AN ECOPHYSIOLOGICAL STUDY OF THE MEIOFAUNA OF THE SWARTKOPS ESTUARY.

2. THE MEIOFAUNA: COMPOSITION, DISTRIBUTION, SEASONAL FLUCTUATION AND BIOMASS

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ABSTRACT

Environmental correlations with mean, as well as seasonal, distribution and abundance of the meiofauna in two exposed beaches in the Swartkops Estuary, near Port Elizabeth, were elucidated. Population densities showed a direct relationship with particle size. Consequent on this, oxygen appeared to be the controlling factor although desiccation played a role in the intertidal distribution of meiofauna in sandy areas. Seasonal fluctuations in numbers were characterized by peaks occurring in spring and autumn. Variations of temperature and oxygen were found to be responsible for this pattern. The presence of the sand prawn *Callianassa kraussi* affected both vertical penetration and seasonal fluctuation of the meiofauna. Since fluctuation in nitrogen and chlorophyll *a* content of the substrate bore little relationship to the fluctuation of the meiofauna, it is concluded that food is not limiting in these areas. Biomass determinations revealed that nematodes, which were the dominant taxon, weighed 0,42 μg individual mean ash-free dry mass and harpacticoid copepods 0,47 μg. On this basis the standing crop biomass was 0,40 g/m^2 in the sandy areas and 0,07 g/m^2 in the muddier areas, both to a depth of 20 cm.

INTRODUCTION

A number of papers on quantitative meiofauna surveys have appeared since the 1940's. Subtidal distribution is dealt with by McIntyre (1964), Coull (1970) and Warwick & Buchanan (1970). The intertidal distribution and composition of the meiofauna in exposed beaches is well documented by Janssen (1967, 1968) in the Baltic, Gray & Rieger (1971) in Yorkshire, Wieser *et al.* (1974) in Bermuda, and Giere (1975) in the North Sea. In South Africa the only work of this nature is that of McLachlan (1975) in Algoa Bay. The distribution of brackish water meiofauna has also been studied, although, to the author's knowledge, not in this country, and workers include Rees (1940) in the Exe estuary, England, Tietjen (1966) in a North American estuary, Teal & Wieser (1966) in a Georgia salt marsh, and Damodoran (1974) and Kurian (1974) both on the west coast of India.

Although dealing quantitatively with meiofauna distribution few of these works have attempted long term studies with the object of correlating fluctuations with environmental parameters (Tietjen 1966; Barnett 1968). To this end, therefore, a number of environmental parameters were used to explain the distribution and seasonal fluctuation of the meiofauna in the Swartkops estuary near Port Elizabeth. A full description of the sampling sites and methods is given in Part 1 of this series (Dye 1978).

METHODS

Samples for faunal analysis were collected as described by Dye (1978). The meiofauna was extracted by means of an Oostenbrink flotation extractor modified by Furstenberg. Samples from Station A, near the mouth of the estuary, being of medium sand (175 μm) could be efficiently extracted by this method alone. At Station B, near the head of the estuary, the substrate was finer (130 μm) and an additional centrifugation process was required to remove silt and detritus. This was done in a sucrose solution according to the method of Hiep *et al.* (1974). The animals were trapped on a 45 μm sieve and washed into beakers. An equal volume of boiling sea water was added to kill the animals without distortion and the samples were then made up to 5% formalin. A few drops of 0,025% rose bengal (tetrachloro, tetra-iodo flourescein) was added and the samples left overnight to allow penetration (Warwick 1971). Counting was done in a perspex dish the sides of which formed angle of 45° with the bottom, which was divided into squares. This eliminated edge effects (Koen & Furstenberg 1970). Since the volume of sand from each depth zone was 200 cm^3 the animal density was expressed in numbers/200 cm^3. Corrections were made for extraction efficiency which was 80% for nematodes and harpacticoid copepods (Furstenberg pers. comm.), and centrifugation efficiency which was on average 93% for these taxa (Hiep *et al.* 1974). An attempt was made to assess the percentage missed by not sampling below 20 cm by plotting the animal density in each depth zone against the lower limit of that zone and extrapolating the resulting line to a depth at which no animals could be expected. The area below 20 cm, expressed as a percentage of the total area, gave the proportion missed. Although not completely accurate, such an estimation is preferable to ignoring the deeper part of the population.

The ash-free dry mass of the various meiofauna groups was determined as follows. Ten replicate samples of 30 organisms from each group were placed in drops of distilled water on a coverslip after rinsing briefly in distilled water. The samples were dried at 60°C for 24 hours, weighed to the nearest microgram on a Sartorius microbalance Model 4431, ashed at 500°C for 12 hours, and reweighed when cool. The ash-free dry mass thus obtained was divided by the number of organisms to give the average individual mass.

In addition, the ash-free dry mass of the macrofauna was determined. At each sampling level two areas of 0,25 m^2 were dug out to a depth of 30 cm and passed through a 1,0 mm sieve. All animals retained were kept for identification and biomass determinations. In areas where the prawn *Callianassa kraussi* occurred a population estimate was made by counting the number of holes and assuming a one-to-one relationship with prawns (Hanekom pers. comm.). Biomass was determined by drying the organisms at 80°C for 24 hours and ashing at 500°C for 12 hours. Shells were removed where relevant and digested in 25% HCl until effervescence had stopped. The residue was filtered, dried and ashed. The ash-free dry mass of the prawns was estimated from the mean values of animals collected and treated as described.

RESULTS

Table 1 gives the results of extrapolations to determine the percentage meiofauna below 20 cm. The meiofauna may be expected to occur to an average depth of 34 cm $\pm$ 10 at Station A and 26 cm ± 8 at Station B. This difference is, however, not significant ($p \leq 0,25$); its importance will be discussed below.

The contribution of the major meiofauna taxa is given in Table 2. Nematodes dominate the meiofauna at both stations and account for 84% of the community. Harpacticoid copepods account for 12% of the total at both stations. Those at Station A were mainly interstitial while those at B were of the burrowing type. The remainder of the meiofauna, referred to as "others", consisted of polychaetes, oligochaetes, flatworms and a small number of gastrotrichs, ostracods and amphipods. At Station A the dominance of nematodes decreases from HW to MW, due to an increase in the number of "others", but at Station B nematodes decrease in importance from HW to UW. The numerical importance of the nematodes increases with depth at all tidal levels of Station A but only at LW of Station B. The highest contribution by nematodes at B occurred in the 0 - 6,5 cm zone at HW, the 6,5 - 13 cm zone at MW and the 13 - 20 cm zones at LW and UW. The harpacticoids increase in importance from HW to UW at both stations and decrease in importance with depth at all tidal levels at Station A. At Station B, however, the highest contributions by harpacticoids occurred in the 13 - 20 cm zone at HW and MW, the 0 - 6,5 cm zone at LW and the 6,5 - 13 cm zone at UW. The proportion of the community accounted for by "others" was highest at MW at Station A and at UW at Station B. There is considerably more

TABLE 1

Estimation of the percentage meiofauna occurring below 20 cm as well as the maximum theoretical depth limit and correction factors for Stations A and B. *Variances are to the 90% confidence level.

Sampling level		Percentage missed	Max. depth*(cm)	Correction factor
A	HW	21 ± 5	38 ± 8	1,27
	MW	15 ± 3	43 ± 10	1,18
	LW	16 ± 6	28 ± 12	1,19
	UW	8 ± 2	28 ± 8	1,09
B	HW	0 ± 5	20 ± 9	1,00
	MW	3 ± 2	25 ± 11	1,03
	LW	14 ± 4	32 ± 5	1,16
	UW	8 ± 6	28 ± 6	1,09

TABLE 2

Mean percentage composition of the meiofauna communities and numbers per 200 cm^3 at Stations A and B.
a = 0 - 6,5 cm; b = 6,5 - 13,0 cm; c = 13,0 - 20,0 cm.
Numbers in brackets are animals / 200 cm^3.

Sampling station	Taxon	Mean percentage composition/sampling level and depth zone.															
		HW				MW				LW				UW			
		a	b	c	mean	a	b	c	mean	a	b	c	mean	a	b	c	mean
A	Nematoda	90,64 (699)	91,13 (471)	91,71 (466)	91,12 (545)	71,09 (600)	83,46 (531)	85,89 (453)	80,15 (528)	78,83 (955)	83,80 (632)	89,31 (405)	84,00 (664)	73,31 (638)	78,90 (487)	90,64 (312)	80,95 (479)
	Harpacticoida	6,39 (33)	5,38 (26)	5,26 (18)	5,69 (25)	19,51 (163)	7,89 (40)	7,52 (32)	11,55 (78)	18,30 (176)	13,55 (84)	8,67 (43)	13,51 (101)	25,05 (208)	12,89 (58)	8,09 (24)	15,34 (96)
	Oligochaeta Polychaeta Platyhelminthes Gastrotricha	2,97 (11)	3,49 (15)	3,30 (10)	3,20 (12)	9,40 (55)	8,65 (56)	6,59 (27)	8,30 (46)	2,87 (15)	2,65 (12)	2,02 (7)	2,49 (11)	1,64 (9)	8,21 (5)	1,27 (2)	3,71 (5)
B	Nematoda	94,51 (329)	92,45 (83)	77,51 (23)	88,19 (145)	83,98 (115)	91,68 (47)	76,88 (31)	84,17 (64)	81,26 (104)	81,30 (79)	88,82 (76)	83,59 (86)	81,65 (85)	55,63 (42)	86,41 (48)	74,34 (58)
	Harpacticoida	3,53 (9)	5,26 (2)	16,97 (2)	8,85 (4)	10,42 (13)	5,16 (2)	14,75 (3)	10,11 (5)	14,70 (7)	11,52 (10)	8,94 (3)	11,53 (6)	8,89 (7)	21,95 (12)	6,38 (3)	13,14 (7)
	Amphipoda Oligochaeta Polychaeta Platyhelminthes Gastrotricha Ostracoda	1,69 (7)	2,20 (2)	5,52 (1)	2,96 (3)	5,60 (7)	3,16 (2)	8,73 (3)	5,72 (4)	7,18 (6)	4,04 (2)	2,24 (4)	4,88 (4)	9,46 (9)	22,42 (12)	7,21 (4)	13,03 (8)

meiofauna at Station A than at B, the mean standing crops being 9,6 x 10^5 individuals/m^2 and 1,38 x 10^5 individuals/m^2 respectively.

A comparison between mean meiofauna distribution and environmental parameters was made using least squares. The results of the statistical analysis (t-tests) are given in Table 3. Three types of distribution were distinguished, i.e. gross distribution (a comparison between Station A and B), intertidal distribution and vertical distribution. It became clear that one of the most important parameters determining the distribution of the meiofauna is substrate particle size. The finer the substrate, the lower the population. The relationship between oxygen and gross distribution is consequent on the increased fineness of the substrate at Station B. Although oxygen was important in determining the intertidal distribution of meiofauna at Station B, desiccation appeared to be the overriding factor at Station A. No relationship could be found between meiofauna and nitrogen or chlorophyll *a*. The distribution of macrofauna at both stations, however, had a significant effect on the vertical depth penetration of the meiofauna. Apart from very low numbers of hermit crabs *(Diogenes brevirostris)* and the bivalve *Psammotellina capensis* at Station A, the macrofauna consisted exclusively of sand prawns *(Callianassa kraussi)* (Table 4). Figure 1 shows the relationship between the sand prawns and the maximum depth of penetration of the meiofauna. This relationship is highly significant for both stations (A: $p \leq 0,10$; B: $p \leq 0,05$).

The seasonal fluctuation of the total meiofauna (mean of four sampling levels) at Station

TABLE 3

Relationships between environmental parameters and mean total meiofauna distribution. (+ indicates a positive relationship, – indicates a negative relationship and "O" indicates no relationship). The criterion for significance is the 90% confidence level.

Parameter	Distribution				
	Gross	Infra-intertidal		Vertical	
		A	B	A	B
Particle	+	+	+	0	0
Silt %	–	0	0	0	0
Permeability	+	+	0	0	0
Oxygen	+	0	+	0	+
Temperature	–	0	0	+	+
Desiccation	0	–	0	0	0
Salinity	+	0	0	0	0
Nitrogen	0	0	0	not investigated	
Chlorophyll *a*	0	0	0	"	"

A and B is shown in Figure 2. The meiofauna exhibited two peaks, one in spring (August to October) and one in autumn (April and May). A brief drop in numbers occurred at both stations in September and October due to flooding. The lowest population densities occurred in mid-summer (December and January) but significant decreases also occurred in winter (May to July). The harpacticoids and "others" varied in a more or less random fashion, but their contribution to the community is relatively small and the obvious trends are entirely due to the nematodes.

TABLE 4

Infra- and intertidal distribution, percentage composition and ash-free dry mass per m² of the macrofauna at Stations A and B. Numbers in brackets are animals/m².

Station	Mean percentage composition		Ash-free dry mass in g/m²
	C. kraussi	Others	
A HW	-	-	-
MW	100 (28)	-	5,69
LW	-	*Diogenes brevirostris:* 50 (4) *Psammotellina capensis:* 50 (4)	0,23
UW	-	-	-
B HW	100 (8)	-	1,62
MW	100 (312)	-	63,45
LW	100 (480)	-	97,62
UW	100 (370)	-	75,25

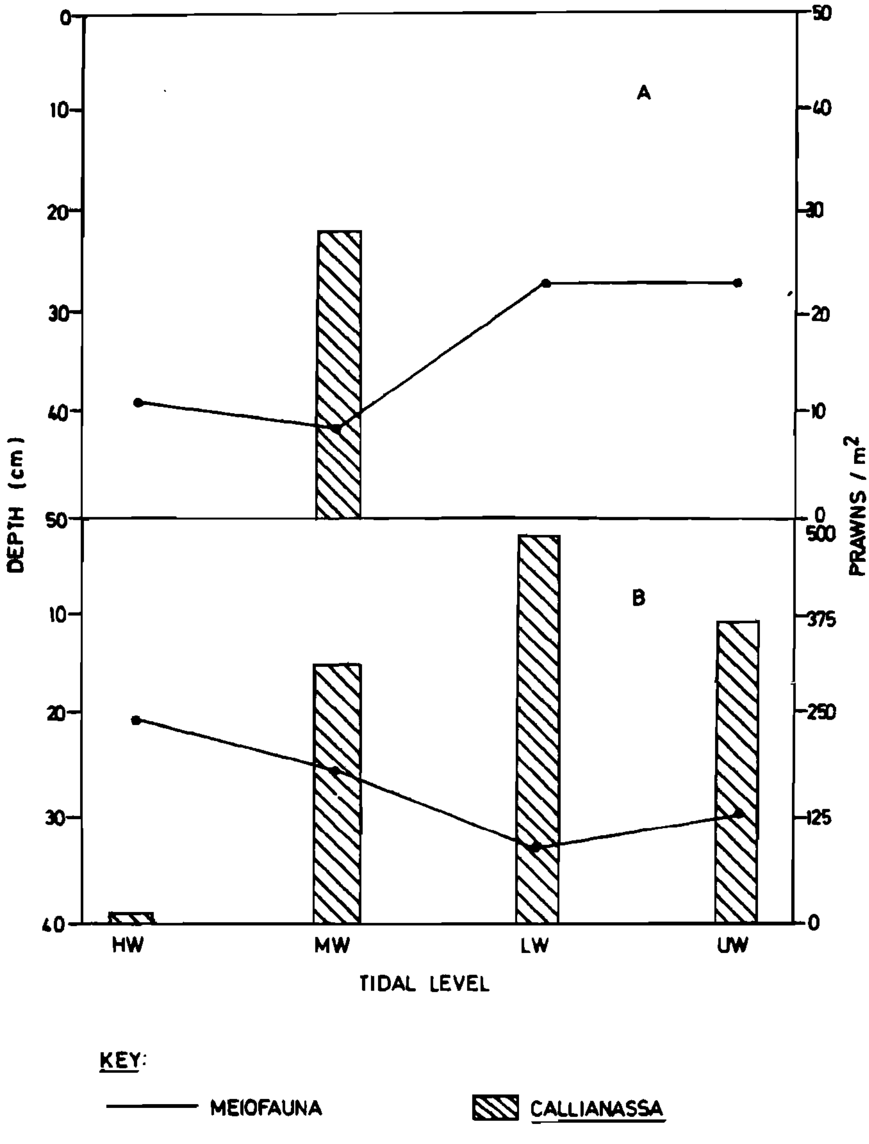

FIGURE 1
Relationship between *Callianassa kraussi* and the maximum depth of penetration of meiofauna at Stations A and B.

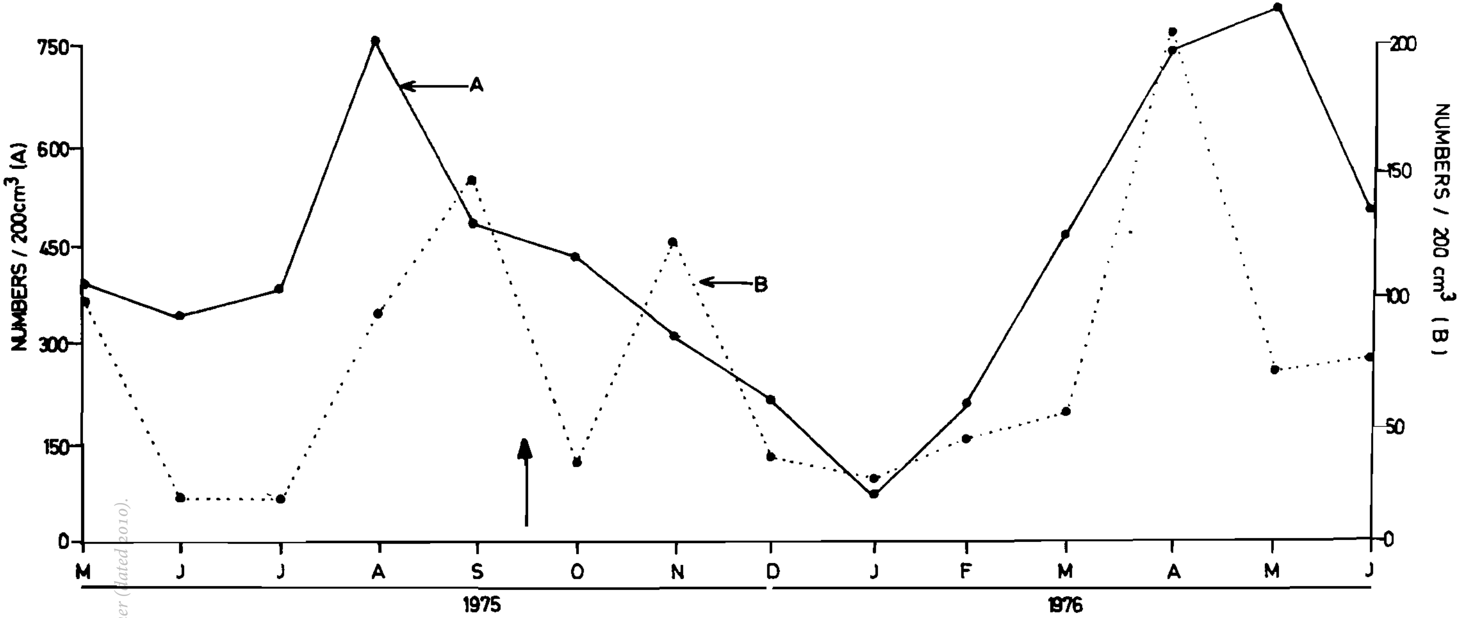

FIGURE 2
Seasonal fluctuations in mean total meiofauna numbers at Stations A and B. Arrow indicates flood conditions.

The results of the biomass determinations of macrofauna are given in Table 4 and of meiofauna in Table 5. Station B is much richer in macrofauna than Station A, by a factor of 40. Prawns dominate the macrofauna at both stations, the peaks being at MW at Station A and LW at Station B. No macrofauna other than prawns was found at Station B. Table 5 shows the average individual ash-free dry mass of the nematodes to be 0,42 μg. The interstitial harpacticoids characteristic of Station A weighed 0,47 μg, while the burrowing forms of Station B weighed 1,65 μg. The "others" weighed approximately 0,42 μg. By far the heaviest group was the amphipods at 10,38 μg but they occurred in such low numbers that they had no significant impact on the biomass of the meiofauna. These determinations put the ash-free dry mass standing crop at 0,4 and 0,07 g/m² for Stations A and B respectively.

TABLE 5

Ash-free dry mass of the major meiofauna taxa.
n = 10 (x 30); I = interstitial; B = burrowing

Taxon	Ash-free dry mass (μg)
Nematoda	0,42 $\pm$ 0,05
Harpacticoida (I)	0,47 $\pm$ 0,05
Harpacticoida (B)	1,65 $\pm$ 0,35
Amphipoda	10,38 $\pm$ 4,00
"Others"	0,42 $\pm$ 0,05

DISCUSSION

The meiofauna composition is typical of most such communities and the dominance of nematodes at all tidal levels is well known (Wieser 1959; Jansson 1968; Kurian 1974 ; McLachlan 1975). This is probably due to a large number of species enabling the group to utilize a great number of microhabitats. Although not investigated in the present study, it is well known that large numbers of nematode species occur in brackish water (Teal & Wieser 1966; Warwick 1971). The remainder of the meiofauna varies from one area to another but harpacticoid copepods are usually well represented, particularly in sandy areas (McIntyre 1969; Jansson 1971).

It is well known that substrate particle size is an important factor controlling the distribution and abundance of meiofauna (Wieser 1959). Particle size exerts its effect through mechanical restrictions on the movement of animals. In coarse substrates the pore spaces are larger and the meiofauna is predominantly interstitial. Wieser (1959) postulated a size barrier of 200 μm separating sliders from burrowers. McLachlan *et al.* (1977) calculated this barrier to be 160 μm. Interstitial harpacticoids and nematodes were found in 175 μm sands in the present study but the harpacticoids were exclusively burrowers at a median particle size of 130 μm. This suggests that the lower limit for interstitial life, excluding nematodes, is considerably lower than 200 μm. The nematodes, however, are capable of sliding in very small spaces and it has been postulated that the lower limit for these forms is 125 μm (McIntyre & Murison 1973).

Apart from the purely mechanical effects, substrate particle size has far-reaching effects on other parameters such as porosity, permeability, desiccation and oxygen content. Fine substrates, characterized by low permeability and oxygen levels, have the effect of reducing meiofauna populations. For these reasons Station A has approximately seven times more meiofauna than Station B. The good drainage at Station A accounts for the fact that desiccation is important in the intertidal distribution of meiofauna.

The effect of *Callianassa kraussi* on the meiofauna depth distribution is striking. The pumping action of the prawn draws aerated water into the substrate and this increases the effective permeability of the beach which allows the meiofauna to penetrate more deeply than would be expected. This accounts for the fact that there is no significant difference between the stations in terms of maximum depth penetration of meiofauna despite the great difference in permeability. It appears, therefore, that both beaches are equally "permeable", Station A due to the relatively coarse substrate, and Station B due to the prawns. Certain relationships between temperature, salinity and gross distribution of meiofauna can only be evaluated when analysed in terms of seasonal fluctuations of the parameters measured. In order to explain the seasonal fluctuations in meiofauna numbers the data in Figure 2 were compared by the method of least squares with the monthly physical and chemical data. However, such an *in toto* analysis did not reveal any relationships between meiofauna and environmental parameters. This is simply because the meiofauna fluctuations are bimodal whereas the fluctuations in environmental parameters are unimodal. For the same reason, multiple regression analysis also failed to reveal any relationships. The data were thus divided into two sections, the boundaries being the meiofauna peaks themselves. In this way the data could be divided into a summer period and a winter period on an ecological, rather than strictly chronological, basis.

Since a similar analysis of nitrogen, chlorophyll *a* and salinity produced no results it is concluded that, if nitrogen and chlorophyll *a* are considered indicators of available food, then food is not limiting in the areas studied. Similarly, salinity appears to have little bearing on meiofauna seasonality although it may be important for gross distribution in the estuary as a whole. A significant relationship between meiofauna and oxygen and temperature was revealed by this method of analysis. It was found that a significant inverse relationship exists between meiofauna density and temperature during the summer period (August to May) at both stations (A: $p \leq 0{,}005$; B: $p \leq 0{,}01$). During the same period, however, a positive correlation exists between oxygen and meiofauna (A: $p \leq 0{,}005$; B: $p \leq 0{,}05$). In the winter period (April to August) no relationship was found between meiofauna and temperature but the dependence on oxygen continued (A: $p \leq 0{,}01$; B: $p \leq 0{,}005$). These findings hold for all the tidal levels of Station A but become progressively less significant towards the lower tidal levels of B. When the individual taxa data were analysed in the same way, the above relationship held for the nematodes but, due to the random fluctuation of the harpacticoids and "others", no relationship could be found with the remainder of the meiofauna. From these results the following chain of events may be postulated. In the winter substrate oxygen levels are high due to the low temperatures. With the onset of summer, temperatures begin to rise and the combined effect of the high oxygen content and slightly raised temperatures results in a peak of meiofauna, particularly nematodes. However, as temperatures continue to rise, the oxygen levels decrease, inhibiting nematode reproduction (Cooper *et al.* 1970). This will, of course, have an effect on the whole community since nematodes are dominant. The population continues to decline until mid-summer when temperatures are highest and oxygen lowest. Towards the end of summer the situation is reversed, i.e. temperatures drop and oxygen increases, resulting in a second peak of meiofauna. Temperatures continue to drop and nematode reproduction is again inhibited (Tietjen & Lee 1972) reducing the population to its previous winter level. It appears that oxygen is more of a limiting factor than temperature since the summer minimum is lower than the winter one. Figure 3 illustrates the above chain of events diagrammatically.

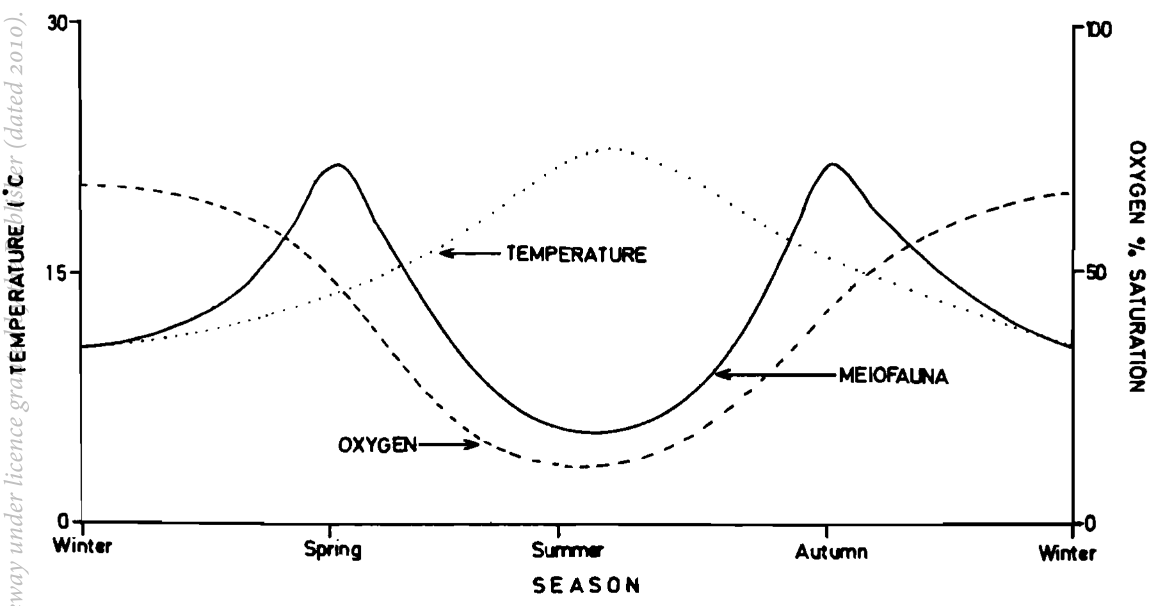

FIGURE 3
Diagrammatic representation of the chain of events leading to the observed twin peak fluctuation of the meiofauna.

Variations on this theme may be caused by a number of factors, among which are tidal level, position in the estuary, floods and macrofauna. Due to varying degrees of exposure, different tidal levels will experience different temperature and oxygen regimes. This, in turn, causes both the time and amplitude of the peaks to vary within a small range. Position in the estuary has much the same effect as tidal level since the ranges of environmental parameters are greater in the upper reaches than near the mouth. Flooding has a very temporary and, depending on the position in the estuary, localized effect. At Station B, where the beach was narrow, the whole intertidal zone was affected by flooding whereas at Station A, with its wide beach, only the lower tidal levels were affected. The above sequence of events may also be altered or abolished by the presence of macrofauna such as sand prawns. Since the prawns are actively pumping aerated water into the substrate throughout the year, areas with high densities of prawns do not experience the summer decrease in oxygen to the same extent as other areas. The removal of this limiting factor means that the meiofauna will not exhibit a twin peak seasonality. Furthermore it may be postulated that in low temperature areas where oxygen is not limiting, the meiofauna will exhibit only a summer, or late summer, peak. Similarly in tropical areas where oxygen is limiting, only a winter peak will be evident. The Swartkops estuary thus lies in a transition zone between these two extremes.

The dry masses obtained for the nematodes correspond closely to those obtained by Wieser (1960) who estimated an average of 0,6 μg. Mare (1942) found a wet mass of 1,6 μg (0,4 μg dry mass) for nematodes, and McLachlan (pers. comm.) estimated meiofauna mass in general to be between 0,4 and 0,6 μg dry mass. As far as the "others" are concerned, Wieser (1960) estimated ostracod and copepod dry mass to be 18 and 1,7 μg respectively, the latter probably reflecting a proponderance of burrowing copepods.

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REFERENCES

BARNETT, P R O 1968. Distribution and ecology of harpacticoid copepods of an intertidal mud flat. *Int. Revue ges. Hydrobiol.* 53: 177 - 209.

COOPER, A F, VAN GUNDY, S D & STOLZY, L H 1970. Nematode reproduction in environments of fluctuating aeration. *J. Nematol.* 2: 182 - 188.

COULL, B C 1970. Shallow water meiobenthos of the Bermuda Platform. *Oecologia,* 4: 325 - 357.

DAMODORAN, R 1974. Meiobenthos of the mudbanks of the Kerala coast. *Proc. Indian Natn. Sci. Acad.* 38(B): 288 - 297.

DYE, A H 1978. An ecophysiological study of the meiofauna of the Swartkops estuary. I. The sampling sites: Physical and chemical features. *Zool. afr.* 13: 1 - 18.

GIERE, O 1975. Population structure, food relations and ecological role of marine oligochaetes, with special reference to the meiobenthic species. *Mar. Biol.* 31: 139 - 156.

GRAY, J S & RIEGER, R M 1971. A quantitative study of the meiofauna of an exposed beach at Robin Hood's Bay, Yorkshire. *J. mar. biol. Ass. U.K.* 51: 1 - 19.

HIEP, C, SMOL, N & HAUTEKIET, W 1974. A rapid method of extracting meiobenthic nematodes and copepods from mud and detritus. *Mar. Biol.* 38: 79 - 81.

JANSSON, B O 1967. The significance of grain size and pore water content for the interstitial fauna of sandy beaches. *Oikos,* 18: 311 - 322.

JANSSON, B O 1968. Quantitative and experimental studies of the interstitial fauna of four Swedish sandy beaches. *Ophelia,* 5: 1 - 71.

JANSSON, B O 1971. The "umwelt" of the interstitial fauna. In: *Smithson. Contr. Zool.* 76: 129 - 140.

KOEN, H & FURSTENBERG, J P 1970. 'n Beknopte laboratorium handleiding vir nematologie. *Tech. Commun. Dep. agric. tech. Serv. S. Afr.* 92.

KURIAN, C V 1974. Ecology of benthos in a tropical estuary. *Proc. Indian Natn. Sci. Acad.* 38(B): 156 - 163.

MARE, M F 1942. A study of a marine benthic community with special reference to the micro-organisms. *J. mar. biol. Ass. U.K.* 25: 517 - 554.

McINTYRE, A D 1964. Meiobenthos of sub-littoral muds. *J. mar. biol. Ass. U.K.* 44: 665 - 674.

McINTYRE, A D 1969. Ecology of marine meiobenthos. *Biol. Rev.* 44: 245 - 290.

McINTYRE, A D & MURISON, D J 1973. The meiofauna of a flatfish nursery ground. *J. mar. biol. Ass. U.K.* 53: 93 - 118.

McLACHLAN, A 1975. Studies on the psammolittoral meiofauna of Algoa Bay. Ph.D. thesis, Univ. Port Elizabeth.

McLACHLAN, A, WINTER, P E D & BOTHA, L 1977. Vertical and horizontal distribution of sublittoral meiofauna in Algoa Bay, South Africa. *Mar. Biol.* 40: 355 - 364.

REES, C B 1940. A preliminary study of the ecology of a mud flat. *J. mar. biol. Ass. U.K.* 21: 185 - 199.

TEAL, J M & WIESER, W 1966. The distribution and ecology of nematodes in a Georgia salt marsh. *Limnol. Oceanogr.* 11: 217 - 222.

TIETJEN, J H 1966. The ecology of estuarine meiofauna with special reference to the class Nematoda. Ph.D. thesis, Univ. Rhode Island.

TIETJEN, J H & LEE, J J 1972. Life cycles of marine nematodes. Influence of temperature and salinity on the development of *Monhystera denticulata* Timm. *Oecologica,* 10: 167 - 176.

WARWICK, R M 1971. Nematode associations in the Exe estuary. *J. mar. biol. Ass. U.K.* 51: 439 - 454.

WARWICK, R M & BUCHANAN, J B 1970. The meiofauna off the coast of Northumberland. I. The structure of the nematode population. *J. mar. biol. Ass. U.K.* 50: 129 - 146.

WIESER, W 1959. The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. *Limnol. Oceanogr.* 4: 181 - 194.

WIESER, W 1960. Benthic studies in Buzzards Bay. II. The meiofauna. *Limnol. Oceanogr.* 5: 121 - 137.

WIESER, W, OTT, J, SCHIEMER, F & GNAIGER, E 1974. An ecophysiological study of some meiofauna species inhabiting a sandy beach at Bermuda. *Mar. Biol.* 26: 235 - 248.