THE DISTRIBUTION AND ECOLOGY OF PSAMMOLITTORAL MEIOFAUNA AROUND THE ISLE OF MAN

by

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Résumé

L'auteur examine, sur six plages sableuses autour de l'Ile de Man, la répartition et la densité de la méiofaune, en rapport avec une analyse physico-chimique du milieu. Ces plages présentent toute une gamme entre les modes battus et abrités et une répartition des sédiments allant du sable moyen au sable fin.

La densité de la méiofaune varie entre 7 655/10 cm^2 et 149/10 cm^2. En général, ce sont les Nématodes qui dominent, bien qu'au niveau de la plage la plus battue, les Copépodes harpacticoïdes soient les plus nombreux. Les Gastrotriches et les Oligochètes dominent localement. En général, les densités les plus élevées se rencontrent sur la basse plage et dans les régions les mieux abritées où la plus grande partie de la population totale se tient au-dessus d'une profondeur de 5 cm. Vers la haute plage, la population maximale se rencontre à un plus bas niveau. En général, les Gastrotriches ont leur centre de répartition, dans le sable, à une profondeur un peu plus grande que les autres groupes.

L'influence des facteurs physico-chimiques sur la distribution de la faune est examinée. De grandes fluctuations de la température et de la salinité, alliées à un manque d'eau dans les vides du sable, sont considérées comme fournissant une barrière puissante au niveau de la haute plage ; néanmoins, certaines espèces d'Oligochètes et de Nématodes peuvent la franchir. Les Copépodes harpacticoïdes sont seulement abondants dans des substrats saturés à plus de 50 p. 100. Un diamètre critique minimal de 2,5 à 2,6 <*Z* s'impose pour l'existence de Copépodes harpacticoïdes interstitiels dans des sables bien classés. L'absence de fait des Copépodes interstitiels et de plusieurs autres groupes sur les plages à sable plus fin de l'Ile de Man est une conséquence de la finesse des sédiments. La distribution des Nématodes se reflète dans celle des détritus visibles. L'influence de l'oxygène sur la répartition est considérée comme se manifestant surtout par l'emprisonnement de la faune aérobie au niveau superficiel du sable.

Introduction

Despite the widespread interest in the distributional ecology of the meiobenthos, there is still little known about the fauna around British coasts. Since the review of Mclntyre (1969) a few additional intertidal meiobenthic surveys have been performed, viz. the River Tees Estuary (Gray, 1971, 1976), Robin Hood's Bay and Filey Bay, Yorkshire (Gray and Rieger, **1971),** Whitsand Bay, Cornwall (Harris, 1972a, b) and several Scottish beaches (Mclntyre, 1971; Mclntyre and Murison, 1973). Platt

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(1977a, b) and Maguire (1977) have recently studied the ecology of meiofauna in Strangford Lough, Northern Ireland. Other European areas which have been studied in more detail generally exhibit a markedly different fauna e.g. the atidal Baltic and Mediterranean Seas, these beaches being comparable to the upper zones of tidal beaches (McIntyre, 1969), although North Sea beaches present more similar conditions (e.g. Renaud-Debyser and Salvat, 1963; Schmidt, 1968, 1969).

This contribution, dealing with the major meiofaunal taxa, is the first of a series of papers based on meiobenthic survey work carried out during 1972-4 in which a range of sandy beaches around the Isle of Man was examined in an attempt to compare the intertidal distribution of the fauna and to identify the roles played by various environmental factors in the determination of distributional patterns. Since this study was completed, McLachlan (1978) has examined the vertical distribution of the meiofauna on one of these beaches in relation to chemical changes.

The study locations

The Isle of Man is situated in the middle of the Irish Sea just north of 54°N and exhibits a number of quartz sand beaches ranging in exposure from very sheltered to moderately exposed. Figure 1 shows the six study

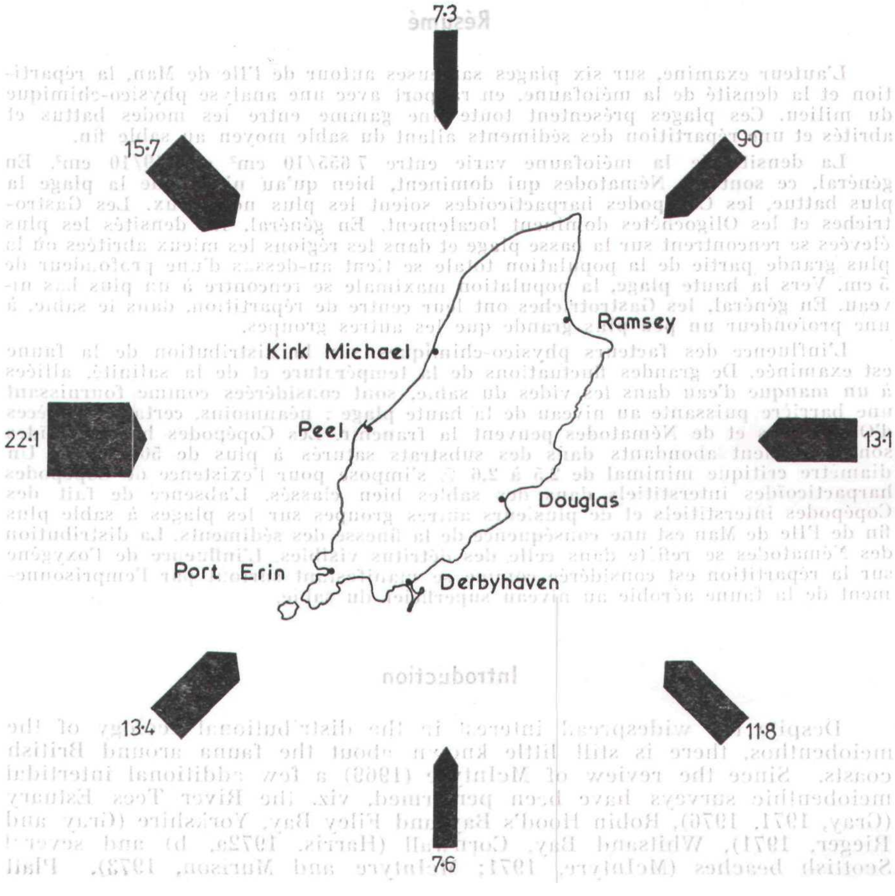


FIG. 1

The Isle of Man, showing study localities and the percentage of Winds in each sector during 1933-1957 (data from Birch, 1964);

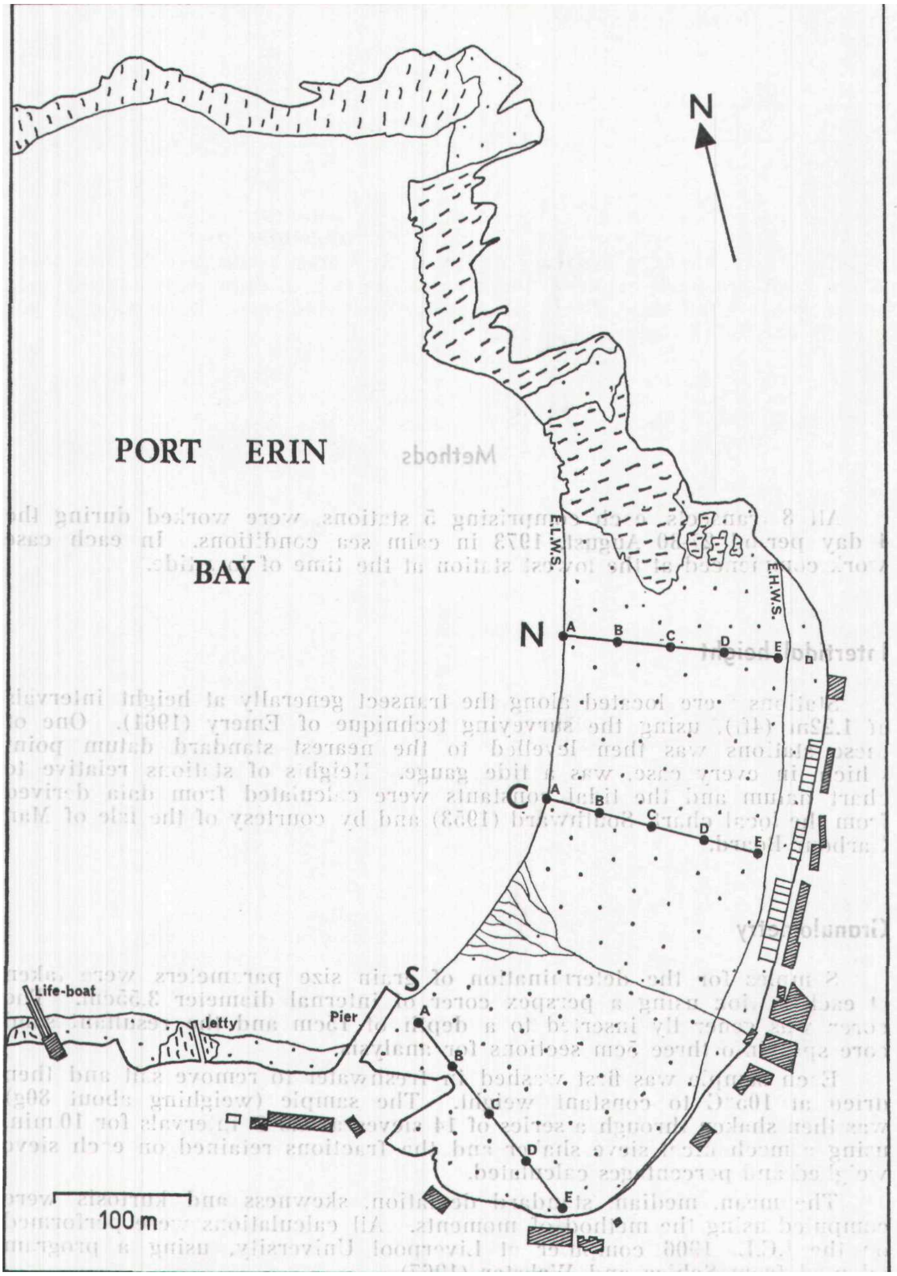


FIG. 2
Port Erin beach, showing sampling stations.

sites in relation to the prevailing winds. One transect was worked at each of these locations apart from Port Erin, where three were worked (Fig. 2). The exact position of these transects with respect to local features and descriptions of the beaches can be found in Moore (1975).

From a consideration of the positions of the sites with respect to the prevailing winds and the degree of local shelter, the following scheme of exposure ranking is proposed:

moderately exposed	Kirk Michael	↑
	Port Erin N	
	Port Erin C	
	Ramsey	
	Douglas	Exposure
sheltered	Peel	
	Derbyhaven	
	Port Erin S	

Due to the small size of the Irish Sea and consequently the small fetch, even the most exposed beaches on the Isle of Man can be described as no more than moderately exposed. The sheltered beaches all show a high degree of localized shelter.

Methods

All 8 transects, each comprising 5 stations, were worked during the 4 day period 27-30 August, 1973 in calm sea conditions. In each case work commenced at the lowest station at the time of low tide.

Intertidal height

Stations were located along the transect generally at height intervals of 1.22m (4ft), using the surveying technique of Emery (1961). One of these stations was then levelled to the nearest standard datum point which, in every case, was a tide gauge. Heights of stations relative to chart datum and the tidal constants were calculated from data derived from the local chart, Southward (1953) and by courtesy of the Isle of Man Harbour Board.

Granulometry

Samples for the determination of grain size parameters were taken at each station using a perspex corer of internal diameter 3.55cm. The corer was generally inserted to a depth of 15cm and the resultant sand core split into three 5cm sections for analysis.

Each sample was first washed in freshwater to remove salt and then dried at 105"C to constant weight. The sample (weighing about 80g) was then shaken through a series of 14 sieves at 0.5 0 intervals for 10 min, using a mechanical sieve shaker and the fractions retained on each sieve weighed and percentages calculated.

The mean, median, standard deviation, skewness and kurtosis were computed using the method of moments. All calculations were performed on the I.C.L. 1906 computer at Liverpool University, using a program adapted from Schlee and Webster (1967).

Porosity and water saturation

Sand samples were taken as for granulometry above and were analysed for water content immediately on return to the laboratory. A subsample weighing approximately 12g wet weight was taken from each 5cm section of core and weighed accurately before and after drying to constant weight at 105°C. The volume of the subsample was determined by slowly cascading the sand through a column of water in a 10cm^3

measuring cylinder. The length of the water column was such that a gentle and even deposition of sand occurred and no air bubbles were trapped within the sediment. The minimum volume of sand was read off, after tapping produced the terminal sand column length.

Minimum porosity was calculated from the knowledge of volume, weight and specific gravity of the samples and water saturation from porosity and water loss on drying. These methods were estimated to be accurate to within +0.5 percent.

Salinity

Two water samples were taken at each station for salinity determination: a $5cm^3$ surface sample by inserting the screened nozzle of a syringe just below the sand surface and a $500cm^3$ sample by collecting the water that drained into a hole dug to an approximate depth of 15cm. Salinity of the water table sample was determined in the field using a portable salinometer (Electronic Switchgear Ltd.) and the surface salinity in the laboratory by titration.

Temperature

Temperature was measured **at** each station at depth intervals of 2.5cm, using a thermistor probe.

Chlorophyll a

Using a perspex corer of internal diameter 3.55cm, duplicate cores were taken to a depth of 10cm at each station along the transect Port Erin S and split into 2.5cm sections. Elsewhere, duplicate 5cm cores were taken only from the middle station along each transect.

The pigment was extracted from **a** 20g subsample of vacuum dried sand in $20cm^3$ of 90 percent acetone (with the addition of $2cm^3$ of a suspension of magnesium carbonate (6g/l) in total darkness for 20h with periodic agitation. Following decantation and centrifugation the extinction at 663µm and 750µm was measured in a 4cm cell before and after acidification with three drops of 4N HC1.

Oxygen

Time limitations prevented the synchronous collection of interstitial water samples for oxygen level determinations with the faunal samples. A survey of the beaches was undertaken at **a** later date (viz. 25-26 May, 1975) when $1cm^3$ water samples were taken at depths of 2.5, 7.5 and 12.5cm at each station, using a syringe screened to avoid entry of sand. Contamination with atmospheric oxygen was prevented by maintaining a continuous phase of liquid paraffin above the samples. The concentration of dissolved oxygen was determined immediately on return to the laboratory by injection into the chamber of an oxygen microelectrode.

Detritus

Relative concentrations of visible detritus were estimated by **ey**e for each 5cm core section at each station. Following stirring of the faunal sediment sample prior to extraction of the fauna, the deposition of detritus on the sediment surface enabled a rough estimation of **concentration** using an arbitrary scale of 0 (no **detritus)** to **5** (much detritus) **and a** reference series **of** concentrations.

Fauna

Preliminary work (Moore, 1975) indicateci that the bulk of the fauna was contained in the upper 15cm of the sand, that duplicate cores were sufficient to yield the required degree of accuracy and that the fauna recorded within a quadrat of side lm was representative of an area of at least 4m^2 (see Harris, 1972a and McIntyre and Murison, 1973 for methodology). This knowledge permitted the adoption of the following sampling strategy.

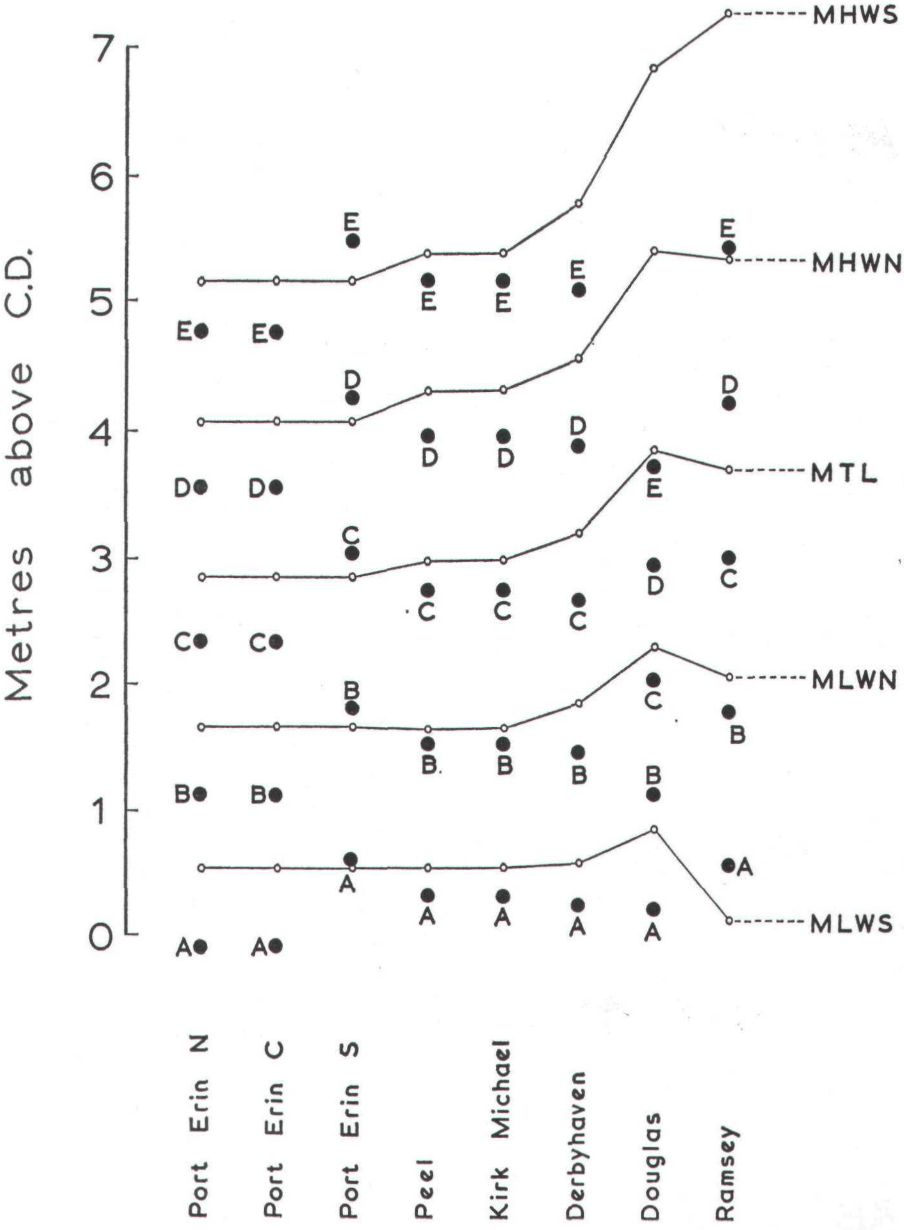


FIG. 3
Sampling stations in relation to chart datum and the tidal constants.

Using a perspex corer of internai diameter 3.55cm, duplicate cores were taken to a depth of 15cm within an area of 1m^2 at each station. Each core was immediately split into three 5cm sections, preserved in 5 percent seawater formalin. Along one transect (Port Erin S) the vertical distribution of the fauna was studied in greater detail by sampling to a depth of 25cm and splitting the sand core into sections of only 2.5cm.

The fauna was extracted by decantation. Four washes of filtered seawater were found to be sufficient for 100 percent extraction of all taxa. The number of meiobenthic organisms retained on a nylon screen of 63μm was counted by scanning the sample contained in a Bogorov tray. Periodic examination of the filtrate revealed only a few small nematodes. The counting efficiency was estimated to be within 90-100 percent. The value for most taxa was near 100 percent, the lower value being sometimes reached for the smaller taxa such as tardigrades, nauplii and small nematodes, particularly in the presence of large amounts of detritus. All densities are quoted as No./10cm^2, each being the mean of two cores.

RESULTS

Environmental factors

Intertidal heights of stations are plotted in relation to chart datum and the tidal constants in Figure 3. The neap and spring ranges can be seen to increase moving north and east from Port Erin, from a minimum of 2.41m and 4.63m respectively at Port Erin to a maximum of 3.29m and 7.16m at Ramsey. Nevertheless the stations adequately span the tidal range at each beach apart from Douglas, where only the lower half of the beach was studied.

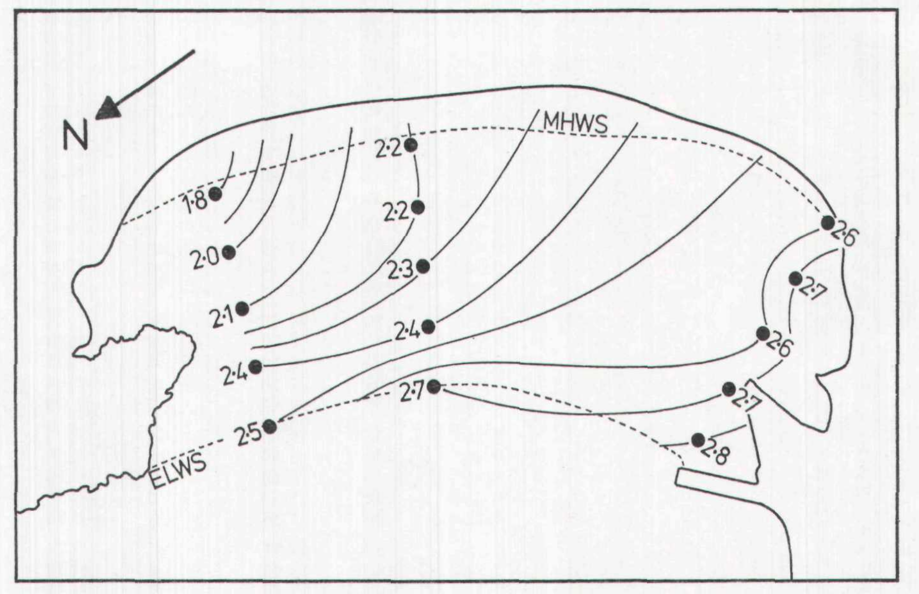


FIG. 4
Distribution of median grain size values (phi units) over Port Erin beach. Isomegeths join points of equal value, intermediate values being interpolated.

TABLE 1

Grain size parameters for Manx beaches.

Transect	Station	Depth (cm)	Median diameter Ø	Mean diameter Ø	Standard deviation Ø	Skewness	Kurtosis
Port Erin N	A	0-5	2.51	2.05	1.23	—0.72	0.91
		5-10	2.60	2.20	1.16	—0.82	1.80
		10-15	2.68	2.57	0.67	—1.21	9.18
	B	0-5	2.41	2.06	1.06	—0.68	1.10
		5-10	2.23	1.86	1.10	—0.60	0.63
		10-15	1.39	1.05	1.37	—0.10	—1.34
	C	0-5	2.07	1.88	0.85	—0.70	2.57
		5-10	1.87	1.52	1.14	—0.42	—0.15
		10-15	2.17	1.80	1.10	—0.59	0.73
	D	0-5	1.98	1.68	1.05	—0.69	1.26
		5-10	2.16	2.03	0.74	—1.11	6.87
		10-15	2.07	1.81	0.95	—0.72	1.85
	E	0-5	1.83	1.59	0.96	—0.69	1.48
		5-10	1.79	1.42	1.11	—0.52	0.07
		10-15	1.91	1.59	1.06	—0.70	1.13
Port Erin C	A	0-5	2.72	2.58	0.74	—1.32	9.60
		5-10	2.68	2.57	0.64	—1.06	7.71
		10-15	2.63	2.53	0.63	—1.12	9.03
	B	0-5	2.39	1.89	0.98	—0.50	0.73
		5-10	2.06	1.85	0.94	—0.56	1.23
		10-15	1.99	1.77	0.97	—0.48	0.71
	C	0-5	2.27	2.26	0.51	—0.21	1.30
		5-10	2.25	2.23	0.51	—0.30	2.61
		10-15	2.29	2.25	0.54	—0.41	2.19
	D	0-5	2.20	2.17	0.53	—0.65	6.48
		5-10	2.35	2.34	0.52	—0.59	5.65
		10-15	2.31	2.23	0.68	—0.95	6.75
	E	0-5	2.17	2.15	0.46	—0.24	2.58
		5-10	2.11	2.07	0.56	—1.00	9.70
		10-15	2.07	2.00	0.63	—0.94	7.09
Port Erin S	A	0-5	2.75	2.72	0.46	—0.42	2.61
	B	0-5	2.70	2.65	0.47	—0.59	4.73
	C	0-5	2.64	2.62	0.38	—0.05	0.98
	D	0-5	2.69	2.67	0.36	—0.13	2.48
	E	0-5	2.55	2.54	0.40	—0.15	2.40
Peel	A	0-5	2.44	2.47	0.42	—0.28	4.14
	B	0-5	2.07	1.96	0.71	—0.66	3.37
	C	0-5	1.69	1.40	1.07	—0.36	—0.34
	D	0-5	1.49	1.25	1.13	—0.26	—0.67
	E	0-5	2.14	2.11	0.46	—0.07	0.45
Douglas	A	0-5	2.76	2.77	0.34	—0.16	3.64
	B	0-5	2.53	2.44	0.57	—0.80	4.62
	C	0-5	2.63	2.61	0.37	—0.23	3.03
	D	0-5	2.59	2.53	0.51	—0.95	7.99
	E	0-5	2.63	2.59	0.42	—0.74	7.69
Kirk Michael	A	0-5	2.50	2.39	0.66	—0.65	2.84
	B	0-5	2.19	2.15	0.50	—0.34	2.35
	C	0-5	2.05	2.01	0.50	—0.38	2.01
	D	0-5	1.34	1.01	1.06	—0.32	—0.64
	E	0-5	1.53	1.32	0.84	—0.53	1.02
Derbyhaven	A	0-5	2.55	2.46	0.63	—0.81	4.62
	B	0-5	2.84	2.73	0.67	—1.18	7.29
	C	0-5	2.71	2.49	0.88	—1.33	7.46
	D	0-5	0.68	0.70	1.08	0.06	—0.85
	E	0-5	1.70	1.30	1.26	—0.26	—0.94
Ramsey	A	0-5	2.65	2.58	0.51	—0.97	7.74
	B	0-5	2.54	2.43	0.64	—1.08	6.32
	C	0-5	2.33	2.29	0.56	—0.91	6.14
	D	0-5	2.17	2.13	0.43	—0.52	4.96
	E	0-5	1.62	1.45	0.81	—0.59	1.51

Table 1 shows the statistical parameters of grain size along the transects studied. Due to the vertical homogeneity of the sand, these parameters relate only to the upper 5cm, although the whole depth range is shown for the exposed northern half of Port Erin beach, where a varying admixture of gravel leads to heterogeneity.

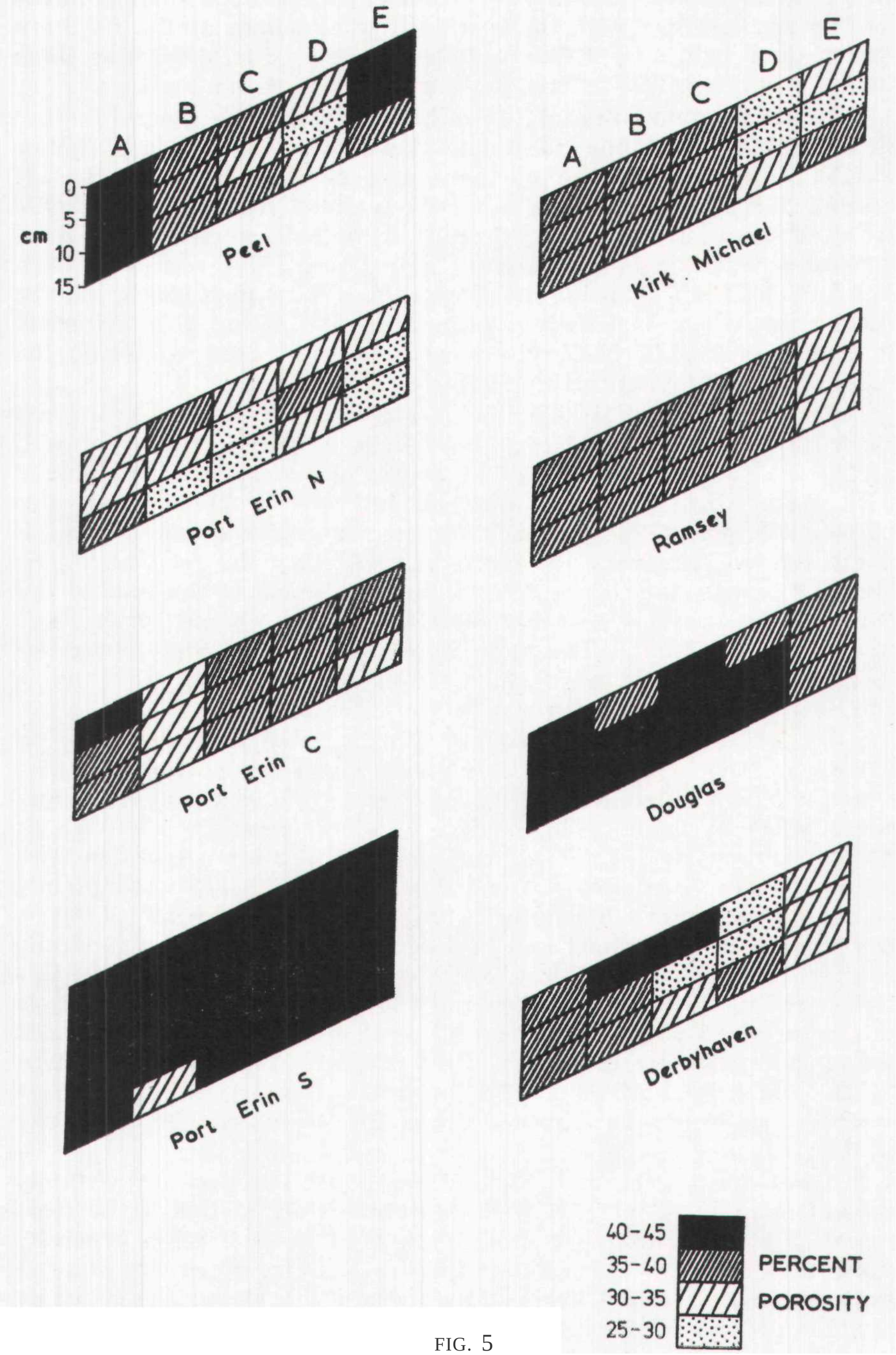


FIG. 5
Maximum porosit}· profiles along each transect.

Distribution of the median particle size of the surface 5cm of sand is shown for Port Erin beach in the form of isomegeths (Fig. 4). Two overlying trends are evident: an increase in grain size with height up the beach and a decrease from north to south. This north-south gradation of medium to fine sand was first noted by Bruce (1928) and is evidently due to the clockwise flood current in the bay which, together with the increased wave action at the northern end of the beach, retains fine particles in suspension, depositing them in the progressively sheltered southern region of the beach.

Considering now the totality of beaches studied, a general feature is the presence of fine sand low down on every beach (below M.L.W.S.) except for the northern end of Port Erin beach. At around M.H.W.N. and above a relatively steep rise in beach profile is often associated with a sharply delimited coarser sand zone, generally containing an admixture of pebbles. The region between M.L.W.S. and M.T.L., being the most extensive on each beach, may be considered when designating each transect. Using this criterion, Peel and Port Erin N can be termed medium sand transects, the remainder fine (Wentworth, 1922).

Employing the classification scale in Folk (1968), sediments range from poorly sorted (e.g. Port Erin N transect) to very well sorted sand (e.g. Douglas A). The degree of sorting is closely linked with grain size, decreasing with an increase in mean grain size ($r=-0.768$; $p<0.001$). Virtually all samples analysed produced negatively skewed frequency distributions, reflecting the relative importance of coarse material in determinine the shape of the tails of the curve. Skewness is weakly correlated with mean grain size ($r=-0.306$; $p<0.05$). The majority of samples are leptokurtic, although the coarsest sand exhibits strong platykurtosis. Kurtosis is correlated with mean grain size ($r=-0.688$; $p<0.001$).

Minimum porosity values are illustrated diagrammatically in Figure 5. The complexity of this diagram can be explained by first considering the relationship between mean grain size and minimum porosity, there being a high degree of correlation ($r=-0.900$; $p<0.001$), porosity increasing with decreasing grain size. The two finest-sand transects, Douglas and Port Erin S, are composed mainly of sand with a minimum porosity in excess of 40 percent. Ramsey, Derbyhaven, Kirk Michael and Peel beaches have porosities generally greater than 37 percent below the coarse sand/pebble band. In this latter region, porosities are generally low and variable falling to a minimum of 28 percent, although at Peel, where such a zone is not found, porosities are in excess of 40 percent. The porosity pattern of the northern half of Port Erin beach (transects N and C) is complex, as would be expected from the grain size heterogeneity of this region.

Apart from Peel and Kirk Michael, all beaches are virtually saturated up to about M.H.W.N. (approximately station D in most cases) (Fig. 6). The upper shore stations of these beaches generally show an increase in saturation with depth. The upper dry zone at Peel and Kirk Michael begins lower down the shore, the anomaly at station D at Kirk Michael being due to the presence of freshwater.

The surface and water table salinities are compared for each

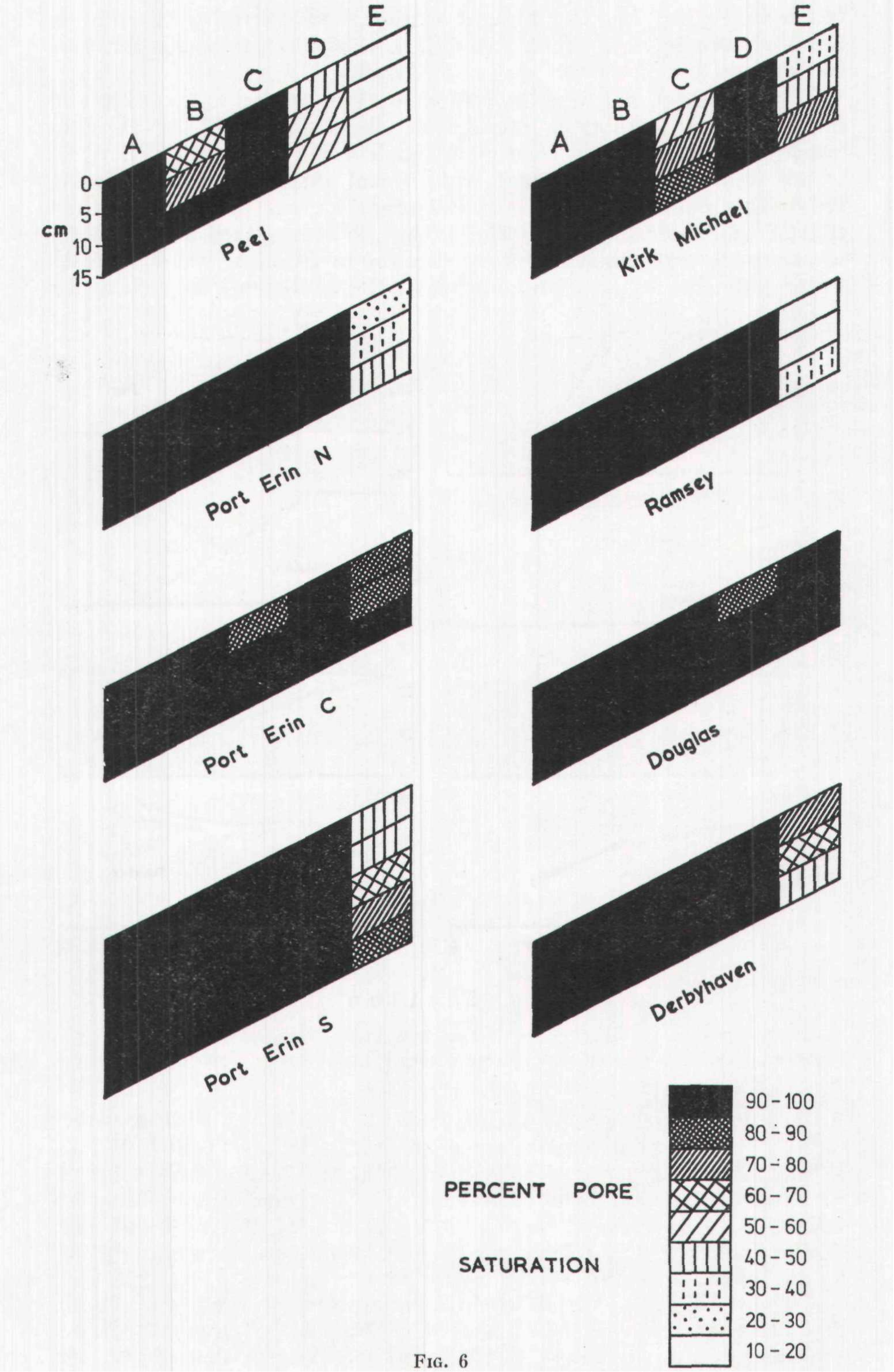


FIG. 6

Percentage pore saturation profiles along each transect.

beach in Figure 7. The highest station was generally too dry to allow a sample to be taken and this was also occasionally the case for surface samples lower down the beach.

The beaches are seen to consist of two types: those with and those without freshwater seepage at about M.H.W.N. Port Erin beach has a well-defined zone of brackish water at around M.H.W.N., which is often quite apparent from visual inspection of the beach. Below this point the surface salinity is always a little higher than that of the water table, the relationship being reversed at M.H.W.N., where the lower salinity water overlies the more saline water. Freshwater influence is most pronounced at the southern end, where the surface salinity drops to 14 percent at M.H.W.N. Full seawater salinity is essentially maintained at Kirk Michael below M.T.L., although the emergence of subsoil water at M.H.W.N. forms a brackish zone with a salinity of 4 percent. On Peel and Ramsey beaches salinities do not differ markedly from that of the adjacent sea; the low salinity at M.L.W.S. on Ramsey beach was presumably due to the influence of the nearby Sulby River.

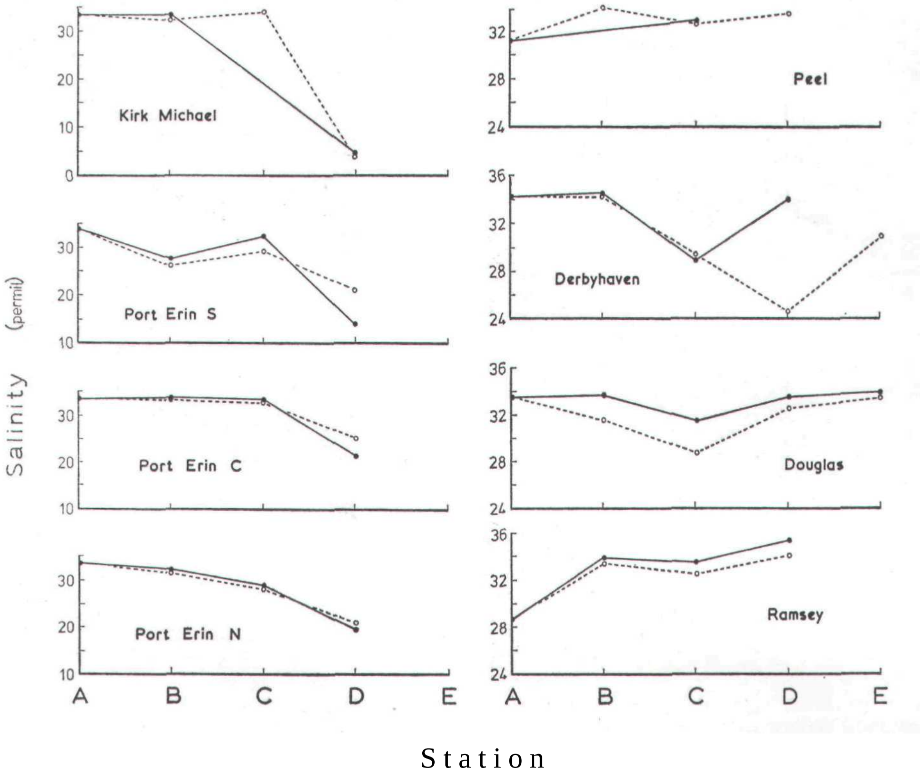


FIG. 7
The surface (solid line) and water table (broken line) salinity along each transect.

There is little variation in temperature on any one beach, this being no greater than about 3°C (Fig. 8). Temperatures are generally within the range 13-16"C and are close to that of the sea. In general, surface/bottom temperature differentials increase in size up the beach. The anomalous station D measurement on Kirk Michael and Port Erin N transects are presumed to be a consequence of the local influence of upwelling freshwater.

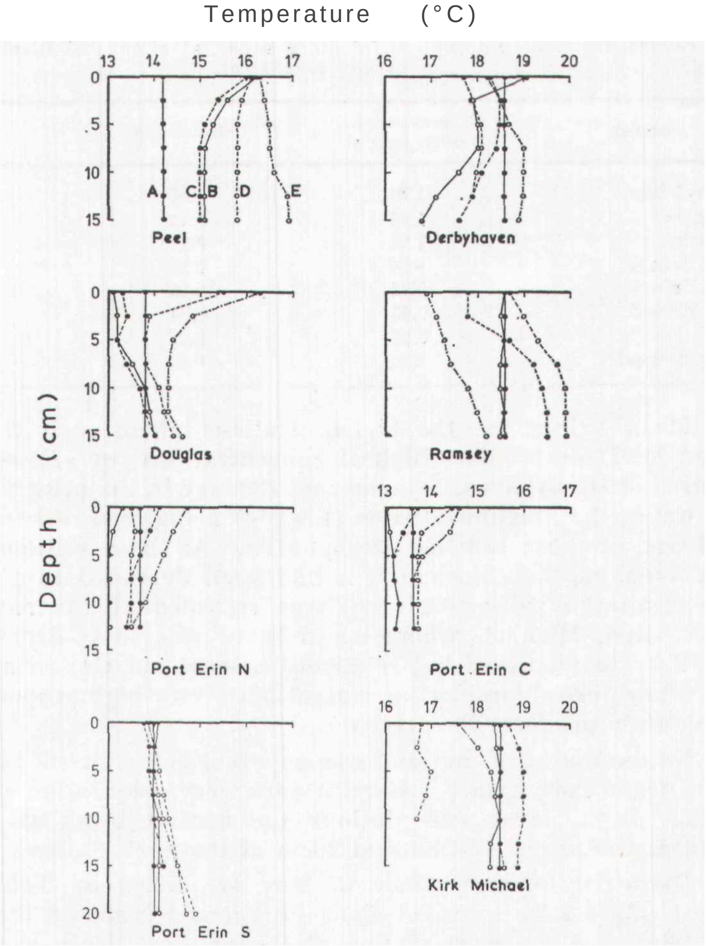


FIG. 8
Temperature profiles along each transect.

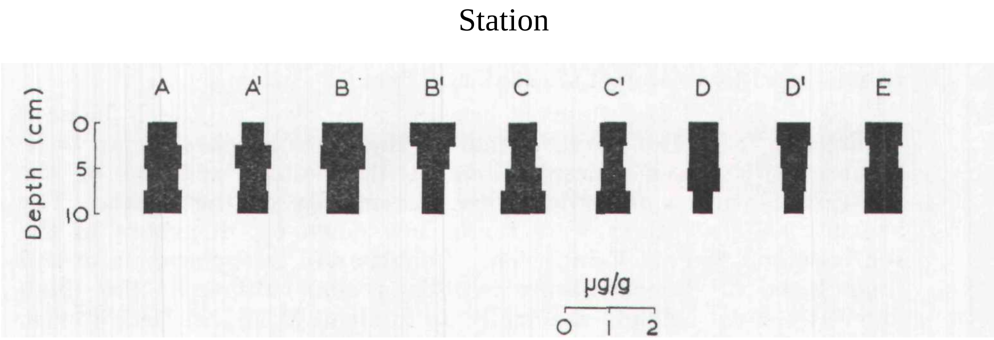


FIG. 9
Distribution of chlorophyll a along Port Erin S transect.

The distribution of chlorophyll a along Port Erin S transect on the 19th March 1973 (Fig. 9) is uniform to a depth of at least 10cm. The mean concentration is 0.71µg/g sand and no horizontal or vertical trends are apparent.

TABLE 2

The concentration of chlorophyll 'a' (µg/g sand) at about M.T.L. at each of the study localities.

location	undegraded chlorophyll 'a'	phaeophytin	total
Derbyhaven	1.81	0.00	1.81
Douglas	1.47	0.11	1.58
Ramsey	1.26	0.11	1.37
Port Erin S	0.69	0.21	0.90
Port Erin N	0.45	0.25	0.70
Port Erin C	0.65	0.04	0.69
Peel	0.23	0.24	0.47
Kirk Michael	0.22	0.01	0.23

Mean values for the M.T.L. stations along each transect are listed in Table 2. The highest concentrations (in excess of 1µg/g) occured at Derbyhaven, Douglas and Ramsey in the presence of standing water, the maximum value (1.8µg/g) being recorded for the most sheltered of these beaches, Derbyhaven. At these stations less than 10 percent of the chlorophyll a had been degraded to phaeophytin. The minimum value (0.23µg/g) was recorded at the most exposed beach, Kirk Michael, where again there was little degraded chlorophyll. The sheltered but relatively coarse-sand station at Peel also had a low pure chlorophyll a content but a very high proportion of the breakdown product (51 percent).

No darkening of the sand was apparent along any of the transects apart from Port Erin S. Here, a dark grey colouration reached the surface at the lower two stations and became black at a depth of 10cm at the lowest station and 20cm at the next station.

Dissolved oxygen values in May are listed in Table 3. The lowest values were recorded along Port Erin S transect, the minimum occurring at the lowest station at the greatest depth sampled. On all the other transects the values were more variable. The three coarsest beaches (Kirk Michael, Peel and Port Erin N) exhibited the highest overall values. As the values recorded seemed high, a series of samples was collected in deep black sand inside the pier at Port Erin. From a concentration of 1.2ml/l at 0.5cm, virtually anoxic conditions were indicated at 7.0cm.

Kirk Michael and Ramsey beaches were clearly little influenced by detritus (Fig. 10). Distribution on the other beaches seems to be bipolar, with heavy concentrations at the bottom and top of the shore, but with a reduction over the middle of the shore. The heaviest concentrations were found low down on the shore at the southern end of Port Erin beach. Douglas and Derbyhaven also had their heaviest concentrations in this region, although the high detritus content extends uniformly up to about M.T.L. at Derbyhaven. Peel and Port Erin N, on the other hand, had maximum concentrations at the top of the shore, as did Kirk Michael.

TABLE 3

The oxygen content (ml 0_2/l) of interstitial water along each of the transects worked.

Transect	Station	Depth (cm)			
		2.5	7.5	12.5	Mean
Port Erin S	B	2.65	2.83	2.19	2.56
	C	2.66	2.89	2.61	2.72
	D	2.62	2.42	2.76	2.60
Port Erin C	B	6.83	3.40	2.88	4.37
	C	4.71	3.42	2.93	3.69
	D	3.56	4.08	3.73	3.79
Port Erin N	B	4.88	3.73	4.02	4.21
	C	7.07	6.59	4.36	6.01
	D	6.26	6.31	6.41	6.33
Kirk Michael	B	—	—	5.63	5.63
	C	—	—	6.53	6.53
	D	7.10	6.85	6.71	6.89
Peel	B	4.03	4.50	4.03	4.19
	C	—	—	6.35	6.35
	D	—	—	5.07*	5.07
Ramsey	B	5.20	3.79	3.42	4.14
	C	6.43	5.40	4.11	5.31
	D	3.25	3.11	2.99	3.12
Douglas	B	4.91	4.58	4.40	4.63
	C	4.01	3.85	3.72	3.86
	D	4.46	4.35	4.53	4.45
Derbyhaven	B	5.76	5.08	4.72	5.19
	C	3.91	3.91	3.11	3.64
	D	—	4.74	4.50	4.62

* Denotes water table sample (30cm).

The fauna

The density of meiofauna at each transect is compared in Table 4. The three finest-sand transects, Douglas, Derbyhaven and Port Erin S, harboured the richest meiofauna with a maximum of 7655 individuals/10cm^2 being recorded at Douglas. Apart from Ramsey, highest densities occurred either at the top or the bottom of the shore.

TABLE 4

Number of meiobenthic individuals per 10cm^2 along each transect. Letters in parentheses refer to stations.

Transect	Mean	Max.	Min.
Douglas	2939	7655(A)	488(E)
Derbyhaven	2844	5401(A)	1332(D)
Port Erin S	1638	3600(A)	197(E)
Peel	1604	4431(E)	466(C)
Ramsey	1063	1717(C)	149(E)
Port Erin N	1021	1375(A)	719(B)
Kirk Michael	853	1262(E)	192(E)
Port Erin C	802	1173(E)	413(A)

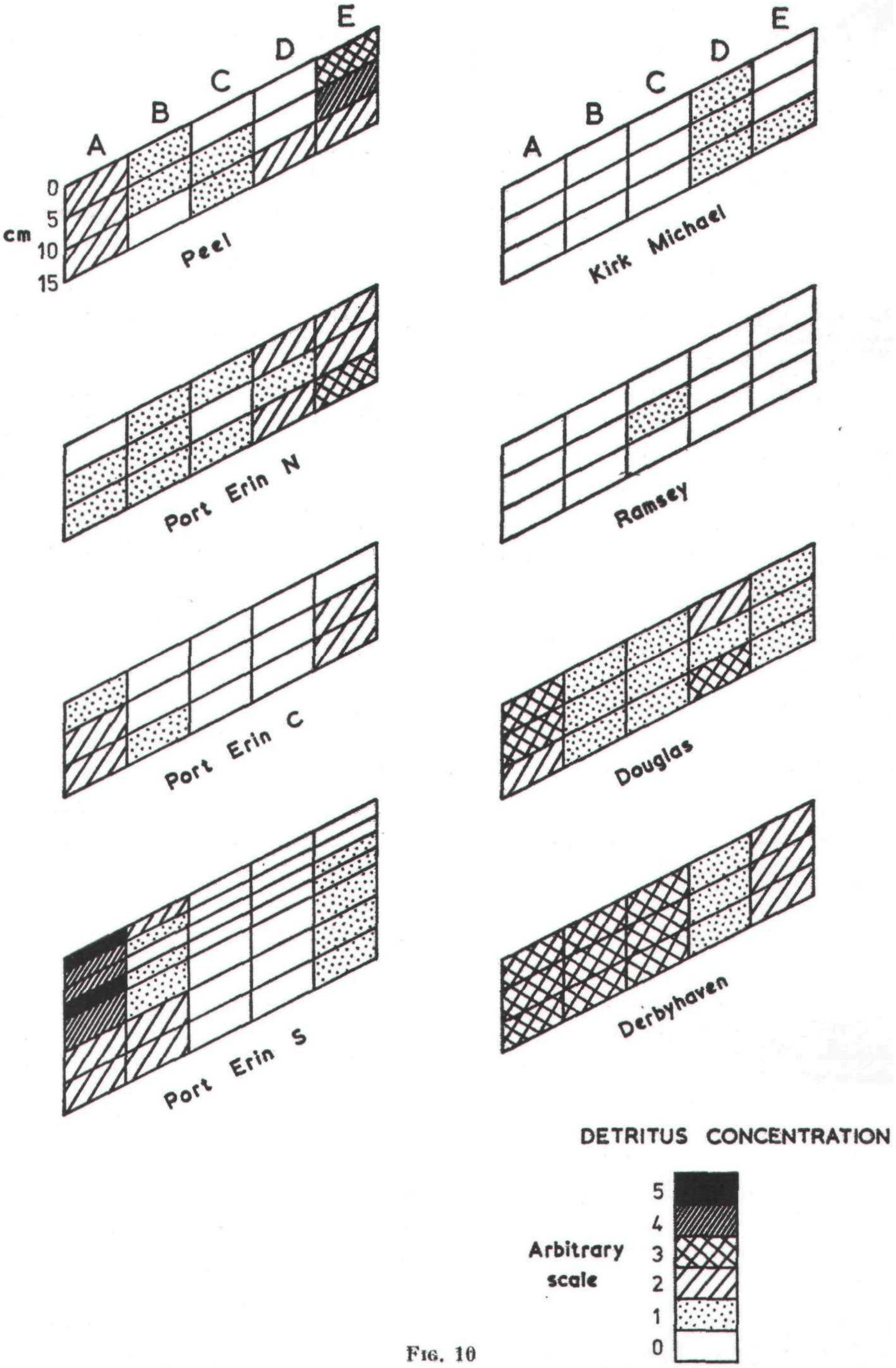


FIG. 10
Detrital concentration profiles along each transect.

Figure 11 shows the Nematoda to be dominant taxon at most localities, particularly at the four most sheltered beaches, where mean densities ranged from 2771/l0cm^2 at Douglas to 1091/l0cm^2 at Port

Erin S. At the other localities, the mean nematode density did not exceed 600/10cm^2, the lowest mean value being recorded at the most exposed beach, Kirk Michael. Harpacticoid copepods were next in importance, this group being dominant at Kirk Michael with a mean density of 353/10cm^2. Virtually all copepods here were of the interstitial type. The four most sheltered beaches had the lowest densities of copepods. Of these beaches, the coarsest sand at Peel harboured the highest density, most of which were interstitial forms, whilst Port Erin S, Derbyhaven and Douglas beaches contained burrowing and interstitial forms in roughly equal numbers, although copepods as a whole were virtually absent from Port Erin S.

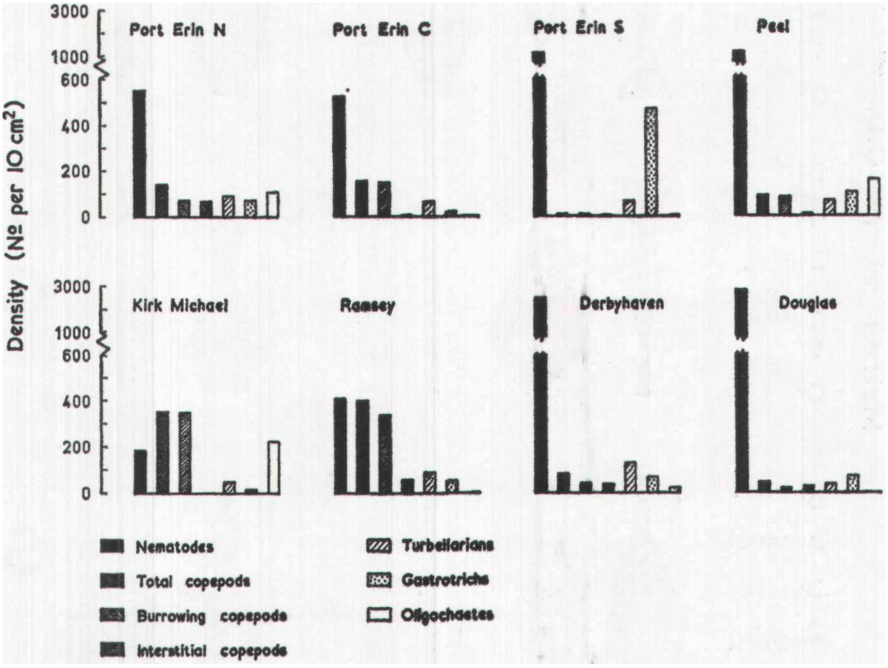


Fig. 11
Mean density (No./10cm^2) of each meiofaunal group along each transect.

The remaining taxa were generally present in relatively low numbers, Turbellaria and Gastrotricha having mean densities mostly below 100/10cm^2, although gastrotrichs were a very important group at Port Erin S (mean density, 468/10cm^2).

Horizontal distribution

Port Erin (Fig. 12)

Most of the meiofauna was concentrated on the lower half of the beach, the marked exception being the Oligochaeta. The centre of distribution of the Copepoda was somewhat higher than that of the Nematoda. On the central portion of the beach, copepods were mostly of the interstitial type and showed a well defined peak between

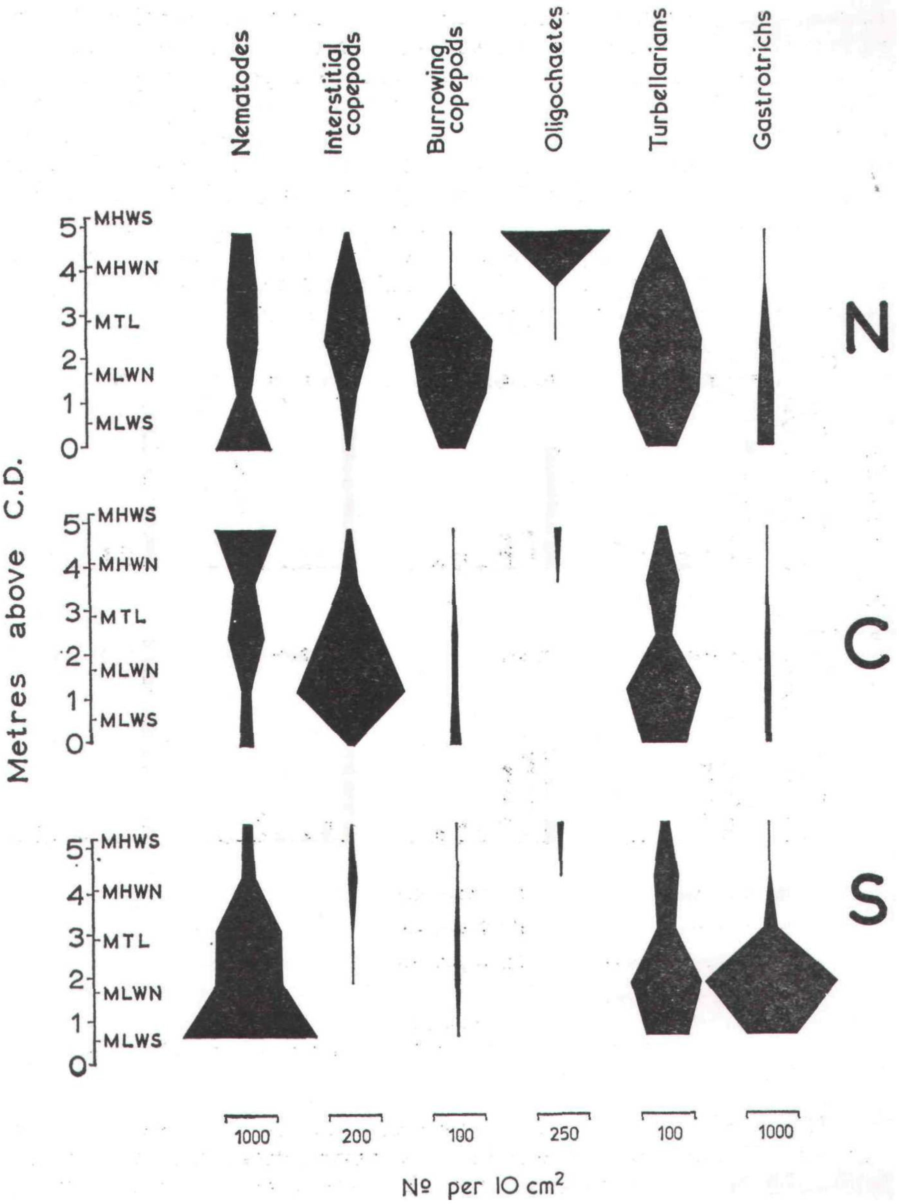


FIG. 12
Distribution of the most abundant meiofaunal groups along three transects at Port Erin.

M.L.W.N. and M.L.W.S. As already mentioned, copepods were barely represented at the south end. Over the whole of the beach it is clear that progression into the subtidal was associated with virtual elimination of interstitial harpacticoids.

Over the southern half of the beach, Turbellaria and Gastrotricha showed clear affinities for the lower shore. Many of the species were determined from qualitative samples and are listed in Table 5.

TABLE 5

Some species of Turbellaria and Gastrotricha identified from Port Erin beach.

Turbellaria	Gastrotricha
Cicerina remanei Meixner	*Cephalodasys turbenelloides* (Boaden)*
Diascorhynchus rubrus Boaden	*Pseudostomella roscovita* Swedmark*
Diascorhynchus sp.	*Thiodasys sterreri* Boaden*
Proschizorhynchus arenarius Beauchamp	*Neodasys* sp.*
Proschizorhynchus sp. A	*Turbanella cornuta* Remane
Proschizorhynchus sp. B	*Turbanella* sp.
Proschizorhynchus sp. C	*Paraiurbanella* sp.
Schizochilus choriorus Boaden	*Chaetonotus* sp.
Schizochilus marcusi Boaden	
Schizochilus sp.	
Thylachorynchus conglobatus Meixner	

* From McLachlan, 1978.

Coelenterates were extremely rare. *Halammohydra octopodides* Remane and *H. vermiformis* Swedmark and Teissier occurred between M.T.L. and M.H.W.N. on the northern half of the beach.

Archiannelids were also rare on Port Erin beach, the only occurrence being the occasional specimen of *Protodriloides symbioticus* (Giard) at M.T.L. at the north end. Polychaetes were also absent at the south end but increased in numbers northwards to reach a maximum of 67/10cm^2 just below M.T.L. The species included macrobenthic juveniles and the interstitial *Micropthalmus listensis* Westheide. No polychaetes were recorded above M.H.W.N.

All the tardigrades recorded belong to one genus, *Batillipes*—*B. littoralis* Renaud-Debyser, B. *pennaki* Marcus, B. *phreaticus* Renaud-Debyser and B. *tubernatis* Pollock. The highest numbers (37/10cm^2) were found between M.L.W.N. and M.H.W.N. on the northern half of the beach. B. *phreaticus* and *B. tubernatis* were generally found to coexist, with B. *phreaticus* the dominant species along Port Erin C and B. *tubernatis* along Port Erin N. Up to three species of tardigrade were found to cohabit within the same 5cm core section.

Kirk Michael (Fig. **13)**

The bulk of the fauna was again found to occur on the lower half of the beach, with the exception of the Oligochaeta which reached a very high maximum density of 1121/l0cm^2 at M.H.W.S. Both nematodes and interstitial copepods reached a peak just below M.T.L. of 357/10cm^2 and 764/10cm^2 respectively, although unlike Port Erin beach the decrease in density of the interstitial harpacticoids with progression into the subtidal was gradual and indicated the existence of a well developed interstitial fauna at least in the shallow subtidal. Burrowing copepods were virtually absent.

The gastrotrich fauna was mainly composed of *Turbanella cornuta,* with *Paraturbanella teissieri* Swedmark and *Turbanella* sp.

higher up the shore. The maximum density of Tardigrada attained was only 9/10cm^2 on the lower half of the beach; again, several species were found to coexist: ***Batillipes mirus*** Richters, ***B.** tubernatis*, *B. phreaticus* and *B. pennaki*. All other groups were represented by less than 2 individuals/10cm^2.

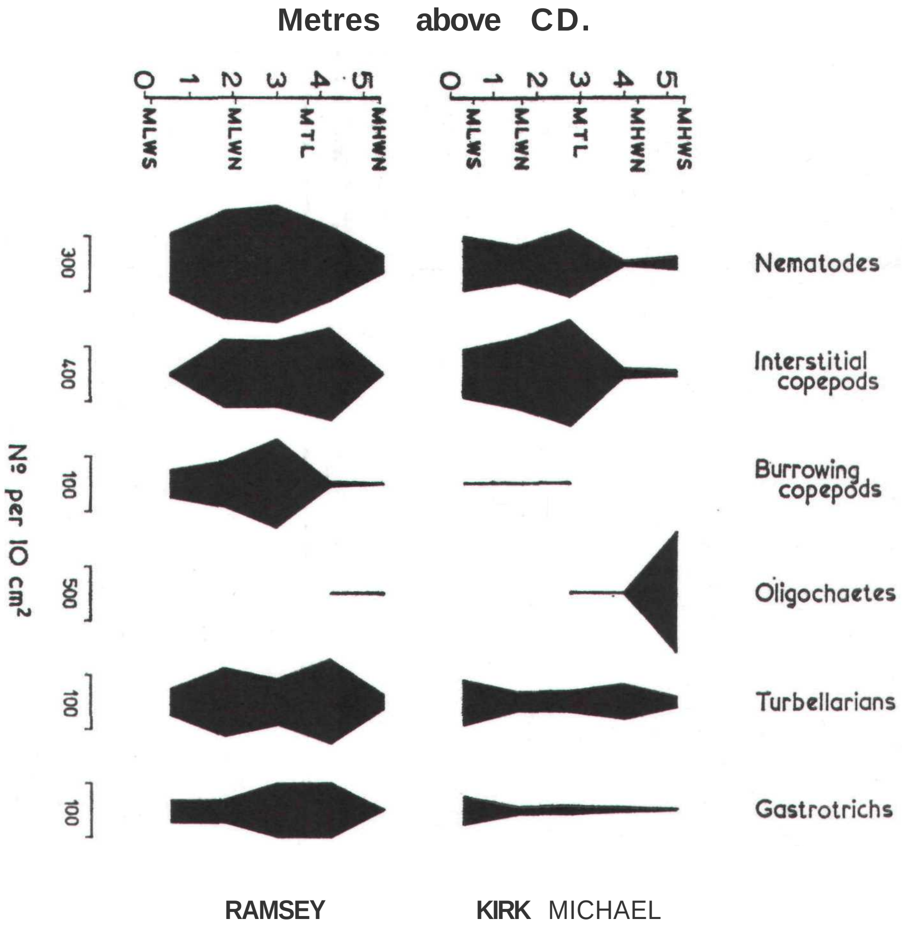


Fig. 13
Distribution of the most abundant meiofaunal groups along transects at Kirk Michael and Ramsev.

Peel (Fig. **14)**

Nematodes were much more abundant on the upper shore, reaching a maximum of 3737/10cm^2 at **M.H.W.S.** At this station, copepods were completely absent, whilst oligochaetes also attained their maximum of 693/10cm^2. The bimodal pattern of the distribution of the interstitial copepods was a result of the well defined nature of the zonation of the predominant species (Moore, 1978), the peak occurring at M.L.W.N. (184/10cm^2) and thereafter dropping strongly seaward. As at Kirk Michael, turbellarians and gastrotrichs attained maxima at the lowest station at M.L.W.S. (121/10cm^2 and 421/10cm^2 respectively).

Of the less well represented taxa, meiobenthic polychaetes were the most abundant, being found up to M.H.W.N. and attaining a maximum density of 146/10cm^2 at M.T.L. The interstitial polychaete *Micropthalmus listensis* and the archiannelid *Trilobodrilus axi* Westheide were distributed between M.L.W.N. and M.T.L. and the tardigrades *Batillipes tubernatis* and *B. phreaticus* between M.T.L. and M.H.W.N.

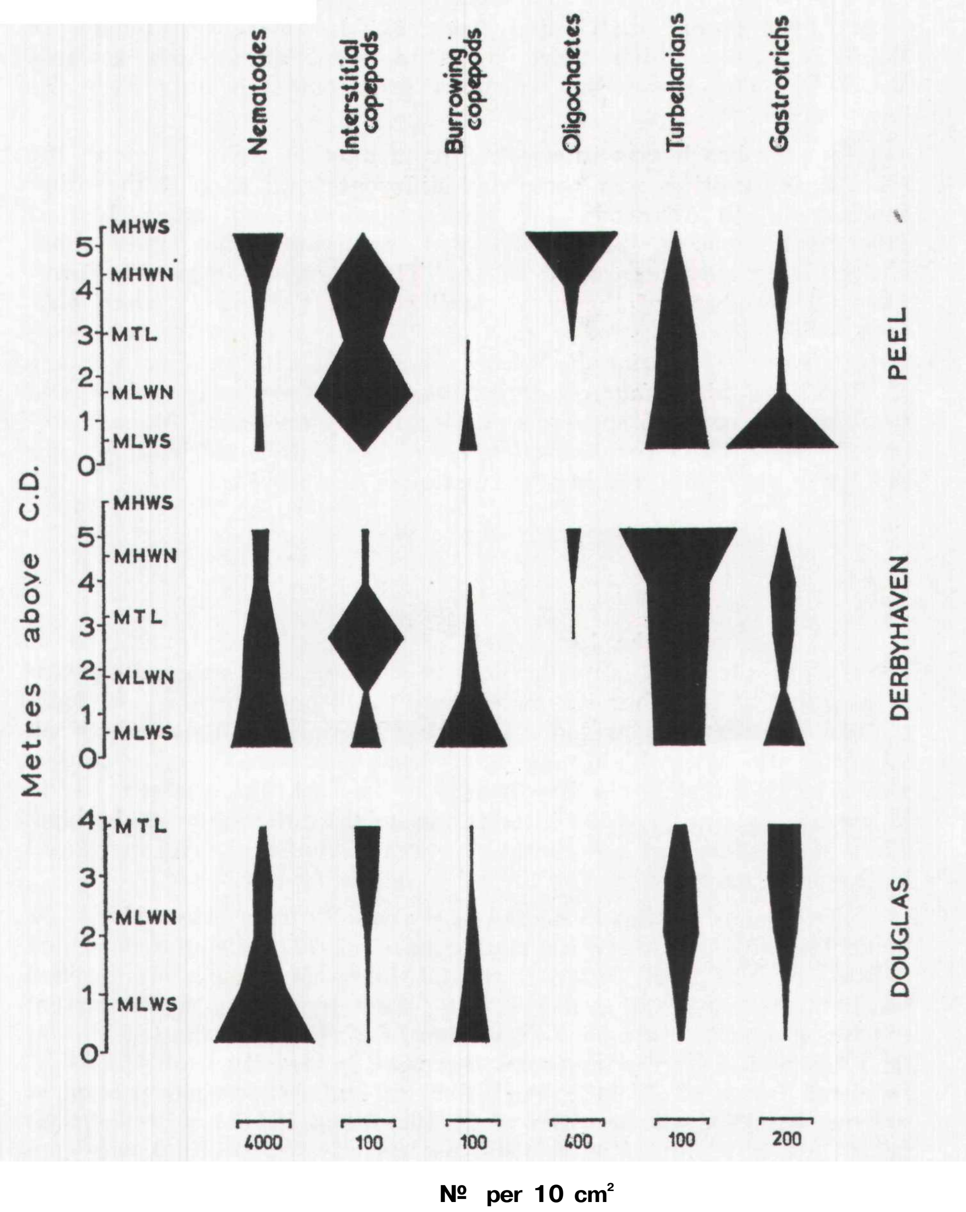


FIG. 14
Distribution of the most abundant meiofaunal groups along transects at Peel, Derbyhaven and Douglas.

Ramsey (Fig. 13)

The faunai distribution at Ramsey was rather different from those already discussed. There was a general raising of the maxima up the beach and a more uniform distribution. Nematodes attained their highest concentration near M.T.L. (644/10cm^2) and the maxima of the interstitial copepods, turbellarians and gastrotrichs occurred just on the upper half of the beach. The interstitial harpacticoids were fairly evenly distributed from M.T.L. (max. 685/10cm^2) to M.L.W.N., after which there was the usual attenuation towards M.L.W.S. The burrowing copepods were common only over the lower shore.

Ramsey beach was interesting from another point of view; the species composition was somewhat different from that of the other beaches. Both ostracods and tardigrades achieved their highest concentrations here, being distributed mainly over the lower shore but attaining maxima around M.T.L. The ostracods (max. 48/10cm^2) were all members of the very small species *Cytherois fisheri* G.O. Sars, whilst the tardigrades (max. 64/10cm^2) were mostly composed of *Orzeliscus septentrionalis* Schulz (58/10cm^2), with smaller numbers of *Batillipes phreaticus, B. tubernatis, B. littoralis, B. mirus* and *Batillipes* sp., up to 5 species occurring in any one core. Polychaetes (mostly *Micropthalmus listensis)* were also distributed mainly over the lower shore but reached a maximum of only 14/10cm^2.

Douglas (Fig. 14)

Although only the lower half of the beach was examined at Douglas, this transect is particularly interesting as it was consequently sampled at a higher intensity than the other beaches. In spite of this, there was no evidence of wide variations in density between adjacent stations, which may have been dampened by the wider-spaced stations of the other beaches. In fact, the pattern would be essentially similar if the interstation height difference was doubled. Thus, it was felt that a reasonable degree of confidence can be placed in the patterns produced for the other beaches.

Nematode densities increased fairly rapidly from below M.L.W.N. to achieve the extremely high maximum of 7577/10cm^2 near chart datum. As at Peel, interstitial and burrowing copepods showed an inverse relationship, interstitial forms increasing from virtual absence at chart datum to a maximum of 47/10cm^2 at the top station (M.T.L.), whilst burrowing forms increased in density from M.L.W.N. to chart datum 63/10cm^2). Turbellarians and gastrotrichs peaked at around M.L.W.N. (at densities of 65/10cm^2 and 131/10cm^2 respectively), below which densities fell to near zero as the subtidal was approached. Polychaetes, all of which were mixobenthic, also attained their highest density at M.L.W.N. (36/10cm^2). Tardigrades were only represented by scattered individuals of *Batillipes tubernatis, B. similis* Schulz and *Batillipes* sp.

Derbyhaven (Fig. **14)**

As at Douglas nematode densities were very high, being in excess of 2500/10cm^2 over the whole of the lower shore and reaching a peak at about M.L.W.S. (4588/10cm^2). Both interstitial and burrowing copepods were more common below M.T.L., the latter exhibiting a marked increase with progression into the subtidal (max. 137/10cm^2). Oligochaetes were again only found on the upper shore. Turbellarians were uniformly distributed along most of the transect but reached the highest recorded density for this group (224/10cm^2) at the top station. Within the zone of distribution of the gastrotrichs there was a minimum at the same station (about M.L.W.N.) that yielded particularly few interstitial harpacticoids. Polychaetes reached their highest density at Derbyhaven. They were all of the mixobenthic type and from a maximum of 325/10cm^2 at the bottom station, steadily decreased up to M.H.W.N. Ostracods also reached relatively high numbers over the lower shore (max. 25/10cm^2). There were a few specimens of *Cytherois fisheri* but they were mostly the much more robust *Leptocythere macallana* Brady and Robertson. Halacarids and tardigrades occurred in very low numbers, the latter sporadically along the entire transect. *Batillipes littoralis* was the dominant species, with *B. pennaki* recorded only from the top station.

Vertical distribution

Port Erin (Fig. **15)**

Trial cores indicated that the bulk of the fauna was contained within the upper 15cm over most of the beach at this time of year. In fact, coring was often impraticable below this depth anyway. It is evident from Figure 15 that most taxa reached a peak in their vertical distribution within the top 10cm of sand. This is particularly clearly illustrated at the south end of the beach, where cores of 25cm were taken. The topmost station was an exception however, where it is felt that there was inadequate examination of the fauna.

Over the whole beach there was an overall trend of submergence with increase in intertidal height. The population density peak for nematodes was generally within the top 5cm up to M.H.W.N. This is shown in greater detail for the south transect, where it can be seen that this peak varied between 0-2.5cm and 2.5-5.0cm. Exactly the same trend was followed by the total meiofauna (most of which were nematodes) and the turbellarians. Gastrotrichs, on the other hand, had a somewhat lower and more uniform distribution. Copepods were rare at the southern end of the beach, but where they were found they were restricted to the top 5cm, usually to the first 2.5cm. Over the rest of the beach, there was a marked difference in the distribution of the interstitial and burrowing forms. The burrowing copepods were virtually restricted to the top 5cm, whereas the interstitial species exhibited submergence up the shore. The

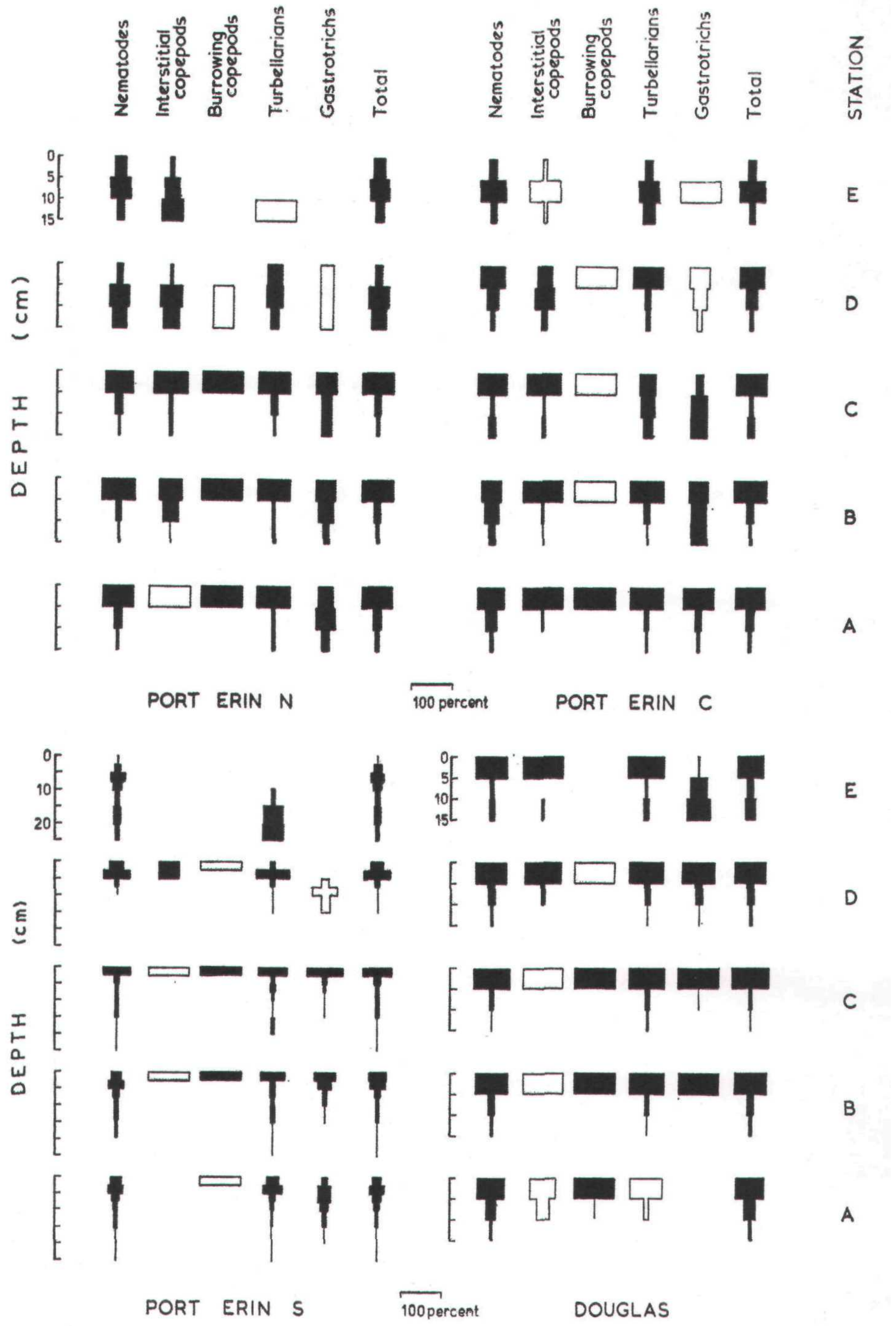


FIG. 15
Vertical distribution of the most abundant meiofaunal groups along transects at Port Erin and Douglas.
Open blocks represent percentages based on <10 individuals.

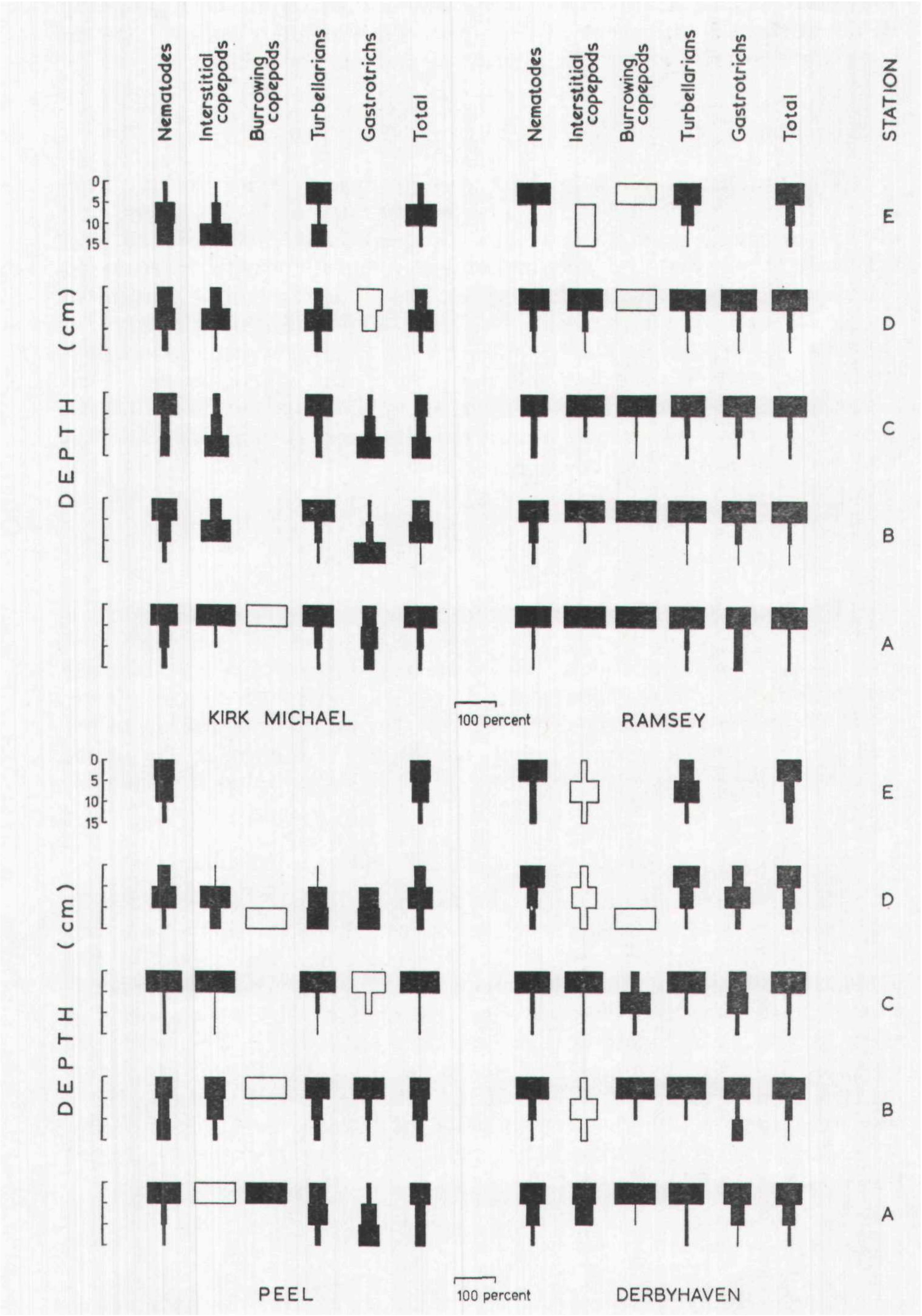


FIG 16
Vertical distribution of the most abundant meiofaunal groups along transects at Kirk Michael, Ramsey, Peel and Derbyhaven.
Open blocks represent percentages based on <10 individuals.

majority of oligochaetes appeared in the surface 10cm of sand. Polychaetes and tardigrades were distributed similarly, generally in the surface 5cm, except at the upper limit of distribution. Ostracods were usually above the 5cm level, halacarids below.

Kirk Michael (Fig. 16)

The pattern at Kirk Michael was not as clear as that at Port Erin. Submergence did occur and led to the inadequate sampling of harpacticoids and gastrotrichs in particular. Nematodes and tubellarians showed a deepening of the population with increase in intertidal height. As on Port Erin beach, gastrotrichs tended to occur deeper in the sediment. The vertical distributional pattern of the total meiofauna was a function of the dominant interstitial harpacticoids and, at the top of the shore, the oligochaetes. The harpacticoid population was restricted to the surface 10cm up to M.L.W.N., above which the peak varied between 5 and 15cm depth. The oligochaetes exhibited a very sharp vertical peak at 5-10cm. The tardigrades showed a similar pattern to that of the copepods.

Peel (Fig. 16)

The pattern at Peel is the most complex yet considered as a result of the variability in the water saturation of the sand (see discussion). Over the lower shore most groups showed a marked population maximum above a depth of 5cm. Higher up the shore, apart from the Nematoda, the bulk of the fauna was found below 5cm and was probably inadequately sampled. At the top of the shore, the oligochaetes achieved a strong peak within the surface 10cm.

Ramsey (Fig. 16)

The vertical distribution of the fauna at Ramsey differed markedly from those of the other beaches above. There was little variation among the different taxa, which can therefore be summarized by the pattern exhibited by the total meiofauna. The fauna was concentrated in the surface 5cm of sand throughout the beach, with a slight degree of submergence towards the backshore. The copepods were particularly abundant towards the surface, the burrowing forms being essentially absent below 5cm. At the lowest station, there was once again a significant proportion of the gastrotrich population at a deeper level than the other taxa. The rarer groups followed the common trend.

Douglas (Fig. 15)

Douglas beach presented a very similar picture, the only maximum not occurring within the top 5cm of sand being that of the gastrotrichs at M.T.L. Burrowing copepods were again essentially restricted to the surface 5cm, with small numbers of interstitial copepods below this depth.

Derbyhaven (Fig. 16)

This beach also contained the bulk of the fauna within the **first** 5cm of sand, although there was submergence of some groups above M.T.L., notably the turbellarians. Gastrotrichs **were** again an excep-ion, the proportion inhabiting the first 5cm diminishing with increase in intertidal height. At the top station, oligochaetes and halacarids increased in density with depth.

DISCUSSION

The primary requirement for the existence of a meiobenthic population is an adequate volume of pore water in which to live. On these Manx beaches, the fine nature of the sand is responsible for this factor seldom exerting a limiting influence except towards the top of the shore. **By** comparing the distribution of water saturation values (Fig. **6)** with the horizontal and vertical distributional patterns of the main taxa (Figs. **12-16)** several salient points emerge. The influence of a low pore water content may be masked at the top of the shore by other powerful limiting factors. Thus, on all beaches, most taxa are poorly represented at about **M.H.W.S.,** irrespective of the water saturation value. At Port Erin C transect, the water content does not fall below 80 percent and yet only nematodes succeed in forming a significant population at the top of the shore. The critical factors at this level are more likely to be temperature and salinity acting directly or indirectly on the fauna.

The influence of pore water content is better studied on the lower shore, where other factors are less variable. Values down to 80 percent clearly have no effect on the fauna. At Kirk Michael (station C) and Peel (station B), the lowest values were recorded for this region of the beach and at each station there was clear submergence of the interstitial harpacticoid element. However, the driest sand at Kirk Michael **(51** percent saturated) still contained a fairly dense population of interstitial harpacticoids (134/50cm^3). In fact, the susceptibility to low water content probably varies amongst the different species of interstitial copepods (Moore, 1978), although this group in general seems the most susceptible to low pore water content and none of the species encountered attained significant population densities in sand of below 50 percent saturation. This compares well with the value of about 45 percent found by Pennak (1942), Enckell (1968) and Jansson (1968). At the other end of the scale, high populations of oligochaetes and nematodes are found in sand as low as **16** percent saturation. Ganapati and Rao **(1962),** studying a number of Indian sand beaches, found the richest interstitial populations in sand of intermediate water saturation. It is interesting that on the beaches in this study where such a situation occurred on the lower shore interstitial harpacticoids reached their maximum density.

It is difficult to isolate the effects of temperature and salinity. More detailed information concerning the degree of variability is required, together with a knowledge of the physiological tolerances of the organisms. On Manx beaches, intertidal height is probably a good overall measure of the variability encountered in these two factors, although several other parameters will also be included. It is possible, however, that temperature and salinity will play key roles in the determination of the zonation patterns observed, perhaps being responsible for the restriction of many species to the lower shore. Oligochaetes must clearly be resistant to considerable fluctuations in these factors.

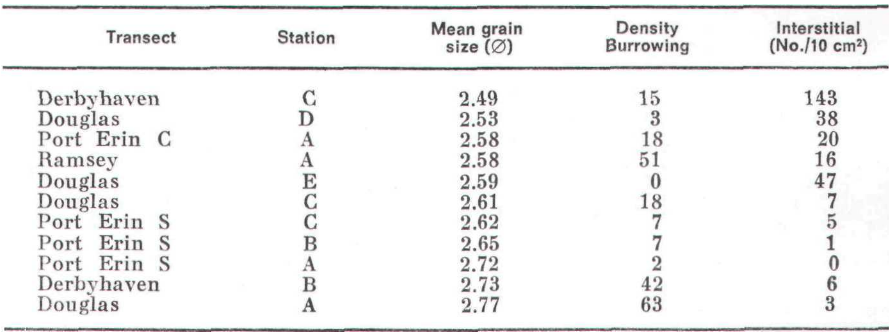
Salinity plays a more obvious role in the context of upwelling freshwater. The upper shore brackish zone marks the upper limit for many species of harpacticoids (Moore, 1978). On Ramsey beach, in the absence of such a zone, several typical inhabitants of the lower shore can extend their distribution almost to M.H.W.N. The presence of much standing water on this beach is also believed to be a contributory factor (cf. Boaden, 1963).

The significance of grain size as a limiting factor lies in the provision of void diameters which may be too narrow or too wide for the interstitial fauna (McIntyre, 1969). The importance of this factor, however, is difficult to isolate due to other environmental factors which tend to vary in parallel (e.g. wave action, sorting efficiency, oxygen concentration). Due to the diversity of forms within each taxon and the varying degrees of constrictability, the influence of grain size is perhaps best studied with reference to the interstitial harpacticoids. On these beaches, they have very similar maximum widths (viz. 50µm) and appear incapable of any marked constrictive ability.

A comparison of the distribution of interstitial harpacticoids with the distribution of grain size (Table 6) reveals the virtual absence of the group in sand of the lowest mean grain diameter. A well developed interstitial harpacticoid fauna is clearly capable of being maintained in sand as fine as 2.49 ø, whereas below 2.61 ø the group is effectively absent, although populations of burrowing copepods may flourish. This data would suggest then a lower critical

TABLE 6

The density of harpacticoid copepods at the lower shore stations exhibiting the finest deposits.



Transect	Station	Mean grain size (∅)	Density Burrowing	Interstitial (No./10 cm²)
Derbyhaven	C	2.49	15	143
Douglas	D	2.53	3	38
Port Erin C	A	2.58	18	20
Ramsey	A	2.58	51	16
Douglas	E	2.59	0	47
Douglas	C	2.61	18	7
Port Erin S	C	2.62	7	5
Port Erin S	B	2.65	7	1
Port Erin S	A	2.72	2	0
Derbyhaven	B	2.73	42	6
Douglas	A	2.77	63	3

grain size in the region 2.5-2.6 ø (165-177µm). Sand only a little in excess of this range can support a very rich interstitial copepod fauna. For example, Ramsey station B, with a mean grain diameter of 2.43 0 contains $501/10cm^3$. Whilst this theoretical limit only pertains to sand of this particle morphology, sorting and packing, it is interesting to note that McLachlan et al (1977) postulate a similar figure (viz. 160µm Md ø) for subtidal sand in Algoa Bay, South Africa.

Oxygen concentration does not appear to be implicated in the establishment of this barrier as the interstitial water of some sediments below this critical level has an oxygen concentration greater than sediments harbouring well developed interstitial harpacticoid faunas. On Derbyhaven beach, a zone of fine sand below this critical level interrupts the horizontal distribution of four species of interstitial harpacticoid, only a few juveniles being found here, although the sediment is capable of supporting a moderately rich population of burrowing copepods.

When considered as a group, the distributional pattern of the burrowing copepods does not appear to be tied to that of grain size. In several cases, the species compose the upper boundary of a shallow subtidal population, this component extending up the beach to varying levels. For the more common species, this is independent of the granulometry of the sediment. Thus, on the fine sand beaches of Derbyhaven and Douglas, this significant component is present at the bottom of the shore. On the coarser beach at Ramsey, the whole distribution is raised higher up the shore and, in fact, reaches a maximum population density around the middle of the shore. However, on the still coarser beach at Peel, the component is barely represented and only extends to M.L.W.N. However, this distribution must at least in part be explicable in terms of pore water content as this group is restricted to the superficial layer of sand (Figs. 15-16). Burrowing meiobenthic species are incapable of performing large vertical migrations to compensate for extensive water table fluctuations (Wieser, 1959) and their size is too great to permit residence within a water film. Burrowing copepods are hence found to be absent on those parts of the beach where the pore spaces of the surface sand do not remain almost saturated at low tide. However, as there are also some true intertidal burrowing species (e.g. causing the abundance of this group on the northern half of Port beach) the discussion warrants a detailed examination of the species composition (Moore, 1978).

The void diameters of the fine sand beaches are no doubt limiting for the larger interstitial species. Thus, many of the forms found in abundance on coarser beaches elsewhere are only represented here in the coarsest sand. This is true particularly for the Annelida. The relatively coarse beaches around the Isle of Sylt exhibit a well developed annelid fauna with *Micropthalmus listensis* and *Trilobodrilus axi* characterizing the lower and middle shore (Schmidt, 1969). These species are present chiefly on the middle shore around the Isle of Man, where they attain significant population densities only in the coarsest sand at Peel *(T. axi* and *M. listensis)* and the northern end of

Port Erin beach *(M. listensis).* All such species were completely absent on the fine sand beaches of Derbyhaven, Douglas and Port Erin S.

With decreasing grain size, it has often been found that the predominance of nematodes increases, the highest densities being recorded on mud. Capstick (1959) recorded mean nematode densities in the River Blyth varying from 300/10cm^2 in muddy sand to 2590/10cm^2 in mud. Similarly, Rees (1940) recorded very high densities with a maximum of 10440/10cm^2 on a mud flat in the Bristol Channel. Teal and Wieser (1966) recorded a nematode density of 16300/10cm^2 in the mud of a Georgia salt marsh. At the other extreme, Jansson (1968) encountered a virtual absence of nematodes on a very coarse sandy beach in Sweden. The factors directly responsible for such enormous variations are difficult to identify. Williams (1972) found a general reduction in nematode numbers with a decrease in the amount of fine material in a series of shell gravels on Anglesey, Wales. He implicated the amount of organic matter rather than the pore dimensions of the deposit. McIntyre (1971), studying a series of Scottish beaches, found an inverse relationship between exposure to wave action and nematode density, although the particle size was also clearly related to exposure. Gray (1971) demonstrated a significant positive correlation between nematode density and the percentage of fine sand in a sheltered silt deposit in the Tees Estuary.

In the absence of knowledge of the species composition of the nematode populations, theories proposed in this investigation must be of a tentative nature; nevertheless, certain points of interest arise which are worthy of comment. In general, nematodes attain their highest density over the lower shore, particularly on the fine sand beaches, where the highest values are recorded. Considering the mean numbers of nematodes recorded however, markedly higher concentrations were found on the four least exposed beaches, viz. Derbyhaven, Douglas, Peel and Port Erin S. Peel is, in fact, the coarsest beach studied. The high mean at this locality is largely due to a dense concentration of nematodes at the top of the shore in an area of very high detritus content. If the comparison of nematode (Figs. 12-14) with detritus (Fig. 10) distributions is carried farther, it can be seen that the nematode maxima on Derbyhaven, Douglas and Port Erin S transects correspond to dense concentrations of detritus. Furthermore, the relatively uniform distribution of nematodes over the lower shore at Derbyhaven is mirrored by the even distribution of detritus. The two markedly cleanest beaches, Kirk Michael and Ramsey, exhibit the poorest nematode populations. Thus the pattern of detritus distribution matches that of nematode distribution better than any other factor measured, although a causal relationship must not necessarily be inferred. The predominance of the various feeding types *(sensu* Wieser, 1953) was unfortunately not recorded.

The importance of the oxygen content of interstitial water in affecting the horizontal distributional pattern of the meiofauna is most clearly marked at the south end of Port Erin beach, where the lowest values recorded are considered chiefly responsible for the reduction in diversity along the transect, the fauna being composed of only nematodes and gastrotrichs, with a smaller number of tubellarians. Representatives of these taxa are known from the thiobios (Boaden and Platt, 1971) or the "living system of the sulfide biome" (Fenchel and Riedl, 1970). Gastrotrichs, in particular, attain a very high population density at the bottom of the shore in sand of dark grey to black appearance. Copepods, which are more susceptible to low oxygen tensions (e.g. McLachlan, 1978), are virtually absent from this region of the beach. The major influence of oxygen at the other localities is considered to be in the control of vertical distribution. Indeed, McLachlan (1978) has shown that the vertical distribution of the chief meiofaunal taxa on Port Erin beach correlates well with redox potential. Brafield (1964) found a very low concentration of oxygen (lml/1) at a depth of 5cm on the poorly drained beaches studied by him, although the surface water was fully saturated. There must therefore be a very strong oxygen gradient in the surface horizons of the sand. The poorly drained sand at Ramsey harboured a very rich and diverse fauna, which was concentrated in the upper 5cm. The fairly high oxygen values recorded at greater depths in May may not be expected to persist throughout the summer. Although no darkening of the sediment was observed, oxygen deficiency is considered to be responsible for this pattern of vertical distribution. Similar superficial concentrations of the fauna were observed at the other two poorly drained beaches, Derbyhaven and Douglas, and, to a lesser extent, over the lower shore in the northern half of Port Erin beach, which had a drainage efficiency intermediate between these beaches and the beaches at Peel and Kirk Michael. The sand at these latter two localities had markedly better drainage qualities, the highest levels of oxygen recorded and the most uniform distribution of fauna within the surface 15cm.

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Summary

The distribution and density of the meiofauna was studied on six sandy beaches around the Isle of Man in association with several environmental factors. The beaches ranged from moderately exposed to sheltered and from medium to fine sand.

Meiofaunal densities ranged from $7655/10cm^2$ to $149/10cm^2$. Nematodes were generally the dominant taxon, although at the most exposed beach harpacticoid copepods predominated. Gastrotrichs and oligochaetes attained dominance locally. Densities were generally higher over the lower shore and in the more sheltered areas, where the bulk of the fauna was contained within the surface 5cm of sand. Submergence occurred on the upper shore. Gastrotrichs were generally found to have their centre of distribution a little deeper in the sand than the other groups.

Where possible the influence of the environmental factors on faunai distribution was examined. Wide temperature and salinity fluctuations, together with a low pore water content were deemed likely to provide a powerful faunai barrier at the top of the shore, which was nevertheless overcome by some oligoch-

aete and nematode species. Harpacticoid copepods were found to be particularly susceptible to a low pore water content (below 50 percent). A minimum criticai grain size of 2.5-2.6 0 is postulated for the existence of interstitial harpacticoids in well-sorted sand. The virtual absence of interstitial harpacticoids and certain other groups on the finer Manx beaches was presumed to be a consequence of the low grain size. The distribution of nematodes was mirrored by the distribution of visible detritus. The influence of oxygen on distribution was considered to be chiefly manifest in the restriction of the aerobic fauna to the surface layers.

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