evident in the first experiment where the two-hour sampling intervals allowed more precise estimates of the turning points of upward and downward movements. Comparing Figures 3 and 8 it can be seen that the meiofauna was at its deepest just before the rising tide reached the experimental area (5 hours), i.e. when the sand was at its driest. Further, the time when the retreating tide left the area corresponds in time to the highest point reached by the harpacticoids (10 hours).

It therefore appears that desiccation, coupled with the tidal cycle, is the dominant factor controlling the vertical migrations of the meiofauna. Bearing in mind the importance of available oxygen (McLachlan 1975) it may be suggested that the meiofauna try to remain in conditions of optimum oxygen availability but that in doing so they have to adapt to the desiccation experienced in these areas. They do this by migrating away from desiccated areas during low tide. Because of the importance of desiccation the depth of migration may be greatly modified by factors affecting the drying-out of the sand, such as temperature differences coupled with seasons and with day and night. Some further deductions may also be made from Figures 4-7 and 10-13. In all of these figures it can be seen that the vertical movements were not confined to the surface layers. Large numbers of animals were in fact moving at depths of 15-24 cm and probably below 24 cm as well. Movement of the deeper meiofauna is hardly surprising if vertical movement is coupled with the tides and as the water table drops deeper than 60 cm below the surface and is below 25 cm for more than 60% of the time. Further, Figures 7 and 13 indicate that the minor taxa also moved with the tides, although their numbers were too low, and in some places too patchy, to allow precise estimates of vertical movement. It is therefore suggested that all of the meiofauna living above the depth of the permanent water table undergo vertical movements coupled with the tidal cycle.

Renaud-Debyser (1963) and Boaden (1968) also found migration to be related to the tides. Boaden suggested that the animals move down when the surge zone crosses their habitat in order to avoid being swept out of the sand by the action of the waves. He, however, only studied the surface 5 cm and 2 cm of sand for a short part of the tidal cycle. Renaud-Debyser had conflicting results, with vertical migrations related to the tides at one station but opposite to the tides at the other station. Harris (1972) found no significant change in the distribution of the meiofauna at different states of the tide, but this was on a beach where the sand was always saturated. Light, which is one of the main factors controlling vertical migrations of zooplankton, penetrates only 10-15 mm in the sand (Pennak 1951 in Boaden 1963) and can therefore not be a factor of direct importance in meiofauna migrations below 1-2 cm depth. At the lower tide levels on Kings Beach and Sundays River, where the sand is always saturated, there might be no migration or there might be migration related to wave action as suggested by Boaden (1968). For all other tide levels, however, desiccation, coupled with the tidal cycle would appear to be responsible for distinct vertical movements of the meiofauna.

Bush (1966) found that almost all the meiofauna just above the MW level moved below

the top 6 cm of the sand after heavy rain. McLachlan (1975), however, found that rain lowered salinities of interstitial water in only the top 5 cm at higher tide levels on Kings Beach and unpublished experiments suggest that this slight dilution has almost no effect on the meiofauna. It thus appears unlikely that anything but the very heaviest rain would cause the meiofauna to migrate downwards and even then this migration would be confined to the superficial layers near high tide.

Three basic conclusions may be drawn from the results of the horizontal migration experiment (Figure 15). Firstly, the very low numbers of animals entering the cores relative to the numbers in the sand indicate that very little horizontal movement of the meiofauna takes place. Secondly, the small amount of movement that was found (i.e. the few animals that did enter the cores) appears to have been random as approximately equal numbers of animals entered both ends of the cores in all cases and in none of the series of cores did high numbers enter one side and very low numbers enter the other side. Thirdly, there seems to have been more horizontal movement on the outgoing tide than on the incoming tide. This appears to be due to the sand having more moisture on the outgoing tide and the animals therefore being both more numerous and more active.

Although low numbers of animals entered the cores relative to the numbers in the sand (see Figures 4-7), some of these moved at least 6 cm during the 5-hour period. During the vertical migration experiment in summer the animals moved on average 10 cm in 10 hours (between 4 hours and 14 hours in Figure 8). This amounts to a rate of approximately 1 cm/hour, which is a surprising amount of movement considering the small sizes of these animals and their restriction to the interstitial spaces. Some of this movement may, however, be due to the animals being 'washed' through the sand by the action of the tide.

It may thus be concluded that the only important migrations undertaken by the meiofauna of Kings Beach are vertical migrations related to the tidal cycle. The main purpose of these migrations appears to be to allow the animals to remain in conditions where oxygen is plentiful but to escape desiccation. It is also possible, however, that feeding activity may be coupled to this vertical tidal migration.

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