

A Quantitative Analysis of the Meiofauna and the Chemistry of the Redox Potential Discontinuity Zone in a Sheltered Sandy Beach

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The vertical distribution of meiofauna in relation mainly to chemical changes in the upper 20 cm of deposit has been investigated at three sites on a sheltered beach of fine sand. There were strong vertical gradients in redox potentials, oxygen availability, hydrogen sulphide and the different oxidation states of nitrogen. Distinct redox potential discontinuities (RPD) were found at two sites in winter. RPDs moved up by 5-10 cm at all three sites in summer probably due to depletion of oxygen by increased benthic metabolism at the higher temperatures. The meiofauna showed distinct vertical distribution patterns strongly correlated with chemical gradients and also moved up to assume a shallower distribution in summer; harpacticoids were the most sensitive taxon. Oxygen is considered the 'super parameter' responsible for these chemical gradients, but numbers of the main meiofauna taxa correlated better with redox potentials than with oxygen availability readings, suggesting that the former is the most sensitive measure. The harpacticoid and gastrotrich faunas also showed vertical compositional changes correlated with chemical gradients. The meiofauna were more contagiously dispersed in winter than in summer and harpacticoids had more random dispersal than nematodes.

Introduction

Although open sandy beaches are generally well oxygenated areas or 'high energy windows' (Fenchel & Riedl, 1970) in the marine environment, reduced layers occur in sheltered beaches with fine sands. In the past most attention has been paid to the fauna of oxygenated areas and only relatively recently has the thibios of low oxygen zones been the subject of detailed studies. Fenchel (1969) and Fenchel & Jansson (1966) have studied particularly the vertical distribution of ciliates in low oxygen and reduced areas. Most metazoan meiofauna, however, decrease drastically in numbers, or even disappear, in the redox potential discontinuity zone (RPD) before fully reducing conditions appear and this boundary has been little studied. Many workers have noted the rapid vertical decline in metazoan meiofauna numbers, even

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in sands (e.g. Harris, 1972; McIntyre & Murison, 1973; Moore, 1975), but, other than Jansson (1968), Ott & Scheimer (1973), Giere (1973) and Wieser *et al.* (1974), have not tried to relate this to vertical oxygen changes or to vertical chemical changes resulting from decreasing oxygen tensions. The work reported here is the first detailed investigation of the relationships between the abundance and composition of metazoan meiofauna and the chemical changes that occur in the critical zone of the RPD.

The range of interstitial conditions from well oxygenated to reduced over a short distance on a sheltered beach at Port Erin, Isle of Man which is the result of small changes in grain size and shelter has enabled a detailed study of the RPD layer to be made. Bruce (1928a) did early work on sulphides and the black layers on this beach and Moore (1975) studied the ecology of the meiofauna, but paid no particular attention to reduced areas. The purpose of the present work is to quantify the effects of a series of oxygen tensions, decreasing over that critical range where reduced conditions first appear, on the meiofauna and chemistry of the interstitial water.

Study locality

The sandy beach at Port Erin (Figure 1) is nearly 500 m long and composed of 'more or less rounded grains of quartz with a coating of iron oxide and a greater or less admixture of calcareous matter, in the form of fragments of chalk, limestone, or comminuted shells . . .'

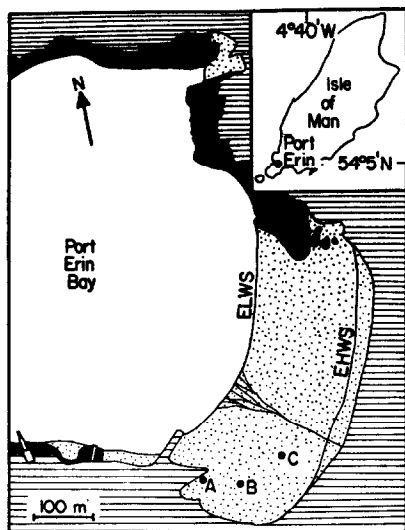


Figure 1. Map showing the positions of the three sampling sites on Port Erin beach.

(Bruce, 1928b). The bay is sheltered from all except westerly winds and its southern end is further protected by the Raglan Pier. Turbulence and sand particle size therefore tend to be lowest at the south end of the beach behind the pier and to increase towards the northern end of the beach (Moore, 1975). Only south of the stream running down the centre of the beach are reduced conditions encountered in the upper 20 cm of sand and in this area three sites were selected for study. Located just above mean tide level, 3 m above chart datum or ELWS, they were named A B and C in order of increasing exposure. On initial selection of

the sites (in January) they had respectively distinct, moderate and no dark layers in the upper 20 cm. All three remained almost saturated with interstitial water throughout the tidal cycle.

Methods

Sampling was done in the mornings in winter (February) and summer (July) shortly after the retreating tide left the study area. All samples were taken in an area approximately 1 m². Four 20 cm cores were taken at random with a perspex corer of internal cross-sectional area 11 cm² and divided into four vertical 5 cm sections each. Each section was placed in 100 ml 7% MgCl₂ solution (Uhlig *et al.*, 1973) and the meiofauna extracted within one hour by decantation using four rinses and a 63 µm screen. This extraction was more than 90% efficient. The meiofauna so collected was fixed in 5% hexamine-neutralized formalin and stained for counting by addition of a little rose bengal solution.

Depths of the dark layers were noted and four sets of oxygen availability (see Hulings & Gray, 1971) readings were taken at depths of 2.5, 7.5, 12.5 and 17.5 cm using a naked platinum electrode (surface area 0.115 cm²) and a calomel reference electrode (for which 250–260 mV must be added to *Eh* readings at temperatures of 5–15 °C). No corrections were made for pH differences. Temperatures were taken with a mercury thermometer to 0.1 °C. In winter two 20 cm cores were pooled, mixed and a 50–100 g subsample wet sieved through a nest of screens at 0.5ϕ intervals. Median (Morgans, 1956) and mean (Hulings & Gray, 1971) particle diameters and related parameters were calculated from the cumulative curves. A further two cores at each site were cut into 5 cm sections which were pooled and a 40-g sample used for estimation of organic matter by loss on ignition at 550 °C for 6 h after 24 h drying at 105 °C.

Interstitial water samples were collected from just below the centre of each 5-cm depth range using a modified pipette sampler (Makemson, 1972) or a 30 cm 16 gauge stainless steel needle with eight 250 µm pores near the sealed tip. By taking a number of 10 ml samples from each depth range, cumulative samples of 100 ml could be collected. PH was measured in the laboratory on a Dynacap pH meter and salinities determined using a bench salinometer or standard chloride titrations (Strickland & Parsons, 1968). Spectrophotometric analyses were carried out for nitrate (Strickland & Parsons, 1968), nitrite (Bendschneider & Robinson, 1952), total ammonia (Koroleff, 1970) and hydrogen sulphide (Cline, 1969). Attempts were made to measure sulphate by precipitation with barium chloride but such high values were obtained for all samples that this was abandoned. Great care was taken to minimize contact with air but most samples had to be filtered to remove suspended matter and slight oxidation of reduced samples may have occurred.

All meiofauna samples were counted and harpacticoid copepods and gastrotrichs identified to species. These two taxa were selected for ease of identification and because harpacticoids seemed representative of oxygenated upper layers and gastrotrichs of more reduced deeper layers. Morisita's index of dispersion (Elliott, 1971) was calculated on the count data and departures from randomness analysed using the χ^2 test ($P < 0.05$). Further, the faunal similarity between the different zones was calculated with the harpacticoid and gastrotrich data (expressed on an arbitrary abundance scale) using the Czekanowski or Bray Curtis coefficient and the results plotted in dendrogram form using group average and nearest neighbour clustering (Field, 1971). Finally, the meiofauna count data and physical and chemical data was compared using least squares linear regression analysis.

Results and discussion

Results of the substrate analyses are given in Table 1 together with depths of the dark layers. All three sites have well sorted fine sands with less than 0.5% subsieve material and hardly any skewness. Median and mean particle diameters are approximately the same for each site and increase with exposure from A to C, but only by 20 μm . Despite these small differences in particle diameters between sites there are noticeable differences in the depths of the dark

TABLE 1. Depths of dark layers and results of substrate particle size analysis at three sites on Port Erin beach. Md = median, QD = quartile deviation, Sk = skewness, Mz = graphic mean, σI = inclusive graphic standard deviation, SK = inclusive graphic skewness

Station	Depths of dark layers (cm)		Particle size analysis							
	Winter	Summer	Md(μm)	Md ϕ	QD ϕ	Sk ϕ	Mz(μm)	Mz ϕ	$\sigma\text{I}\phi$	SK ϕ
A	9-12	2-3	175	2.52	0.15	0.00	175	2.52	0.22	+0.07
B	10-16	not clear	179	2.48	0.16	-0.02	182	2.46	0.25	-0.08
C	below 20	18-20	194	2.37	0.20	-0.02	198	2.34	0.31	-0.13

TABLE 2. Results of physical and chemical analysis of sediments and interstitial waters. W = winter; S = summer; Oxygen availability in $\text{g cm}^{-2} \text{min}^{-1} \times 10^{-7}$, nutrients in $\mu\text{g l}^{-1}$

Station and depth (cm)	Temp. $^{\circ}\text{C}$		Sal. ‰		pH		Organics %		Eh mV	
	W	S	W	S	W	S	W	S	W	S
A 0-5	5.0	17.5	22.6	35.2	7.7	7.6	2.26	1.58	+290	+110
A 5-10	5.4	15.1	24.6	35.0	7.9	7.8	2.38	1.01	+205	-66
A 10-15	5.6	14.4	23.5	35.7	7.9	7.8	1.54	0.88	+75	-177
A 15-20	6.0	14.0	23.5	35.3	7.9	7.9	1.58	1.00	+60	-187
B 0-5	6.0	17.4	28.9	31.6	7.9	7.4	1.93	0.85	+405	+319
B 5-10	5.9	15.9	30.3	31.2	7.9	7.6	1.83	0.85	+360	+160
B 10-15	5.7	14.9	28.5	30.7	8.0	7.6	2.11	0.76	+250	+86
B 15-20	5.6	14.8	26.4	32.4	8.0	7.5	2.11	0.85	+125	+41
C 0-5	5.5	15.2	27.4	21.0	8.2	8.6	2.20	0.90	+450	+330
C 5-10	5.3	15.2	26.6	25.4	8.3	8.2	2.18	0.98	+410	+222
C 10-15	5.2	15.1	27.6	23.3	8.3	8.1	2.12	1.03	+355	+118
C 15-20	5.1	15.3	26.0	24.6	8.1	7.7	2.27	1.02	+200	+69

Station and depth (cm)	Oxygen		Hydrogen sulphide		Ammonia		Nitrite		Nitrate	
	W	S	W	S	W	S	W	S	W	S
A 0-5	0.9	0.7	0	60	150	172	10	5	18	21
A 5-10	0.8	0.6	0	75	166	194	10	1	40	0
A 10-15	0.7	0.6	0	85	211	204	13	0	66	0
A 15-20	0.5	0.5	40	85	331	323	23	0	53	0
B 0-5	2.3	2.0	0	0	0	97	7	10	1072	349
B 5-10	1.8	1.9	0	0	30	140	36	1	673	56
B 10-15	1.6	1.7	0	12	121	194	13	0	40	0
B 15-20	1.4	1.7	0	34	135	323	7	0	0	0
C 0-5	3.5	2.4	0	0	0	0	16	58	2033	749
C 5-10	2.6	2.4	0	0	0	86	59	78	3033	890
C 10-15	2.5	2.3	0	0	0	65	187	352	1798	340
C 15-20	2.4	2.2	0	9	15	237	371	262	1333	328

layers which are shallowest at A and deepest at C. This is the result of permeability differences (between sands of 175 μm to 194 μm median particle diameters), differences in hydrostatic forces due to turbulence and differences in organic input.

Table 2 shows the results of the physical and chemical analyses of stratified sampling from the three sites. Temperatures were 5–6 °C in winter and 14–17 °C in summer. Salinities were mainly below 30‰ in winter, being lowest at site A while in summer they were above 30‰ except at site C where values around 23‰ were recorded, probably due to the proximity of the stream.

pH values were close to 8, even in reduced areas, due to the buffering capacity of seawater and carbonates in the sand. Lowest values were usually around the redox potential discontinuity (RPD) where dark layers appeared. Summer values were lower than those in winter. The percentage organic matter in the sand on a mass basis was higher in winter than summer and tended to be highest in the region of the RPD.

Redox potential values showed a wide range vertically in the sediment, alongshore and seasonally and reasonably distinct RPDs were apparent. Assuming the RPDs to be the 'layer where oxidising processes become displaced by reducing processes' or the 'flattest part of the Eh curve, . . .' (Fenchel & Riedl, 1970), the depths of the RPDs can be estimated from the data in Table 2 and Figures 2, 3 and 4. Eh values vary with the tides (Ott &

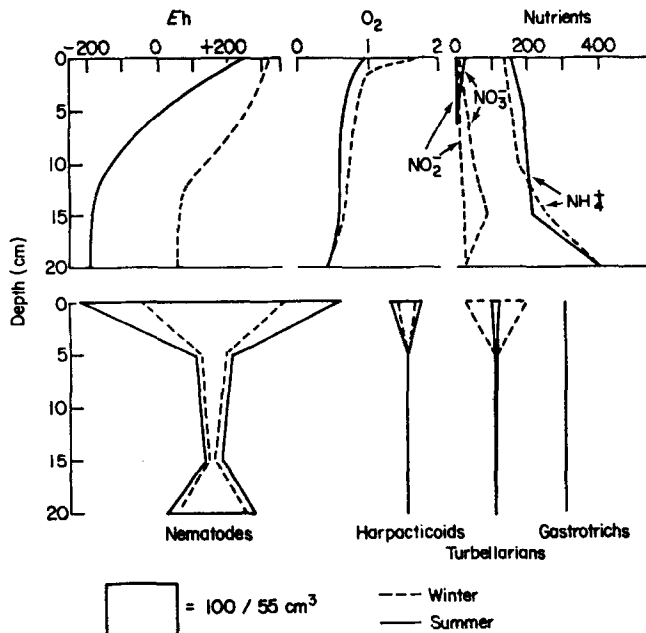


Figure 2. Summary of the main vertical gradients at site A. Eh in mV, oxygen availability in $\text{g cm}^{-2} \text{min}^{-1} \times 10^{-7}$ and nutrient concentrations in $\mu\text{g l}^{-1}$.

Machan, 1971) and the values in Table 2 refer only to the first hour after the sites were exposed. The estimates are 5–20 cm, 11–20 cm and below 18 cm in winter and 1–10 cm, 5–20 cm and 10–20 cm in summer at A, B, and C respectively. These estimates are confirmed by the nutrient analysis discussed later.

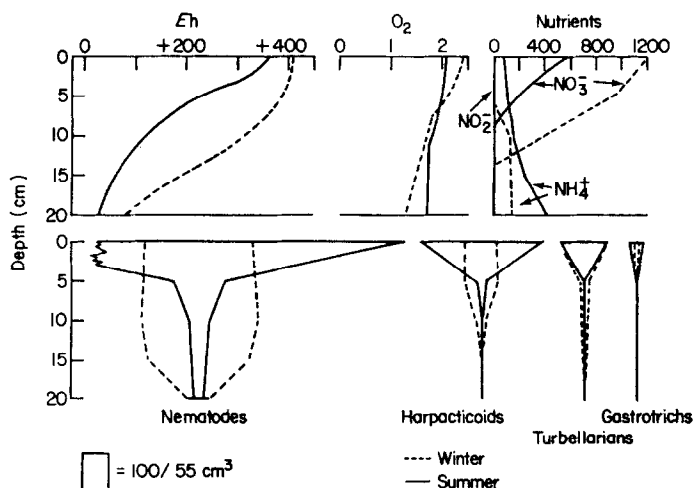


Figure 3. Summary of the main vertical gradients at site B. Eh in mV, oxygen availability in $\text{g cm}^{-2} \text{min}^{-1} \times 10^{-7}$ and nutrient concentrations in $\mu\text{g l}^{-1}$.

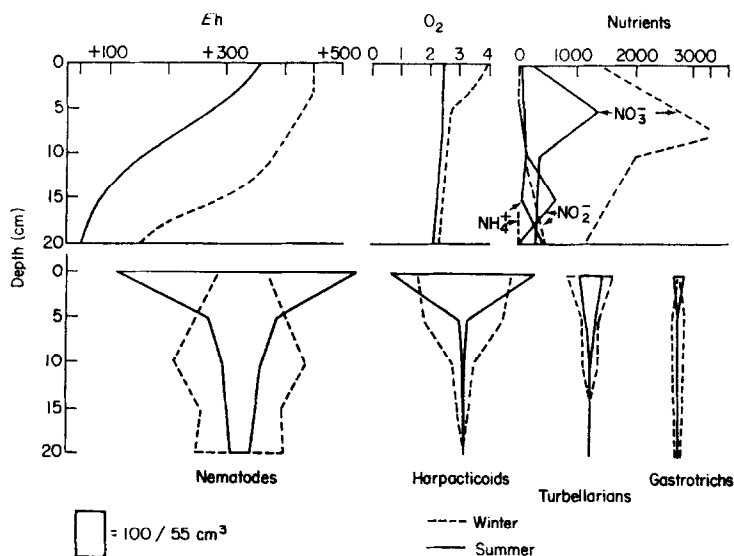


Figure 4. Summary of the main vertical gradients at site C. Eh in mV, oxygen availability in $\text{g cm}^{-2} \text{min}^{-1} \times 10^{-7}$ and nutrients concentrations in $\mu\text{g l}^{-1}$.

Oxygen availability did not appear to be as sensitive a measure of interstitial climate as Eh ; values ranged between 0.5 and $3.5 \text{ g cm}^{-2} \text{min}^{-1} \times 10^{-7}$, being lowest at A 15–20 cm, highest at C 0–5 cm and lower in summer than winter. Even in obviously reducing conditions at A in summer, readings never went below $0.2 \text{ g cm}^{-2} \text{min}^{-1} \times 10^{-7}$, although the general pattern was the same as for Eh .

Hydrogen sulphide was present in small quantities, mainly at site A in summer, and only at site A could it be strongly smelt during sampling. It also occurred in traces at B 10–20 cm and C 15–20 cm in summer. The three oxidation states of nitrogen exhibited some fairly clear patterns, following the Eh profiles as described by Fenchel & Riedl (1970). At site A

at all depths in summer and winter ammonia was dominant. Nitrates recorded at 5–20 cm in winter were probably the result of some ammonia being oxidized during sampling. Site B had clear gradients in both winter and summer: nitrates predominated in the upper 10 cm in winter and 5 cm in summer; nitrites were present in low quantities at 5–15 cm in winter, and ammonia predominated below 10 cm in winter and below 5 cm in summer. At site C nitrates predominated throughout the upper 20 cm in winter, although nitrites reached relatively high proportions below 10 cm. In summer nitrates predominated in the upper 10 cm, nitrites at 10–15 cm and nitrites and ammonia at 15–20 cm. Values of nitrate and nitrite in the sea during winter are about $400 \mu\text{g l}^{-1}$ and $5 \mu\text{g l}^{-1}$ respectively and considerably lower in summer (Slinn & Eastham, 1971), these being about an order of magnitude lower than the maximum values in the interstitial water.

The chemical gradients recorded thus follow the pattern described by Fenchel & Riedl (1970) and indicate that the depth range studied here correspond to the oxygenated layers and RPD except for the 10–20 cm range at site A in summer which may be considered part of the black or sulphide zone.

Various densities of meiofauna were recorded in the top 20 cm (Table 3), ranging from 348 per 11 cm^2 at A in winter to 2137 per 11 cm^2 at C during winter but were generally close to 1100 per 11 cm^2 or 10^6 m^{-2} . In winter numbers increased from A to C but in summer B had highest counts followed closely by C and then A. There were marked seasonal differences in vertical distribution (Figures 2, 3 and 4) with the fauna concentrated in the upper 5 cm at all three sites in summer but deeper lying in winter, as found by Harris (1972) and McIntyre & Murison (1973). One noticeable pattern was the increase in nematode numbers at A 15–20 cm in both summer and winter. The reason for this is uncertain but may be due to small areas of oxygenated or disturbed substrate at these depths or to an anaerobic component (Ott & Scheimer, 1973).

Nematodes were dominant throughout, making up 62–82%, 76–70% and 60–66% of the total numbers at A, B and C in winter–summer respectively, followed by harpacticoid copepods at 5–9%, 11–17% and 25–21%, turbellarians at 21–3%, 7–6% and 8–3% and gastrotrichs at 1–3%, 3–2% and 4–2%. Other forms included unidentified nauplii, the archiannelid *Protodriloides symbioticus* (Giard), acarines, tardigrades, ciliates, gnathostomulids, oligochaetes, amphipods and ostracods.

Analysis of the count data using Morisita's index of dispersion for total counts revealed significant departures from randomness (χ^2 , $P < 0.05$) in many cases. All winter total counts except C 15–20 cm showed contagious distribution, mainly due to contagious distribution of nematodes. Harpacticoids were more randomly distributed, particularly in A samples where they occurred in very low numbers. Summer total counts showed a more random distribution with some samples even exhibiting regular distribution. Nematodes were, however, still mainly contagiously distributed through harpacticoids, occurring in lower numbers, were more randomly distributed. McIntyre & Murison (1973) also found harpacticoids to be more uniformly distributed than nematodes and suggested that this may be as a result of their utilizing fewer environmental niches. Other taxa occurred in too low numbers for similar analysis of their dispersal patterns.

Each parameter measured was compared against all other parameters by linear regression analysis and Table 5 summarizes the significant results. All factors expected to be related to the degree of oxygenation of the substrates showed strong interrelationships: oxygen availability, redox potential, nitrates and ammonia, total meiofauna numbers and numbers of the dominant taxa. Oxygen availability, redox potential, nitrates and ammonia were interrelated as described by Fenchel & Riedl (1970). Oxygen availability, redox potential

TABLE 3. Meiofauna numbers per 55 cm³

Station and depth (cm)	Winter					Summer						
	Nematodes	Harpacticoids	Turbellarians	Gastrotrichs	Others	Total \pm s.d.	Nematodes	Harpacticoids	Turbellarians	Gastrotrichs	Others	Total \pm s.d.
A 0-5	120	15	48	1	10	194 \pm 28	206	29	8	2	10	256 \pm 54
A 5-10	27	2	14	2	9	54 \pm 20	42	2	1	1	2	48 \pm 18
A 10-15	13	1	9	1	11	35 \pm 24	28	1	1	1	2	33 \pm 11
A 15-20	55	1	4	0	5	65 \pm 90	72	5	3	8	1	89 \pm 50
Total						348						433
B 0-5	438	125	115	0	17	695 \pm 224	929	261	95	26	77	1388 \pm 294
B 5-10	450	81	25	2	2	560 \pm 115	140	15	6	2	1	164 \pm 45
B 10-15	422	21	9	32	0	484 \pm 376	65	4	2	2	3	70 \pm 10
B 15-20	237	1	7	38	5	288 \pm 75	47	3	1	2	0	53 \pm 12
Total						2027						1681
C 0-5	239	287	107	22	10	665 \pm 194	513	263	26	17	94	913 \pm 231
C 5-10	384	181	54	34	9	662 \pm 280	181	15	9	3	8	216 \pm 64
C 10-15	361	55	25	28	6	475 \pm 181	115	6	4	4	2	131 \pm 40
C 15-20	291	12	4	20	8	335 \pm 10	79	1	1	1	1	83 \pm 17
Total						2137						1343

TABLE 4. Values of Morisita's index (I_B) for count data from winter (W) and summer (S) samples. * = contagious; ** = random; *** = regular (χ^2 , $P < 0.05$)

	Station and depth (cm)											
	A 0-5	A 5-10	A 10-15	A 15-20	B 0-5	B 5-10	B 10-15	B 15-20	C 0-5	C 5-10	C 10-15	C 15-20
Total (W)	1.012*	1.093*	1.351*	2.418*	1.076*	1.031*	1.450*	1.048*	1.061*	1.132*	1.105*	0.998**
Total (S)	0.972***	1.096*	0.980**	1.220*	0.672***	1.064*	0.984**	0.952***	1.044*	1.052*	1.028*	0.976**
Nematodes (W)	1.359*	1.062*	1.899*	2.859*	1.166*	1.027*	1.521*	1.110*	1.262*	1.077*	1.079*	0.997**
Nematodes (S)	1.014*	1.149*	1.071*	1.286*	1.059*	1.041*	1.017**	1.019**	1.116*	1.051*	1.042*	1.024*
Harpacticoids (W)	1.046**	0.667**	0.400**	0.000**	1.054*	1.172*	2.820*	0.667**	1.009*	1.468*	1.255*	1.036**
Harpacticoids (S)	1.280*	1.000**	0.000**	1.032**	1.037*	1.067**	0.941**	0.889**	1.115*	1.217*	1.319*	1.200**

TABLE 5. Significant regressions between parameters measured during winter and during summer. All have 10 degrees of freedom and significance at 5% = *, 1% = **, 0.1% = *** or 0, 1% = **** levels. Eh in mV, oxygen availability in $g\ cm^{-2}\ min^{-1} \times 10^{-7}$, nutrients in $\mu g\ l^{-1}$ and meiofauna numbers per 55 cm^3

		Winter		Summer		
X	Y	r	X	Y	r	
1	Oxygen	0.79***	24	Oxygen	Eh	0.79***
2	Oxygen	-0.90***	25	Oxygen	log [nitrites] + 1	0.78***
3	Oxygen	0.84***	26	log [nitrites] + 1	[ammonia]	-0.75***
4	Eh	-0.83***	27	Eh	log [nitrites] + 1	0.80***
5	Eh	0.71***	28	Eh	[ammonia]	-0.75***
6	log [ammonia] + 1	-0.82***	29	Eh	log (Total numbers + 1)	0.85***
7	Oxygen	0.86***	30	Eh	log (Nematodes + 1)	0.86***
8	Oxygen	0.66*	31	Eh	log (Harpacticoids + 1)	0.80***
9	Oxygen	0.85***	32	Eh	log (Turbellarians + 1)	0.80***
10	Eh	0.87***	33	log [nitrites] + 1	log (Total numbers + 1)	0.72***
11	Oxygen	0.61*	34	log [nitrites] + 1	log (Nematodes + 1)	0.75***
12	Eh	0.67*	35	log [nitrites] + 1	log (Harpacticoids + 1)	0.59*
13	Eh	0.98***	36	log [nitrites] + 1	log (Turbellarians + 1)	0.74***
14	Eh	0.77***	37	[ammonia]	log (Total numbers + 1)	-0.69*
15	[ammonia]	-0.85***	38	[ammonia]	log (Nematodes + 1)	-0.68*
16	[ammonia]	-0.76***	39	[ammonia]	log (Harpacticoids + 1)	-0.67*
17	[ammonia]	-0.87***	40	[ammonia]	log (Turbellarians + 1)	-0.65*
18	[nitrites]	0.71***	41	Total numbers	Nematodes	0.99***
19	[nitrites]	0.76***	42	Total numbers	Harpacticoids	0.96***
20	Total numbers	0.88***	43	Total numbers	Turbellarians	0.94***
21	Total numbers	0.77***	44	Nematodes	Harpacticoids	0.92***
22	Total numbers	0.67*	45	Nematodes	Turbellarians	0.90***
23	Harpacticoids	0.81**	46	Nematodes	Gastrotrichs	0.94***
			47	Harpacticoids	Turbellarians	0.82***
			48	Harpacticoids	Gastrotrichs	0.93***
			49	Turbellarians	Gastrotrichs	0.91***

TABLE 6. Abundance of harpacticoids and gastrotrichs per 55 cm³ in winter (W) and summer (S) samples: 1 = <5, 2 = 5-15, 3 = 16-50, 4 = >50; W/S

Species	Station and depth (cm)											
	A 0-5	A 5-10	A 10-15	A 15-20	B 0-5	B 5-10	B 10-15	B 15-20	C 0-5	C 5-10	C 10-15	C 15-20
Harpacticoids												
<i>Asellopsis intermedia</i> (T. Scott)	2/3	1/1	1/1	1/1	3/4	3/1	2/1	1/0	4/4	3/1	1/1	1/1
Ectinosomatidae sp.	1/0	1/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
<i>Arenosetella monensis</i> Moore	1/1	0/0	0/0	0/1	4/3	2/1	1/0	0/1	4/4	4/1	1/1	1/0
<i>Paraleptastacus espinulatus</i> Nicholls	0/1	0/0	0/0	0/1	3/4	0/2	0/1	0/1	4/4	4/2	3/1	2/0
<i>Arenocaris bifida</i> Nicholls	0/0	0/0	0/0	0/0	2/2	1/1	0/1	0/1	1/2	1/1	0/1	0/0
<i>Khtopsyllus constrictus</i> (Nicholls)	0/1	0/0	0/0	0/0	1/1	2/1	0/0	0/0	1/0	0/0	0/0	0/0
Gastrotrichs												
<i>Cephalodays turbanelloides</i> (Boaden)	0/1	0/1	0/1	0/2	0/0	0/1	0/0	0/0	2/2	3/1	3/1	2/0
<i>Pseudostomella roscovia</i> Swedmark	0/0	0/0	0/0	0/1	0/2	0/0	0/0	0/0	0/2	0/1	1/0	0/0
<i>Thiodays sterreri</i> Boaden	0/0	0/0	1/0	0/0	0/2	1/1	3/1	3/1	1/0	0/0	0/0	0/0
<i>Neodays</i> sp.	0/0	1/0	0/0	0/0	0/3	1/1	2/0	2/0	1/0	1/0	1/0	2/1
<i>Turbanelia</i> sp.	1/1	1/0	0/0	0/1	0/0	1/0	0/0	0/0	0/0	1/0	0/0	2/1

and nitrates were positively correlated the only difference between summer and winter being that nitrates were logarithmically related to oxygen availability (25) and redox potential (27) in summer and linearly related to them in winter (3), (5). Ammonia was negatively related to oxygen availability, redox potential and nitrates. In winter it was inversely logarithmically related to oxygen availability (2) and to the logarithm of nitrates (6). In summer it increased linearly as nitrates decreased logarithmically (26). This represents total ammonia and no attempt was made to distinguish ionized and unionized fractions although the latter is considered to be more toxic (Hampson, 1977).

Meiofauna numbers showed strong correlations with most of the above factors. In winter relationships with oxygen availability, redox potential, nitrate and ammonia [equations (7) to (19)] were linear for total counts, nematodes and turbellarians but logarithmic for harpacticoids, suggesting the greater sensitivity of this group to the effects of decreasing oxygen tensions. In summer no significant relationships were found between meiofauna numbers and oxygen availability, largely because of the insensitivity (see Giere 1973) and variability of oxygen availability values. There were, however, strong relationships with redox potential [equations (29) to (32)], nitrates [equations (33) to (36)] and ammonia [equations (37) to (40)] for total counts, nematodes, harpacticoids and turbellarians. Since all these relation-

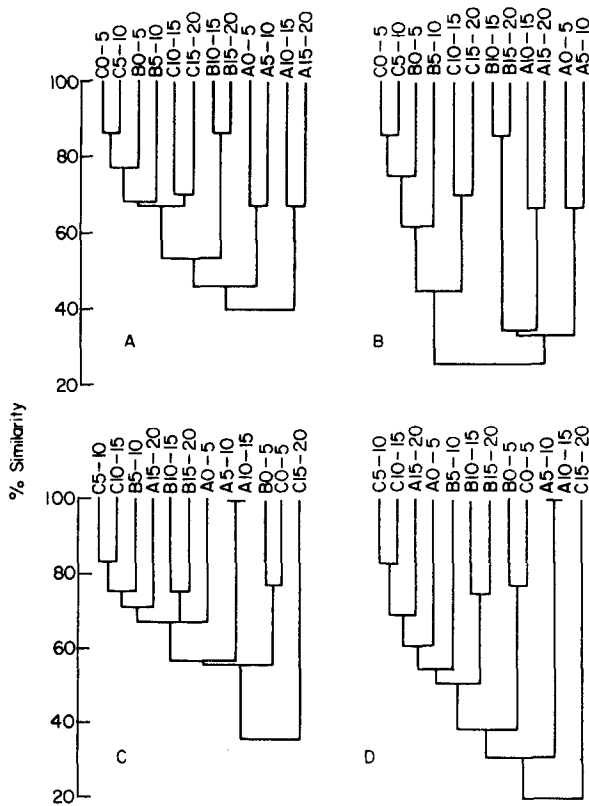


Figure 5. Dendrograms showing harpacticoid and gastrotrich faunal affinities between depth zones at three sampling sites. A = nearest neighbour clustering, winter samples; B = group average clustering, winter samples; C = nearest neighbour clustering, summer samples; D = group average clustering, summer samples.

ships are logarithmic it suggests that these factors are nearer their critical limits in summer thus making the meiofauna more sensitive to small changes. The absence of gastrotrichs from these regressions is because, unlike the other taxa, they tend to concentrate at or just above RPD and not in the most oxygenated layers. It is not certain whether the negative correlations with ammonia are simply a passive result of its negative relationship to oxygenation or whether it actually exhibits a toxic limiting effect. These equations in fact only confirm the great sensitivity of the meiofauna to these chemical gradients and do not allow separation of effects of different parameters as all are interrelated.

The numbers of the main taxa were strongly intercorrelated. Nematodes particularly, being the dominant taxon, were closely correlated to the total counts [equations (20) and (41)]. Even gastrotrichs showed strong correlations to nematode, harpacticoid and turbellarian numbers in summer [equations (46), (48) and (49)]. These correlations between counts for the main taxa were closer in summer than in winter because of the lower oxygen conditions in summer and thus the greater concentration in the surface layer.

The abundances of harpacticoid and gastrotrich species on an arbitrary scale from 0 to 4 is presented in Table 6 and the dendrograms based on this in Figure 5. Although only 6 harpacticoid and 5 gastrotrich species were used some clear patterns can be seen. In winter nearest neighbour and group average clustering show a similar pattern in different ways. Nearest neighbour clustering arranges the sampling points in a series from the most oxygenated (C 0-10 cm) to the most reduced (A 10-20 cm) while group average tends to divide them into two main clusters, one of relatively oxygenated areas (C 0-20 cm & B 0-10 cm) and one of relatively reduced areas (B 10-20 cm & A 0-20 cm). The summer pattern is not quite so clear. Nearest neighbour clustering tends to produce four groups of areas at 60% similarity: (1) C 5-15 cm, B 5-20 cm and A 0-5 cm and A 15-20 cm all having moderate numbers and occurring close to or in the RPD, (2) A 5-15 cm being reduced and having low numbers, (3) B 0-5 cm and C 0-5 cm being relatively well oxygenated and having very high numbers and (4) C 15-20 cm, being in the RPD, with moderate numbers but very few harpacticoids or gastrotrichs. Group average clustering in summer produced the same four groups at a 40-50% level of similarity. Similarities between the same areas in winter and summer were:

A 0-5 cm	62%	B 0-5 cm	71%	C 0-5 cm	83%
A 5-10 cm	33%	B 5-10 cm	60%	C 5-10 cm	50%
A 10-15 cm	50%	B 10-15 cm	33%	C 10-15 cm	53%
A 15-20 cm	25%	B 15-20 cm	20%	C 15-20 cm	43%

At all three sites similarity values decreased with depth, showing that the greatest changes occurred in deeper layers where conditions became more reducing in summer, while in the surface layers conditions remained reasonably oxygenated.

These data show that faunal composition, as well as abundance, is related to the gradients of the RPD. Thus, although the numbers of most species increase with increasing oxygenation, some species are more tolerant of reduced conditions than others. Most typical of the oxygenated layers were the harpacticoids *Arenosetella monensis*, *Paraleptastacus espinulatus* and *Asellopsis intermedia*. *Asellopsis intermedia* was the most tolerant of these three species to reduced levels of oxygen and was fairly common in the upper RPD, as was the gastrotrich *Cephalodasy turbanelloides*. Under moderately reducing conditions the gastrotrich *Thiodasys sterreri* occurred. The intertidal height sampled here falls approximately on the boundary between eulittoral or midshore harpacticoids and upper shore harpacticoids distinguished by Moore (1975). This transition zone is marked by an increase in beach slope associated with brackish water seepage and relatively coarser sand. *Asellopsis intermedia* is the only

burrower amongst these species and this ability may partly account for its dominance at site A where the finest sand may begin to limit interstitial harpacticoids whose lower grain size barrier is around $160\ \mu\text{m}$ (McLachlan *et al.*, 1977).

Conclusions

The sediments sampled here represent the upper oxygenated layers and the RPD (as defined by Fenchel & Riedl, 1970), with the exception of the 10–20 cm depth zone at site A during summer which may be considered part of the black or sulphide zone. The predominant factor or 'super parameter' responsible for the vertical gradients of the RPD is oxygen, the availability of which determines the redox potential as well as the oxidation states of sulphur and nutrients. Despite the fact that oxygen was the most important factor investigated, the oxygen availability values obtained here (which are a measure of the rates of diffusion and not the absolute amounts of oxygen present) appeared to be very insensitive and had poorer predictability and less correlation with meiofauna numbers than redox potential values. The apparatus used for oxygen availability measurements had an applied potential of 600 mV and not the suggested 800 mV (Hulings & Gray, 1971), although this should make negligible difference at the oxygen tensions measured here (see Lemon & Erickson, 1954). It is well known that oxygen availability readings are influenced by a number of factors, most notably flow (Jansson, 1967), while redox potential readings are generally accurate, simple and reliable (Ott & Machan, 1971). The sensitivity of oxygen availability readings to water movement is such that in a rapidly draining beach they may be considered more a record of rates of drainage than actual oxygen content. On the other hand, in a more restricted or stagnant environment, even a small probe consumes oxygen faster than a small organism and thus quickly depletes its immediate environment. Oxygen availability is then more a measure of the rate of diffusion of oxygen from the surroundings to a point than of the amount available to a tiny organism that can move around. Further, these readings are insensitive and fluctuations often exceed the limits of error of the method at low oxygen tensions (Giere, 1973). For these reasons it is felt that actual oxygen content, as measured by titrations or a polarographic method in the laboratory, is a more sensitive and a more meaningful measure of interstitial oxygen conditions.

In both summer and winter the meiofauna showed strong vertical gradients in numbers and species which appear to be mainly in response to chemical gradients in the interstitial water. Harpacticoids were the most sensitive group to the effects of decreasing oxygen tensions in winter and were followed by turbellarians and nematodes. Calmer seas reduce turbulence and mixing and higher temperatures probably raise benthic metabolism in summer. This could cause the RPDs to rise by 5–10 cm at each site, as has been recorded elsewhere (Fenchel & Riedl, 1970). All three taxa became more sensitive to chemical changes in summer. Gastrotrichs, however, tended to concentrate towards the RPDs rather than at the surface. Hulings & Gray (1976) postulated that physical and chemical factors control meiofauna abundance in winter and that biological factors are more important in summer. The reverse seems to be the rule in these poorly oxygenated sediments in which chemical factors become more limiting in summer. The greater tendency towards random dispersal in summer, however, suggests that although chemical factors may control both abundance and vertical distribution, horizontal dispersal may be controlled biologically, e.g. by predation and competition, to a greater extent in summer than in winter.

The data presented here show clearly that the RPD is the critical zone for the metazoan meiofauna whose numbers drop rapidly below a redox potential of $+200\ \text{mV}$. As far as

the actual limiting factors controlling vertical distribution are concerned, Fenchel (1969) postulated that the correlation between vertical distributions and redox profile may be due to (1) oxygen requirements, (2) tolerance to toxic reduced compounds and (3) specialization to feed on micro-organisms which require certain redox conditions. All the chemical parameters monitored here are related to oxygen tensions and it is difficult at present to determine which are the most critical. Laboratory experiments to assess tolerances to ammonia, hydrogen sulphide and low oxygen tensions would help to clarify this.

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