

## Studies on the Sublittoral Free-Living Nematodes of Liverpool Bay. I. The Structure and Distribution of the Nematode Populations

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### Abstract

Data collected from a survey of the benthic fauna of Liverpool Bay (UK) have been used to study the distribution and structure, in terms of percent age dominance and percent age frequency, of the nematode populations. Cluster analysis of the faunistic data from individual stations has shown that the populations are not sharply delimited. The relative proportions of their characteristic genera are extremely variable, and apparently influenced by small differences in sediment composition. It is, thus, considered more logical to think in terms of a number of different habitats, each with certain characteristic genera, rather than in terms of a series of discrete associations. Six types of habitat are distinguished on the basis of sediment granulometry: (1) mud and sandy mud; (2) very muddy sand; (3) muddy sand; (4) muddy sand-gravel mixtures; (5) clean sand-gravel mixtures; (6) clean sand. Habitats 1, 2 and 3 were dominated by *Sabatieria* spp., the degree of dominance apparently being related to the percentage of silt-clay. Habitat 4 was dominated by *Neochromadora* sp. and *Sabatieria* spp. and Habitats 5 and 6 by *Desmodora* sp. Both generic and dominance diversity were very much lower for Habitats 1 and 2 than elsewhere.

### Introduction

The sublittoral benthic fauna of Liverpool Bay (UK) was investigated during the period June, 1970 to March, 1971 as part of a survey, commissioned by the Department of the Environment, of the effects of sewage sludge disposal in the area (see Rees *et al.*, 1972). During this investigation, studies were carried out to determine whether any correlation existed between the distribution of free-living nematodes and the presence of sludge in the environment. The data obtained are used here to try to correlate the distribution of the nematode populations with that of the varied substrata occurring in the bay.

### Materials and Methods

A full account of the techniques employed is given in Rees *et al.* (1972). Samples were collected at 94 stations (Fig. 1) fixed by Decca co-ordinates, using a Shipek grab sampler. Duplicate core samples of approximately 25 ml volume (core diameter 2.5 cm) were taken from the sediment *in situ* in the grab bucket in order to obtain two similar subsamples through the relatively undisturbed sediment. The subsamples were pre-

served separately in 5% formalin for transport to the laboratory.

The nematodes were extracted from the sediment by a combination of decantation and sieving. A total count was made for each core, and a subsample of approximately 100 individuals was removed for identification.

Granulometric analysis of sediment samples collected at the same time was carried out by the Hydraulics Research Station. Fines (particles < 0.06 mm diameter) were removed by wet-sieving, settled, dried, and weighed, while the remaining fractions were separated by dry-sieving. Analysis of sediments by dry weight tends to underestimate the volumetric importance, in the natural substratum, of the silt-clay fraction and its associated organic floc. The silt-clay content was thus estimated by simple sedimentation in a column of sea water, the depth of the surface silt layer being measured after 48 h and compared with the total depth of the sample.

Since there are inadequate taxonomic data to identify all the nematodes beyond genus, the nematode populations were analysed at the generic level. However, in the majority of cases, the most commonly occurring genera were either represented by or dominated by a single species.

Faunal association between stations was calculated on the basis of the percentage of similarity (Raabe, 1952). This is a simple approach, based on a comparison of the composition of a pair of samples in terms of individuals of the various species and, as such, places the emphasis on the dominant species. The value of the percentage of similarity between two populations can be found by comparing the percentage dominance of their constituent species (or other convenient taxa) and calculating the element common to both populations, i.e.,

$$\% \text{ Similarity} = \frac{\sum \text{Common}}{\text{Species 1, Species 2, \dots Species } n}$$

A cluster analysis was carried out to group the stations in dendrogram form using a "group average" method (Mountford, 1962). Of the several other

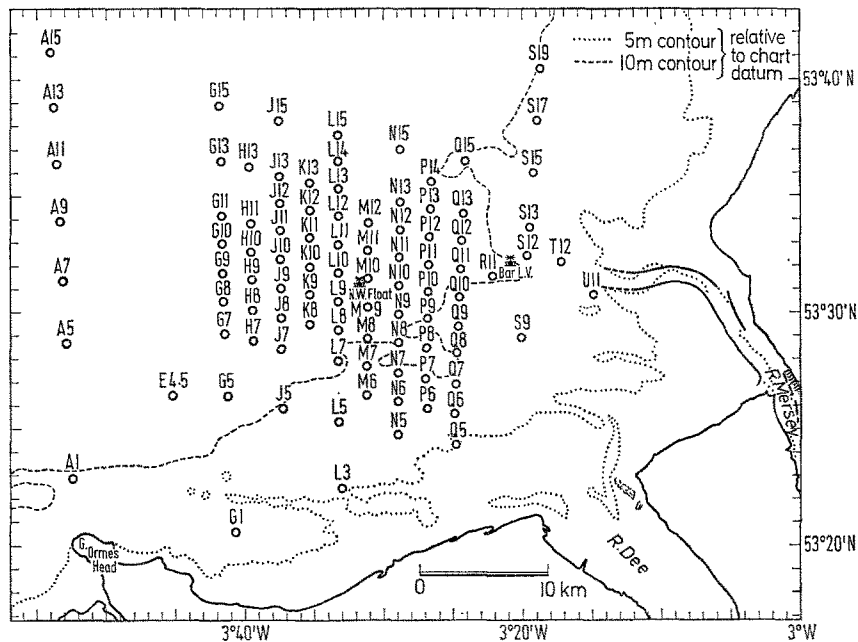


Fig. 1. Location of sampling stations in Liverpool Bay

clustering strategies described by Field and McFarlane (1968), both "nearest neighbour" and "furthest neighbour" techniques were found to produce a number of illogical associations.

## Results

### *The Habitats*

The bottom sediments of Liverpool Bay are extremely diverse. The main part of the area sampled is predominantly medium-to-fine sand, with small or moderate amounts of silt. Near the approach channels to the River Mersey areas of mud or very muddy fine sand occur, whilst in the western part of the sampling area the sediment consists of rather muddy sand-gravel mixtures. Mobile sand waves occur frequently in the southern regions.

There appears to be a continuous variation between these types of sediments but, for the purposes of this study, the stations have been arbitrarily divided, on the basis of granulometry, into 6 main groups, or habitats, each of which may be considered to represent a node of this continuum. The groups are as follows:

(1) Mud and sandy mud. Above 60% silt-clay as determined by sedimentation; less than 5% gravel (particles above 2 mm diameter) dry weight.

(2) Very muddy sand. 15 to 60% silt-clay; less than 5% gravel.

(3) Muddy sand. 7.5 to 15% silt-clay; less than 7.5% gravel. Mainly medium sand.

(4) Muddy coarse bottom. Poorly sorted sediments, with above 7.5% silt-clay and 10 to 50% gravel.

(5) Clean coarse bottom. Sand-gravel mixtures. Less than 7.5% silt-clay; 10 to 70% gravel.

(6) Clean sand. Less than 7.5% silt-clay; less than 5% gravel. Predominantly medium sand.

The distribution of these habitats in Liverpool Bay is illustrated in Fig. 2. Further details of sediment analyses may be found in the report of Crickmore and Kiff (1972). Particle-size distributions of individual samples are available from the Hydraulics Research Station, Wallingford, Berkshire (UK).

### *Nematode Fauna of the Habitats*

The genera occurring in each habitat are listed, in order of total percentage abundance, in Table 1. Details of nematode density and diversity are given in Table 2. The average density (numbers/m<sup>2</sup>) for a genus in any habitat may be obtained by comparing the percentage dominance of the genus given in Table 1 with the average density of nematodes listed in Table 2.

A group-average cluster-analysis of the pooled data for each habitat produced the associations illustrated in Fig. 3. It can be seen that those habitats which are most similar with regard to sediment type are also most similar faunistically.

The very muddy sediments of Habitats 1 and 2 were both dominated by *Sabatieria*. *Tripyloides*, *Crassolaimus*, and *Terschellingia* were important members of the subsidiary fauna in Habitat 1, whilst *Neochromadora* occurred at all stations in Habitat 2. *Sabatieria* was also important in the muddy sands and muddy coarse sediments of Habitats 3 and 4, although it was present with lower dominance, and both these

Table 1. Distribution of nematode genera in Liverpool Bay, ranked in order of total percentage abundance. Dom.: dominance; Freq.: frequency

Genus	Total		Habitat 1		Habitat 2		Habitat 3		Habitat 4		Habitat 5		Habitat 6	
	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.
<i>Sabatieria</i>	12.63	87.2	70.13	100.0	53.20	100.0	15.24	100.0	11.06	100.0	2.26	71.4	4.88	68.0
<i>Desmodora</i>	10.06	85.1	2.03	25.0	—	—	10.18	85.7	5.98	88.2	15.33	92.9	15.16	96.0
<i>Necromadora</i>	7.44	88.3	0.25	25.0	2.36	100.0	6.21	92.9	12.65	97.1	2.34	71.4	5.65	92.0
<i>Microaimus</i>	3.22	86.2	0.51	50.0	4.71	66.7	3.25	85.7	3.83	91.2	2.12	78.6	4.30	96.0
<i>Odonophora</i>	3.15	74.5	0.25	25.0	2.69	66.7	4.84	92.9	4.57	85.3	3.07	100.0	2.70	80.0
<i>Graphonema</i>	3.12	63.8	—	—	—	—	1.88	78.6	1.32	44.1	8.76	100.0	4.01	68.0
<i>Metachromadora</i>	3.00	54.3	3.29	50.0	1.35	66.7	5.56	85.7	0.90	29.4	4.23	57.1	3.89	68.0
<i>Crassolaimus</i>	2.22	58.5	1.52	100.0	1.35	66.7	1.73	71.4	4.19	79.4	1.02	28.6	0.70	32.0
<i>Theristus</i>	2.13	59.6	0.25	25.0	0.67	33.3	1.73	57.1	3.59	82.4	1.17	35.7	1.39	52.0
<i>Richtersia</i>	1.97	48.9	0.25	25.0	7.74	66.7	3.39	85.7	0.48	26.5	1.68	57.1	2.95	56.0
<i>Hypodontolaimus</i>	1.86	53.2	0.76	75.0	0.67	66.7	1.59	71.4	0.51	26.5	3.72	64.3	3.15	68.0
<i>Oncholaimus</i>	1.86	22.3	—	—	3.70	66.7	4.26	21.4	0.21	17.6	5.99	42.9	0.53	16.0
<i>Hatichoncolaimus</i>	1.55	56.4	—	—	—	—	1.01	57.1	2.90	79.4	1.17	64.3	0.66	36.0
<i>Oryonchus</i>	1.48	44.7	1.77	25.0	—	—	4.26	50.0	1.23	58.8	0.66	28.6	0.86	40.0
<i>Actinonema</i>	1.42	41.5	—	—	0.36	14.3	0.36	14.3	3.23	70.6	0.44	35.7	0.49	32.0
<i>Halalaimus</i>	1.38	61.7	0.25	25.0	0.34	33.3	0.51	35.7	2.21	82.4	0.73	50.0	1.39	64.0
<i>Monhystera</i>	1.34	47.9	1.01	50.0	—	—	0.29	21.4	1.79	61.8	2.55	64.3	0.86	40.0
<i>Spirinia</i>	1.29	33.0	0.76	50.0	0.34	33.3	1.08	28.6	2.78	52.9	0.15	14.3	0.20	16.0
<i>Paramonhystera</i>	1.28	57.4	0.51	50.0	—	—	1.01	35.7	1.73	85.3	0.51	35.7	1.52	52.0
<i>Eupoilides</i>	1.27	47.9	—	—	—	—	0.72	50.0	0.54	26.5	3.94	85.7	1.43	68.0
<i>Chromaspirina</i>	1.22	44.7	—	—	0.34	33.3	0.87	42.9	0.39	32.4	1.24	35.7	2.87	76.0
<i>Denticulella</i>	1.14	48.9	—	—	0.67	66.7	0.36	21.4	2.36	85.3	0.73	42.9	0.37	24.0
<i>Halaplanolaimus</i>	1.04	40.4	0.76	25.0	—	—	3.03	78.6	0.45	29.4	0.44	35.7	1.23	44.0
<i>Pomponema</i>	1.01	43.6	—	—	—	—	1.08	50.0	1.02	55.9	1.24	42.9	1.11	36.0
<i>Tripyloides</i>	1.01	31.9	4.05	100.0	1.35	66.7	2.60	21.4	0.42	23.5	0.51	35.7	0.66	32.0
<i>Trejusia</i>	0.96	45.7	—	—	—	—	1.23	28.6	1.55	70.6	0.66	50.0	0.45	32.0
<i>Rhynchonema</i>	0.84	30.9	—	—	—	—	0.14	14.3	0.57	26.5	3.58	78.6	0.33	28.0
<i>Prochromadorella</i>	0.83	40.4	—	—	0.34	33.3	0.36	21.4	0.87	58.8	1.90	42.9	0.66	32.0
<i>Isconema</i>	0.82	28.7	—	—	—	—	0.36	28.6	0.27	17.6	1.82	42.9	1.52	44.0
<i>Terschellingia</i>	0.78	18.1	5.06	75.0	—	—	0.07	7.1	1.52	38.2	—	—	—	—
<i>Chromadorita</i>	0.74	39.4	—	—	0.34	33.3	0.51	35.7	0.75	38.2	1.75	71.4	0.45	32.0
<i>Anticoma</i>	0.74	31.9	—	—	—	—	—	—	1.17	50.0	1.75	71.4	0.20	12.0
<i>Viscosia</i>	0.73	31.9	—	—	—	—	0.29	21.4	1.55	55.9	0.58	42.9	0.12	8.0
<i>Chromadorina</i>	0.67	39.4	—	—	—	—	0.65	35.7	0.90	47.1	1.02	57.1	0.37	32.0
<i>Latronema</i>	0.67	25.5	—	—	—	—	0.14	14.3	0.24	23.5	0.36	28.6	1.93	40.0
<i>Monoposthia</i>	0.66	22.3	—	—	0.34	33.3	0.65	28.6	0.03	2.9	1.46	28.6	1.23	44.0
<i>Camacolinoides</i>	0.66	16.0	—	—	—	—	0.07	7.1	0.15	8.8	0.29	21.4	2.09	32.0
<i>Cybalaimus</i>	0.65	17.0	—	—	—	—	—	—	0.09	8.8	0.44	14.3	2.09	44.0
<i>Paracanthochus</i>	0.58	24.5	1.01	50.0	2.69	33.3	0.43	14.3	0.69	38.2	0.07	7.1	0.49	16.0
<i>Paracyatholaimus</i>	0.58	14.9	—	—	—	—	0.14	7.1	0.06	2.9	1.61	28.6	1.15	32.0
<i>Adoncholaimus</i>	0.58	5.3	—	—	—	—	—	—	0.12	8.8	—	—	2.05	8.0
<i>Xyala</i>	0.56	20.2	—	—	—	—	0.22	14.3	0.33	5.9	0.15	14.3	1.47	52.0
<i>Mononcholaimus</i>	0.51	31.9	0.25	25.0	—	—	0.22	21.4	0.63	50.0	0.58	28.6	0.37	20.0
<i>Linthonaeus</i>	0.51	26.6	—	—	—	—	0.14	14.3	0.90	35.3	0.36	28.6	0.41	28.0
<i>Orystomina</i>	0.50	34.0	0.76	50.0	—	—	0.65	35.7	0.69	41.2	0.36	35.7	0.25	24.0
<i>Vasostoma</i>	0.49	22.3	—	—	—	—	0.22	21.4	0.30	14.7	0.22	14.3	1.19	44.0

Table 1 (continued)

Genus	Habitat 1		Habitat 2		Habitat 3		Habitat 4		Habitat 5		Habitat 6	
	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.
<i>Oncholaimellus</i>	0.48	23.4	—	—	0.94	35.7	0.45	26.5	0.51	21.4	0.37	20.0
<i>Cerwonema</i>	0.44	17.0	—	—	0.07	7.1	1.20	44.1	—	—	—	—
<i>Camacolaimus</i>	0.41	26.6	—	—	0.29	14.3	0.48	29.4	0.88	50.0	0.25	24.0
<i>Metalinhomoeus</i>	0.39	21.3	0.25	25.0	0.14	14.3	0.72	38.2	0.29	14.3	0.12	4.0
<i>Ceramonema</i>	0.36	16.0	—	—	0.07	7.1	0.36	14.7	—	—	0.82	36.0
<i>Diodontolaimus</i>	0.36	12.8	—	—	0.07	7.1	0.03	2.9	0.22	21.4	1.15	28.0
<i>Euploplaimus</i>	0.32	13.8	—	—	0.22	21.4	0.18	2.9	0.36	21.4	0.66	24.0
<i>Amphimomhystrera</i>	0.31	28.7	—	—	0.36	28.6	0.27	26.5	0.36	35.7	0.41	36.0
<i>Gamananema</i>	0.29	21.3	—	—	0.65	42.9	—	—	—	—	0.74	56.0
<i>Pselionema</i>	0.29	20.2	—	—	0.07	7.1	0.21	17.6	0.29	14.3	0.61	40.0
<i>Paralinhomoeus</i>	0.29	16.0	—	—	—	—	0.63	35.3	0.07	7.1	0.20	8.0
<i>Rhabdotemania</i>	0.29	14.9	—	—	0.29	21.4	—	—	0.88	42.9	0.45	20.0
<i>Paraseuratiella</i>	0.28	12.8	—	—	0.58	28.6	0.12	5.9	0.44	14.3	0.33	16.0
<i>Nudora</i>	0.28	10.6	—	—	0.43	28.6	—	—	1.09	14.3	0.20	16.0
<i>Gonionchus</i>	0.27	17.0	—	—	0.22	14.3	0.54	32.4	0.29	21.4	—	—
<i>Aconolaimus</i>	0.26	16.0	—	—	0.58	28.6	0.06	5.9	0.07	7.1	0.53	32.0
<i>Metacanthonchus</i>	0.26	2.1	—	—	—	—	—	—	—	—	0.98	8.0
<i>Leptolaimus</i>	0.25	18.1	—	—	0.22	21.4	0.36	29.4	—	—	0.29	12.0
<i>Thoracostomopsis</i>	0.25	17.0	—	—	0.36	21.4	0.27	20.6	0.51	28.6	0.08	8.0
<i>Dermatolaimus</i>	0.24	14.9	0.51	50.0	0.07	7.1	0.33	23.5	—	—	0.25	8.0
<i>Paradesmodora</i>	0.24	9.6	—	—	0.14	7.1	—	—	0.29	14.3	0.66	24.0
<i>Bathylaimus</i>	0.23	16.0	—	—	0.36	21.4	0.36	32.4	0.22	14.3	0.04	4.0
<i>Diplopeltis</i>	0.23	14.9	—	—	0.22	21.4	0.51	29.4	—	—	0.04	4.0
<i>Heterocyatholaimus</i>	0.23	14.9	—	—	0.65	42.9	0.12	8.8	0.07	7.1	0.25	12.0
<i>Linhomoella</i>	0.23	13.8	—	—	0.22	21.4	0.06	5.9	0.36	14.3	0.45	24.0
<i>Thalassoalaimus</i>	0.22	17.0	0.25	25.0	0.14	14.3	0.21	17.6	0.07	7.1	0.37	24.0
<i>Sphaerolaimus</i>	0.22	14.9	0.25	25.0	0.14	14.3	0.30	17.6	0.15	14.3	0.04	4.0
<i>Chromatorella</i>	0.22	12.8	—	—	0.07	7.1	0.30	17.6	0.29	28.6	0.16	12.0
<i>Mesacanthoides</i>	0.22	11.7	—	—	—	—	0.12	11.8	0.73	28.6	0.25	28.0
<i>Lauratonema</i>	0.19	13.8	0.25	25.0	0.14	14.3	0.03	2.9	0.29	14.3	0.41	—
<i>Ascolaimus</i>	0.18	7.4	1.52	50.0	0.22	21.4	—	—	—	—	—	—
<i>Bradylaimus</i>	0.16	1.1	—	—	—	—	—	—	—	—	0.61	4.0
<i>Eurystomina</i>	0.15	11.7	—	—	0.22	14.3	0.30	23.5	—	—	0.04	4.0
<i>Longicyatholaimus</i>	0.15	10.6	—	—	0.29	28.6	0.06	5.9	—	—	0.33	16.0
<i>Steneria</i>	0.15	8.5	—	—	0.14	14.3	0.15	8.8	0.22	7.1	0.16	8.0
<i>Eleutherolaimus</i>	0.13	10.6	—	—	0.07	7.1	0.21	14.7	0.15	14.3	0.04	4.0
<i>Cobbia</i>	0.13	10.6	—	—	0.07	7.1	0.24	17.6	0.15	14.3	0.04	4.0
<i>Paramicroalaimus</i>	0.13	9.6	—	—	0.22	14.3	0.06	2.9	0.29	21.4	0.08	8.0
<i>Onyr</i>	0.13	8.5	—	—	—	—	—	—	0.73	42.9	0.08	—
<i>Calyptronema</i>	0.13	3.2	—	—	—	—	0.36	8.8	—	—	—	—
<i>Cyfolaimum</i>	0.12	8.5	—	—	0.14	14.3	0.18	11.8	—	—	0.12	8.0
<i>Tricoma</i>	0.12	8.5	—	—	0.07	7.1	0.09	5.9	0.15	7.1	0.20	16.0
<i>Chromadora</i>	0.12	7.4	—	—	0.07	7.1	0.09	8.8	0.15	7.1	—	—
<i>Sphaerocephalum</i>	0.10	7.4	0.25	25.0	0.07	7.1	0.06	5.9	0.07	7.1	0.25	16.0
<i>Parachromogasteriella</i>	0.09	4.3	—	—	0.22	14.3	—	—	0.07	7.1	0.16	4.0
<i>Epacanthion</i>	0.09	3.2	—	—	—	—	0.03	2.9	0.44	7.1	0.04	4.0
<i>Eutelolaimus</i>	0.08	7.4	—	—	0.07	7.1	0.08	8.8	0.07	7.1	0.08	8.0

Table 1. (continued)

Genus	Total		Habitat 1		Habitat 2		Habitat 3		Habitat 4		Habitat 5		Habitat 6	
	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.	% Dom.	% Freq.
<i>Dasyneimoides</i>	0.08	7.4	—	—	—	—	0.07	7.1	0.09	8.8	0.07	7.1	0.08	8.0
<i>Laimella</i>	0.08	6.4	—	33.3	—	14.3	—	—	0.15	11.8	—	—	0.04	4.0
<i>Bairmijer</i>	0.08	4.3	—	66.7	—	—	—	—	—	—	—	—	—	—
<i>Prochromadora</i>	0.08	2.1	—	—	—	—	—	—	0.18	2.9	0.07	7.1	—	—
<i>Diplophutula</i>	0.06	6.4	—	—	—	14.3	—	—	0.06	5.9	0.07	7.1	0.04	4.0
<i>Spilophorella</i>	0.06	6.4	—	—	—	—	—	—	0.12	11.8	0.15	14.3	—	—
<i>Siphonolaimus</i>	0.06	5.3	—	—	—	—	—	—	0.03	2.9	0.22	14.3	0.08	8.0
<i>Dasyneimella</i>	0.06	5.3	—	—	—	—	—	—	0.03	2.9	—	—	0.20	16.0
<i>Disconema</i>	0.06	4.3	—	—	—	—	0.14	14.3	—	—	0.07	7.1	0.12	4.0
<i>Atrochromadora</i>	0.06	4.3	—	—	—	—	—	—	0.03	2.9	0.36	21.4	—	—
<i>Aegialolaimus</i>	0.05	5.3	—	—	—	—	—	—	0.09	8.8	0.07	7.1	0.04	4.0
<i>Rhadinema</i>	0.05	4.3	—	—	—	—	0.07	7.1	0.06	2.9	0.07	7.1	0.04	4.0
<i>Southernella</i>	0.05	3.2	—	—	—	—	0.22	7.1	0.06	5.9	—	—	—	—
<i>Choanolaimus</i>	0.04	4.3	—	—	—	—	—	—	0.06	5.9	0.07	7.1	0.04	4.0
<i>Manuema</i>	0.04	3.2	—	—	—	—	—	—	—	—	—	—	0.12	8.0
<i>Prasacanthionchus</i>	0.04	3.2	—	—	—	—	—	—	—	—	0.15	7.1	0.08	8.0
<i>Neotonchus</i>	0.04	2.1	—	—	—	—	—	—	0.09	2.9	—	—	—	—
<i>Araolaimus</i>	0.03	3.2	—	—	—	—	0.07	7.1	0.07	7.1	0.15	14.3	—	—
<i>Pterygonema</i>	0.03	3.2	—	—	—	—	—	—	—	—	0.15	14.3	0.04	4.0
<i>Comesoma</i>	0.03	3.2	—	—	—	—	—	—	0.03	2.9	—	—	0.08	8.0
<i>Spiliphora</i>	0.03	3.2	—	—	—	—	0.07	7.1	—	—	—	—	0.08	8.0
<i>Trileptium</i>	0.03	3.2	—	—	—	—	0.07	7.1	—	—	—	—	0.04	4.0
<i>Dilepsenella</i>	0.03	3.2	—	—	—	—	—	—	—	—	0.07	7.1	—	—
<i>Polygastrophora</i>	0.03	3.2	—	—	—	—	—	—	0.06	5.9	0.07	7.1	0.04	4.0
<i>Dasyllaimus</i>	0.03	3.2	—	—	—	—	—	—	0.06	5.9	—	—	—	—
<i>Tarvaia</i>	0.03	2.1	—	—	—	—	0.07	7.1	0.06	5.9	—	—	0.08	4.0
<i>Paraterschellingia</i>	0.03	2.1	—	—	—	—	—	—	0.03	2.9	0.07	7.1	—	—
<i>Sauejevica</i>	0.03	2.1	—	—	—	—	—	—	0.06	2.9	—	—	0.04	4.0
<i>Araolaimoides</i>	0.02	2.1	—	—	—	—	—	—	0.06	2.9	—	—	0.04	4.0
<i>Desmoscolex</i>	0.02	2.1	—	—	—	—	—	—	0.03	2.9	—	—	0.04	4.0
<i>Phanoderna</i>	0.02	2.1	—	—	—	—	—	—	0.03	2.9	—	—	0.04	4.0
<i>Mesacanthion</i>	0.02	2.1	—	—	—	—	—	—	0.03	2.9	0.07	7.1	0.04	4.0

Rare genera (restricted to 1 habitat and with overall dominance < 0.10%)

Habitat 2	
<i>Choniolaimus</i> (6) <sup>a</sup> , <i>Paramesacanthion</i> (1)	Habitat 5
	<i>Campylolaimus</i> (2), <i>Hyalacanthion</i> (2), <i>Metoncholaimus</i> (2), <i>Cyatholaimidae</i>
	sp. (1), <i>Metacyatholaimus</i> (1)
Habitat 3	
<i>Didelta</i> (1), <i>Pseudolella</i> (1), <i>Paranticonema</i> (1), <i>Octonchus</i> (1), <i>Pelagonema</i> (1)	Habitat 6
Habitat 4	<i>Stephanolaimus</i> (6), <i>Pseudonchus</i> (6), <i>Pseudochromaspirina</i> (3), <i>Paratricula</i> (3),
<i>Symplacostoma</i> (7), <i>Conistomella</i> (5), <i>Dorylaimopsis</i> (5), <i>Dorylaimus</i> (3),	<i>Omicronema</i> (2), <i>Promonhystera</i> (2), <i>Acanthopharyngoides</i> (2), <i>Filippineinema</i> (1),
<i>Planodermopsis</i> (3), <i>Thoönchus</i> (3), <i>Desmolaimus</i> (2), <i>Synonema</i> (2),	<i>Southernia</i> (1), <i>Metatesmodora</i> (1), <i>Rhinema</i> (1), <i>Xinema</i> (1), <i>Enoplus</i> (1),
<i>Eudesmoscolex</i> (2), <i>Symplacostomella</i> (2), <i>Polysigma</i> (2), <i>Anomonema</i> (1),	<i>Metenoploides</i> (1), <i>Chaetonema</i> (1)
<i>Paratritiploides</i> (1), <i>Metacomsonema</i> (1), <i>Mesonchium</i> (1), <i>Trichronadora</i> (1),	
<i>Chetronchus</i> (1), <i>Thoracostoma</i> (1), <i>Klugia</i> (1), <i>Curvolaimus</i> (1)	

<sup>a</sup> Numbers in brackets represent number of individuals encountered.

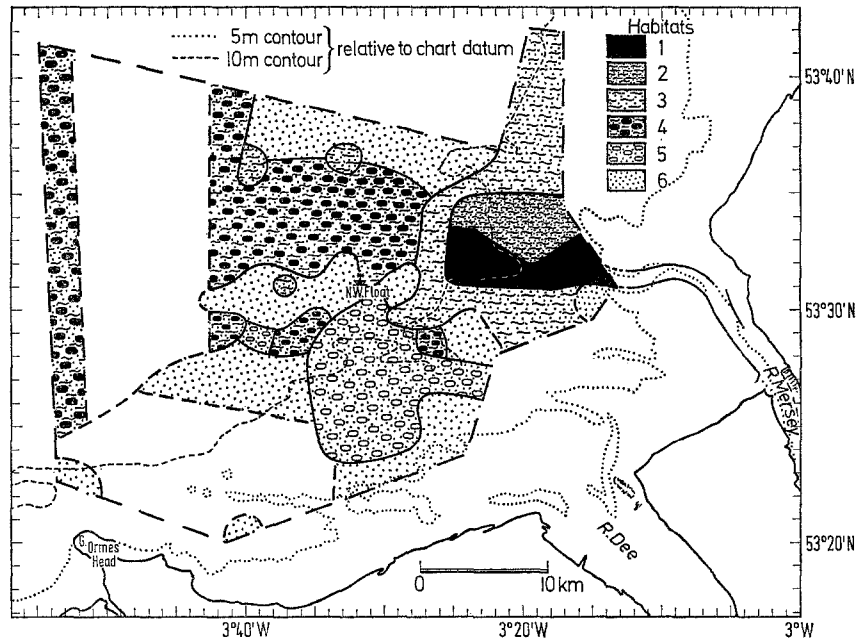


Fig. 2. Distribution of habitats in Liverpool Bay (for description of habitats see text)

Table 2. Nematode abundance and diversity in Liverpool Bay

Habitat*	1	2	3	4	5	6
No. of samples	4	3	14	34	14	25
No. of specimens	395	297	1385	3345	1370	2441
No. of genera	30	33	99	127	102	125
Average density (no./m <sup>2</sup> )	$34 \times 10^4$	$161 \times 10^4$	$56.5 \times 10^4$	$31 \times 10^4$	$29 \times 10^4$	$42.5 \times 10^4$
Diversity index ( $\alpha$ )	7	9	25	27	26	28

\* For habitat description see text.

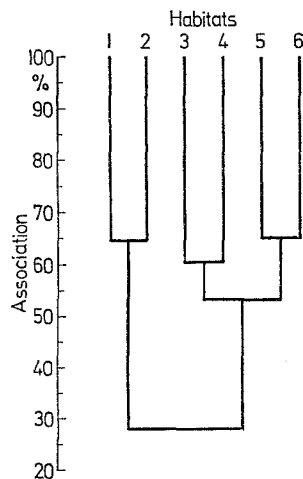


Fig. 3. Faunal affinity between habitats (for explanation see text)

habitats supported a much more heterogeneous fauna than the previous two. *Odontophora*, *Dichromadora*, and *Neochromadora* were the most common sub-dominant genera in Habitat 3, whilst *Micro-laimus*, *Halaphanolaimus*, *Metachromadora*, and *Richtersia* occurred frequently. *Neochromadora* dominated Habitat 4, whilst *Odontophora*, *Dichromadora* and *Micro-laimus* were again common, along with *Theristus*, *Crassolaimus*, *Denticulella*, *Halichoanolaimus*, and *Halalaimus*. *Desmodora* was found frequently in both Habitats 3 and 4, but only occurred in large numbers in areas where relatively high concentrations of sewage-sludge tracer were recorded. The possible significance of this has been discussed in Rees *et al.* (1972). Normally, *Desmodora* was found to be characteristic of clean, coarse substrata, and occurred abundantly at nearly all stations in Habitats 5 and 6, where *Graphonema*, *Dichromadora*, and *Micro-laimus* were also common. *Graphonema* was sub-dominant in Habitat

5, and *Dichromadora* in Habitat 6. Other common genera were *Rhynchonema* and *Enoploides* in Habitat 5, and *Neochromadora* in Habitat 6. *Sabatieria* was poorly represented in both habitats, mainly by *S. hilarula*, a species which Warwick and Buchanan (1970) found to be associated with sandy substrata.

#### Faunal Affinity Between Stations

Cluster analysis of the individual stations produced the associations illustrated in dendrogram form in Fig. 4. The stations fall into 5 main groups which

#### Group Analysis

##### Group I

Two stations only, both with a very high percentage of *Oncholaimus*, which is almost entirely responsible for the 47% similarity between them. In all other respects, the two stations are dissimilar, having only 4 other genera in common.

Habitat 3: S15 - *Oncholaimus* 41% : *Sabatieria* 16%

Habitat 5: M8 - *Oncholaimus* 74% : *Desmodora* 10%

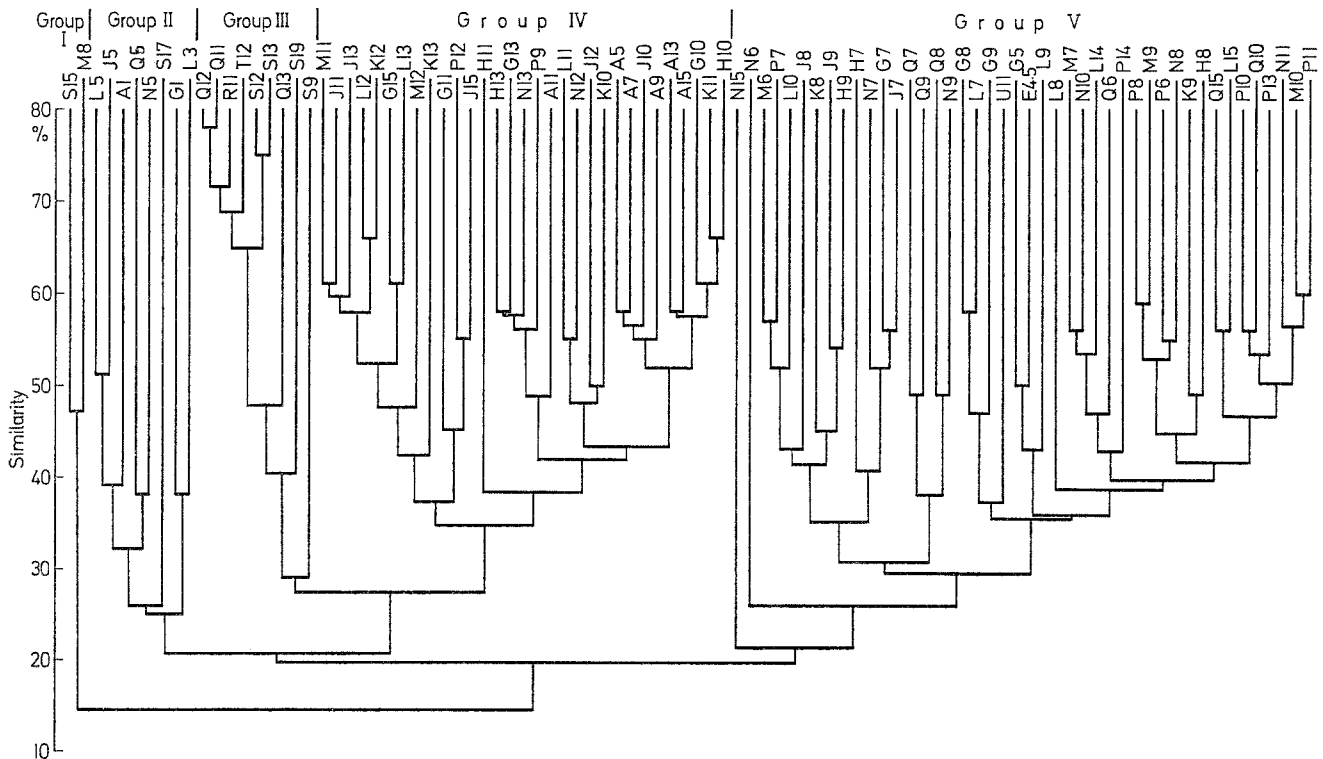


Fig. 4. Dendrogram of faunal affinity between stations (for explanation see text)

conform generally, but not precisely, with the division by habitats.

Group I comprises two stations only, S15 and M8, characterised by an unusually high dominance of *Oncholaimus*. Group II is faunistically rather heterogeneous, but consists of characteristically sandy stations. Group III comprises the muddy, *Sabatieria*-dominated stations of Habitats 1 and 2, together with two from Habitat 3. Group IV consists of Habitat 4 stations with three from Habitat 3. Finally, Group V contains mainly stations from Habitats 5 and 6 with a few from Habitats 3 and 4, particularly those characterised by large numbers of *Desmodora*, the genus which dominates this group.

##### Group II

A rather heterogeneous group of stations, associated at a low level of similarity.

Habitat 3: S17 - *Tripyleoides* 31%

Habitat 5: L5 - *Monoposthia* 11%

N5 - *Hypodontolaimus* 18%

Habitat 6: A1 - *Microlaimus* 13% : *Camacolaimoides* 13% ; *Paramonhystera* 13%

G1 - *Metachromadora* 17%

J5 - *Paracyatholaimus* 12% : *Neochromadora* 10%

L3 - *Metacanthonchus* 22% : *Metachromadora* 12%

Q5 - *Hypodontolaimus* 21% : *Dichromadora* 14% ; *Neochromadora* 12% : *Cyatholaimus* 11%

### Group III

This group, apart from S9, is characterised by the overwhelming dominance of *Sabatieria*. The two Habitat 3 stations are not typical; S9 has only 8% *Sabatieria*, and is attached to the group through S19 at only 28.8% similarity. S19 is associated at 40.4% similarity, much lower than the others, by virtue of the 31% dominance of *Sabatieria*.

Habitat 1: Q11 - *Sabatieria* 69% : *Terschellingia* 11%  
 Q12 - *Sabatieria* 63% (*Terschellingia* 4%)  
 R11 - *Sabatieria* 61% (*Terschellingia* 5%)  
 T12 - *Sabatieria* 84% : *Tripyloides* 10%  
 Habitat 2: Q13 - *Sabatieria* 42% : *Microlaimus* 11%  
 S12 - *Sabatieria* 65% : *Richtersia* 10%  
 S13 - *Sabatieria* 51% : *Richtersia* 13%  
 Habitat 3: S9 - *Oxyonchus* 31% : *Dichromadora* 23% (*Sabatieria* 8%)  
 S19 - *Sabatieria* 31% : *Oxyonchus* 10%

### Group IV

This group comprises 27 stations from Habitat 4, 3 from Habitat 3, and 1 from Habitat 6. The group divides into 6 sub-groups below 40% similarity, as follows:

*Sub-group (i)*. Characteristically dominated by *Sabatieria*, with *Neochromadora* and *Odontophora* present in small numbers. J13 and M11, with larger numbers of *Neochromadora*, appear intermediate with the next sub-group.

Habitat 4: G15 - *Sabatieria* 17%  
 J11 - *Sabatieria* 15%  
 J13 - *Neochromadora* 18% : *Sabatieria* 15%  
 K12 - *Sabatieria* 24%  
 K13 - *Theristus* 38% : *Sabatieria* 19%  
 L12 - *Sabatieria* 24% : *Spirinia* 12%  
 L13 - *Sabatieria* 12%  
 M11 - *Sabatieria* 18% : *Neochromadora* 15% : *Actinonema* 11%  
 M12 - *Sabatieria* 21% : *Spirinia* 17% : *Halichoanolaimus* 10%

*Sub-group (ii)*. *Sabatieria* co-dominant with various genera, notably *Neochromadora*. *Odontophora* still with relatively low dominance.

Habitat 3: P12 - *Sabatieria* 22% : *Neochromadora* 20% : *Metachromadora* 20%

Habitat 4: G11 - *Sabatieria* 23% : *Crassolaimus* 19% : *Cervonema* 15% (*Neochromadora* 9%)

Habitat 6: J15 - *Sabatieria* 21% : *Neochromadora* 21%

*Sub-group (iii)*. A single station, separated from the other sub-groups by the high percentage of *Odontophora*, and most closely related to the next sub-group.

Habitat 4: H11 - *Odontophora* 18% : *Sabatieria* 11%

*Sub-group (iv)*. Characterised by the dominance of *Sabatieria* and/or *Odontophora*. *Neochromadora* more abundant (7 to 9%), but other Chromadoridae still relatively scarce. Perhaps a transitional stage between Sub-groups (iii) and (v). H13 is an atypical sediment, and may represent a more complex transitional stage between the other members of the group and the *Desmodora*-dominated sediments of Group V.

Habitat 3: H13 - *Sabatieria* 16% : *Desmodora* 10% (*Odontophora* 8%)

P9 - *Sabatieria* 12% : *Odontophora* 11% : *Trefusia* 10%

Habitat 4: A11 - *Odontophora* 11% (*Sabatieria* 3%)

G13 - *Spirinia* 17% : *Sabatieria* 12% : *Odontophora* 11%

N13 - *Sabatieria* 25% (*Odontophora* 6%)

*Sub-group (v)*. Relative abundance of *Sabatieria* generally lower than in the previous sub-groups, and that of *Neochromadora*, and sometimes *Odontophora*, rather higher. Chromadoridae in general with much higher dominance. Station K10 was somewhat unusual in the high dominance of *Desmodora*. This may be an effect of sewage sludge, since this station was in the dumping zone.

Habitat 4: J12 - *Odontophora* 19% : *Neochromadora* 15% : *Sabatieria* 11%

K10 - *Desmodora* 10% (*Neochromadora* 9%, *Sabatieria* 7%, *Odontophora* 6%)

L11 - *Neochromadora* 14% (*Sabatieria* 4%, *Odontophora* 1%)

N12 - *Neochromadora* 16% : *Sabatieria* 11% (*Odontophora* 2%)

*Sub-group (vi)*. *Neochromadora* invariably dominant, and the Chromadoridae in general present with high dominance (34 to 47%). *Odontophora* and *Sabatieria* usually with low dominance.

Habitat 4: A5 - *Neochromadora* 19%

A7 - *Neochromadora* 19%

A9 - *Neochromadora* 28%

A13 - *Neochromadora* 26% : *Microlaimus* 13% : *Sabatieria* 10%

A15 - *Neochromadora* 29%



- G10 - *Neochromadora* 24% : *Oxyonchus* 11%  
 H10 - *Neochromadora* 24% : *Denticulella* 15% : *Crassolaimus* 11%  
 J10 - *Neochromadora* 24%  
 K11 - *Neochromadora* 25% : *Crassolaimus* 12%

#### Group V

Group V comprises 19 stations from Habitat 6, 11 from Habitat 5, 7 from Habitat 4, and 7 from Habitat 3. Eleven of the 14 stations from these last two habitats are associated due to high dominance of *Desmodora*, and all are from areas of relatively high sludge-tracer concentration. Two stations diverge from the group almost immediately:

- Habitat 6: N15 - *Adoncholaimus* 48% (*Desmodora* 4%)  
 Habitat 5: N6 - *Graphonema* 26% : *Enoploides* 19% (*Desmodora* 7%)

N6 is closely related to the other *Graphonema*-dominated stations in this group.

Apart from the above stations, Group V divides into 11 sub-groups associated, with one exception, below 40% similarity.

*Sub-group (i)*. Mainly *Desmodora*-*Graphonema* dominated populations, with a fairly high percentage of Chromadoridae (21 to 40%). Station K8 is associated through *Graphonema* and other, subsidiary, elements, and is perhaps a rather atypical Group IV station.

- Habitat 3: J9 - *Desmodora* 14% (*Graphonema* 5%) ("sludge-tracer" station)  
 Habitat 4: K8 - *Neochromadora* 14% : *Dichromadora* 12% : *Graphonema* 11% (*Desmodora* 3%)  
 Habitat 5: M6 - *Graphonema* 19% : *Desmodora* 15%  
 P7 - *Desmodora* 18% : *Graphonema* 15% : *Ixonema* 10% : *Rhynchonema* 10%  
 Habitat 6: H9 - *Graphonema* 10% : *Oncholaimus* 10% (*Desmodora* 9%)  
 J8 - *Graphonema* 13% (*Desmodora* 9%)  
 L10 - *Desmodora* 16% : *Graphonema* 15% : *Monhystera* 10%

*Sub-group (ii)*. Characterised by the generally low dominance of *Desmodora*, and the common occurrence of *Monhystera* together with several chromadorid genera, although, individually, the latter are present with generally low dominance.

- Habitat 4: G7 - *Microilaimus* 12% : *Monhystera* 10%  
 J7 - *Monhystera* 12%  
 Habitat 5: H7 - *Chromaspirina* 13% : *Graphonema* 10% : *Monhystera* 10%

- N7 - *Hypodontolaimus* 13% : *Desmodora* 11% (*Monhystera* 7%)

*Sub-group (iii)*. Mainly *Metachromadora*-*Dichromadora*-*Desmodora*, with *Odontophora* fairly frequent (5 to 7%). Chromadoridae in general well represented.

- Habitat 5: Q7 - *Metachromadora* 29% : *Desmodora* 13% (*Dichromadora* 9%)  
 Habitat 6: Q9 - *Metachromadora* 10% : *Dichromadora* 10% : *Neochromadora* 10% (*Desmodora* 9%)

*Sub-group (iv)*. Characterised by the high dominance of *Richtersia*, together with a low percentage of Chromadoridae. Linked to the preceding sub-group by the dominance of *Metachromadora* and *Desmodora* at Station Q8.

- Habitat 3: N9 - *Richtersia* 18% (*Metachromadora* 6%, *Desmodora* 3%)  
 Habitat 6: Q8 - *Richtersia* 24% : *Desmodora* 15% : *Metachromadora* 10%

*Sub-group (v)*. *Desmodora* dominant. Chromadoridae well represented.

- Habitat 4: G9 - *Desmodora* 11% : *Neochromadora* 10% : *Xyala* 10% ("sludge-tracer" station)  
 Habitat 5: L7 - *Desmodora* 24%  
 Habitat 6: G8 - *Desmodora* 23%

*Sub-group (vi)*. Restricted to a single, somewhat isolated, station situated on a sand bank bordering the entrance to the Mersey Channel. The sediment consists almost entirely of medium sand with a very low silt content.

- Habitat 6: U11 - *Desmodora* 24% : *Bradyilaimus* 15% : *Hypodontolaimus* 14% (*Graphonema* 7%)

*Sub-group (vii)*. All well-sorted medium sands, with virtually no silt. Characterised by the dominance of *Desmodora* and *Camacolaimoides*. Chromadoridae scarce.

- Habitat 6: E4.5 - *Desmodora* 20% : *Camacolaimoides* 11%  
 G5 - *Desmodora* 18% : *Diodontolaimus* 16% : *Camacolaimoides* 10%  
 L9 - *Desmodora* 19% : *Ixonema* 11% (*Camacolaimoides* 7%)

*Sub-group (viii)*. *Desmodora* dominant, *Rhynchonema* sub-dominant.

- Habitat 5: L8 - *Desmodora* 26% : *Rhynchonema* 14%

*Sub-group (ix)*. *Desmodora* with very high dominance. Very few Chromadoridae.

- Habitat 3: L14 - *Desmodora* 33% ("sludge-tracer" station)  
 Habitat 5: M7 - *Desmodora* 42%  
 Habitat 6: N10 - *Desmodora* 44%: *Chromaspirina* 10%  
     P14 - *Desmodora* 25%: *Halaphanolaimus* 10%  
     Q6 - *Desmodora* 39%

*Sub-group (x)*. *Desmodora* again dominant, but slightly less so than in the previous sub-group; dominance of Chromadoridae somewhat higher. Associated with the following sub-group at 41.6%, but logically should be separated. Apart from K9, all the stations show affinity with either Sub-group V(i) (*Desmodora-Graphonema*) or Sub-group V(iii) (*Desmodora-Metachromadora*). Stations N8 and P6 are more akin to V(i) whilst P8, M9, and H8 appear to represent an intermediate stage between the two. These stations probably group together through the greater dominance of *Desmodora* and the composition of the subsidiary fauna. The dominance of *Chromaspirina* at P6 gives this station some affinity with N10 [Sub-group V(ix)], whilst H8 also appears related to the following Sub-group (particularly Station P13) through the dominance of *Sabatieria*. The dominance of *Latronema* at K9 relates this station to L15 in Sub-group V(xi; a).

- Habitat 4: P8 - *Desmodora* 28%: *Metachromadora* 17% (*Graphonema* 7%) ("sludge-tracer" station)  
 Habitat 5: M9 - *Desmodora* 24% (*Graphonema* 9%, *Metachromadora* 8%)  
     N8 - *Desmodora* 18%: *Graphonema* 13%  
 Habitat 6: H8 - *Desmodora* 16%: *Sabatieria* 12%: *Metachromadora* 11% (*Graphonema* 9%)  
     K9 - *Desmodora* 22%: *Latronema* 10%  
     P6 - *Desmodora* 23%: *Graphonema* 12%: *Chromaspirina* 12%

*Sub-group V(xi)*. Characteristically, the *Desmodora-Sabatieria* communities. Although all the stations in this group are associated above 40% similarity, a further sub-division is desirable, and separates two final groups at a level of 46.6% similarity; these are:

(a) The typical *Desmodora* sediments of Habitat 6. *Sabatieria* represented almost exclusively by the sand-inhabiting *S. hilarula*.

- L15 - *Latronema* 14%: *Desmodora* 12%: *Sabatieria* 10%  
 Q15 - *Sabatieria* 22%: *Desmodora* 12%

(b) The muddier sediments of Habitats 3 and 4. *Sabatieria* represented by typically mud-inhabiting species, *Desmodora* dominant or sub-dominant. All these stations lie in areas of high sludge-tracer concentration.

- Habitat 3: P10 - *Oncholaimus* 17%: *Desmodora* 16%: *Sabatieria* 15% (cf. Group I)  
 P11 - *Sabatieria* 26%: *Desmodora* 24%  
 P13 - *Metachromadora* 13%: *Desmodora* 12%: *Sabatieria* 10%  
 Q10 - *Desmodora* 18%: *Sabatieria* 14%: *Dichromadora* 10%  
 Habitat 4: M10 - *Desmodora* 28%: *Sabatieria* 10%  
 N11 - *Desmodora* 22%: *Sabatieria* 14%

#### Faunal Diversity of the Habitats

Sanders (1968) defined two types of diversity measurements, which he designated (after Whittaker, 1965) as dominance diversity measurements and species diversity measurements.

The first group depends on the numerical percentage composition of the species present in the sample; the more these species are represented by equal numbers of individuals, the more diverse is the fauna and the lower is the degree of dominance. As examples of this type of measurement, Sanders quotes the MacArthur "Broken Stick" model (1957), the Preston lognormal distribution (1948) and the Simpson index (1949).

The second type of diversity is determined by the actual number of species present in the sample. The larger the number of species in a sample, compared with the number of individuals, the greater is the diversity. As measurements of this type, Sanders (1968) lists the  $\alpha$  values of Fisher *et al.* (1943), the  $d$  values of Margalef (1957), the methods of Gleason (1922) and of Hessler and Sanders (1967), and his own rarefaction technique (Sanders, 1968).

Sanders developed his rarefaction method in order to eliminate the effects of sample size, and found that the technique gave more consistent results than any of the other species-diversity methods and compared favourably with the Shannon-Wiener information function. The method, slightly modified, is used here to compare the generic diversities of the 6 habitats (Fig. 5). Since the nematodes were only identified to genus, the diversities obtained are necessarily lower than the true values; however, they do serve to demonstrate the differences between the populations. It can be seen that the habitats fall into two groups, the muddy sediments having considerably lower diversities than the remainder. This agrees with the findings of Wieser (1960) and Hopper and Meyers (1967), who concluded that, due to the greater number of ecological niches, coarse sediments support more diverse nematode faunas than those in which the proportion of silt-clay is high.

The rarefaction curves in Fig. 5 are plotted with a logarithmic scale on the horizontal axis instead of the normal scale employed by Sanders. This allows the actual data to be compared directly with the theoretical curves for various values of Williams' diversity

index  $\alpha$ , (Fisher *et al.*, 1943) which are represented by dotted lines.

Sanders (1968) compared the various values of  $\alpha$  for different sized samples from the same population. He found that, when species diversity was high, the values of  $\alpha$  were higher in samples containing few individuals, decreased rapidly as sample size increased, and then decreased more slowly until an approximate equilibrium was reached. In samples with low species diversity, the tendency for higher values of  $\alpha$  with small samples either did not occur at all or was very

theless differ slightly in their subsidiary faunas. The pooled sample thus contains more rare genera than would be expected in a single sample from a single station.

The two clean, coarse habitats, 5 and 6, show an opposite trend. Here the number of genera is much higher at lower sample sizes than might be expected from the theoretical curves, corresponding with Sanders' findings, but decreases very rapidly above the 400 individual level. This again is almost certainly due to the pooling of results from several stations since,

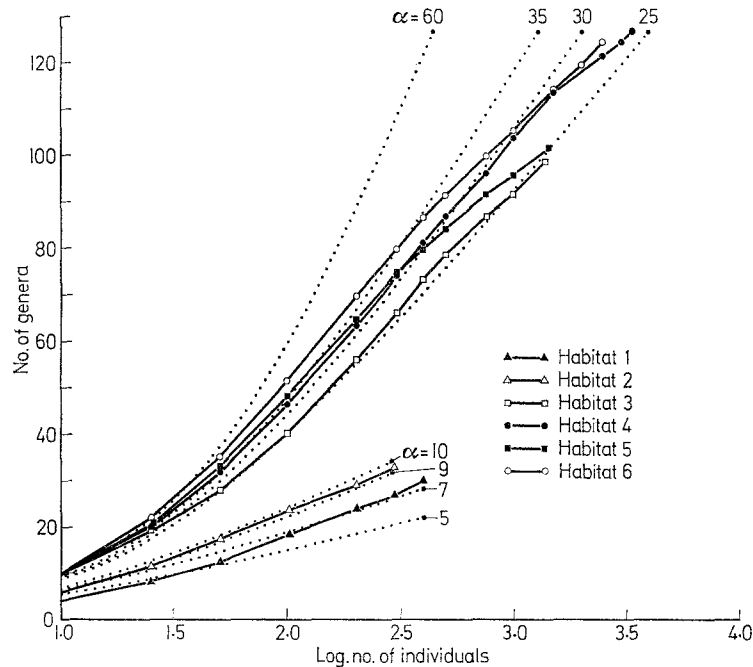


Fig. 5. Rarefaction curves for the fauna of each habitat. Modified after Sanders (1968), and compared with Williams' theoretical curves (Fisher *et al.*, 1943), which are represented by dotted lines

slight, and in some cases the values were slightly lower.

The curve for Habitat 2 (Fig. 5) lies between the curves for  $\alpha = 9$  and  $\alpha = 10$ , and follows these curves very closely, indicating good correlation with the theoretical distribution, apart from the 10 and 25 individual levels, where the theoretical values are slightly higher. The curve for Habitat 1, however, commences at a level equivalent to  $\alpha = 2.5$ , but rises steeply between the 25 and 100 individual levels, eventually exceeding  $\alpha = 7$  at the actual sample values. This can be related to the very high dominance of one genus (*Sabatieria*) combined with a high percentage of genera represented by only one or two individuals. This, in turn, is because the rarified sample represents the pooled individuals from stations which, although very similar in fauna and sediments, none-

in the case of these two habitats, the sub-dominant genera, although qualitatively often the same at each station, vary considerably in their degree of dominance. Thus, more genera are included in the lower sample sizes than might be expected from a single station.

Finally, Habitats 3 and 4 follow a similar pattern to 5 and 6, except that the terminal decrease in diversity compared with the theoretical curves is much less pronounced and appears only at the very end of the curves. These two habitats, and particularly Habitat 4, correspond much more closely with Sanders' findings than do any of the others except Habitat 2.

Ranked cumulative genus-abundance curves for the 6 habitats are shown in Fig. 6. These give an indication of the dominance diversity, or equitability, of the respective nematode faunas. This method of pres-

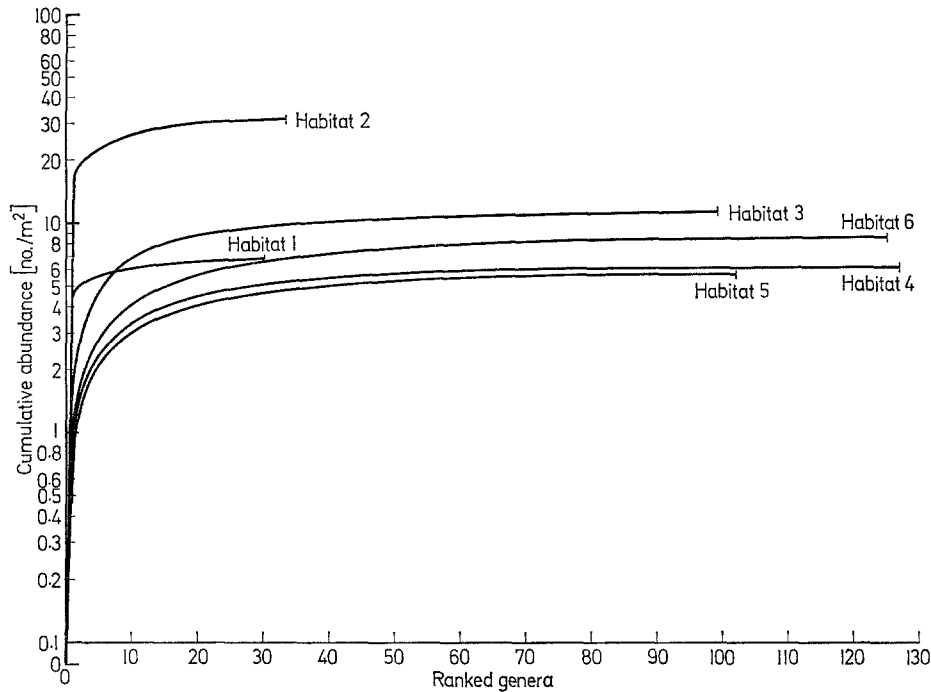


Fig. 6. Ranked cumulative genus-abundance curves for the 6 habitats in Liverpool Bay

entation has been chosen in preference to Lloyd and Ghelardi's equitability value  $\epsilon$  (Lloyd and Ghelardi, 1964) since Sanders (1968) found the latter to be markedly sample-size dependent. The present method depends on a comparison of the shapes of the curves rather than on a numerical value. The cumulative abundance has been plotted on a logarithmic scale in order to lessen the effect of the much greater density of nematodes in Habitat 2. It must again be stressed that these curves, based as they are on an analysis of the populations at the generic level, cannot be directly compared with species-abundance curves from other areas. Their function is simply to indicate the fundamental differences between populations from different types of sediment within the area studied. The very angular appearance of the curves for Habitats 1 and 2 show the low dominance diversities of both these populations due to the very high percentage of *Sabatieria* in the samples. The relative proportions of the subsidiary genera are very similar in both cases. The curve for Habitat 3 shows a much higher diversity, although there is still a slight angularity. The greatest dominance diversity is exhibited by the faunas of the coarse sediments of Habitats 4 and 5, where the proportion of rare species is also much higher.

#### Discussion

Several workers have recognised the correlation between specific types of benthic community and spe-

cific types of substratum. Amongst others, Ford (1923) remarked on the possibility of dividing sublittoral macrofauna communities into coarse and soft-bottom types, whilst Jones (1950) based his nomenclature of macrobenthic communities on the types of substrata which they inhabited. Gerlach (1953) noted a similar correlation between nematode faunas and sediment and distinguished between a considerable number of communities, the compositions of which were shown to depend on the prevailing combination of exposure, grain size, and organic content. He also studied in detail the nematode fauna of several types of habitat in the Bay of Kiel, Germany, listing the species encountered at each on the basis of percentage frequency and percentage dominance (Gerlach, 1958). However, in his final analysis, he considered only two broad types of habitat, the sandy and the muddy, as far as the sublittoral regions were concerned. Many similarities are apparent between the distributions encountered by Gerlach and those found in the present survey.

In his study of the Chilean marine nematodes, Wieser (1959a) divided the sublittoral habitats into 3 main types: soft bottom, coarse bottom, and secondary substrata. However, he remarks on the non-uniformity of these habitats, stating that they are "types of habitats, the nodes, as it were, of an interwoven pattern of environmental conditions". He notes that the number of habitats studied was incomplete, but suggests that these might represent faunal entities even if they were linked by transitional stages.

Wieser (1959a, b) found *Sabatieria* to be characteristic of muddy sediments whilst McIntyre (1961) found *Sabatieria cupida* and *Dorylaimopsis punctatus* prominent in mud samples from Loch Nevis and the Fladen Grounds off the Scottish coast. Off the Northumberland coast, Warwick and Buchanan (1970) found a definite mud fauna characterised by *Dorylaimopsis punctatus*, *Leptolaimus elegans* and *Sabatieria cupida*. *D. punctatus* and *L. elegans* were encountered only rarely during the present study, although *S. cupida* was common. The mud fauna of Liverpool Bay, thus, differs substantially from that found off Scotland and Northumberland, probably because of differences in the granulometry, chemical composition, and organic content of the sediments. It is probable that the main sources of the Liverpool Bay muds are the Rivers Dee and Mersey, together with erosion of the underlying boulder clay of parts of the Irish Sea (Sly, 1966). In addition, variable amounts of organic matter are derived from the Mersey and from sludge disposal in the Bay.

*Odontophora longisetosa* was prominent in Warwick and Buchanan's (1970) sandy habitat, which was actually a rather muddy sand, and the species was also found in similar sediments from the Liverpool Bay area, although it was dominant at only a few isolated stations.

The present investigations suggest that it is possible to identify a number of basic types of nematode population, the compositions of which are correlated with the granulometry of the substrata. These populations are not clearly delimited, but are linked by many transitional stages. Their faunal compositions are not rigid, but they have certain characteristic genera whose degree of dominance may be influenced by small variations in sediment composition. It, thus, seems preferable to think not so much in terms of discrete nematode populations, but rather in terms of a series of habitat nodes, each with a characteristic type of nematode fauna.

### Summary

1. In Liverpool Bay, sampling distinguished 6 main types of habitat on the basis of sediment composition: (1) mud and sandy mud; (2) very muddy sand; (3) muddy sand; (4) muddy coarse bottom (sand-gravel mixtures); (5) clean coarse bottom (sand-gravel mixtures); (6) clean sand.

2. Cluster analysis showed that those habitats which were most similar with regard to sediment type were also most similar faunistically.

3. *Sabatieria* was the dominant genus in the muds and muddy sands of Habitats 1, 2 and 3, the degree of dominance apparently being related to the silt content. Habitat 3 supported a much richer subsidiary fauna than the two very muddy habitats, *Odontophora*, *Neochromadora* and *Dichromadora* being

important genera. *Neochromadora* was dominant in the muddy coarse sediments of Habitat 4, with *Sabatieria* sub-dominant and *Odontophora* also common. *Desmodora* dominated the clean sediments of Habitats 5 and 6, with *Graphonema* sub-dominant in Habitat 5 but rather less abundant in Habitat 6.

4. Cluster analysis of the faunistic data from individual stations produced 5 main groups: (I) *Oncholaimus*-dominated stations; (II) stations associated at a low level of similarity, from mainly sandy areas with various dominant and sub-dominant genera; (III) *Sabatieria*-dominated stations from mud and sandy mud; (IV) mainly muddy, coarse sediments dominated by various combinations of *Sabatieria*, *Neochromadora* and *Odontophora*; (V) mainly *Desmodora* and *Desmodora-Graphonema*-dominated stations.

5. The muddy habitats, 1 and 2, supported a much less diverse fauna than did the other habitats.

6. Nematode populations are not well-defined entities, being linked by transitional faunas and with the relative abundance of their characteristic genera apparently influenced by small differences in sediment granulometry. It, therefore, seems more logical to think in terms of a number of different habitats, each with a characteristic type of nematode fauna.

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### Literature Cited

- Crickmore, M. J. and P. R. Kiff: Bed sediments: particle size. *In*: Out of sight out of mind; report of a working party on sludge disposal in Liverpool Bay, Vol. 2. Appendix 12. pp 273—286. London: Her Majesty's Stationary Office 1972.
- Field, J. G. and G. McFarlane: Numerical methods in marine ecology. I. A quantitative "similarity" analysis of rocky shore samples in False Bay, South Africa. *Zoologica africana*, **3**, 119—137 (1968).
- Fisher, R. A., A. S. Corbet and C. B. Williams: The relation between the number of species and the number of individuals in a random sample from an animal population. *J. Anim. Ecol.* **12**, 42—58 (1943).
- Ford, E.: Animal communities of the level sea bottom in the waters adjacent to Plymouth. *J. mar. biol. Ass. U.K.* **13**, 164—224 (1923).
- Gerlach, S. A.: Die Biozönotische Gliederung der Nematodenfauna an den Deutschen Küsten. *Z. Morphol. Ökol. Tiere* **41**, 411—512 (1953).
- Die Nematodenfauna der sublitoralen Region in der Kieler Bucht. *Kieler Meeresforsch.* **14**, 64—90 (1958).
- Gleason, H. A.: On the relation between species and area. *Ecology* **3**, 158—162 (1922).
- Hessler, R. R. and H. L. Sanders: Faunal diversity in the deep-sea. *Deep Sea Res.* **14**, 65—78 (1967).
- Hopper, B. E. and S. P. Meyers: Population studies on benthic nematodes within a subtropical seagrass community. *Mar. Biol.* **1**, 85—96 (1967).

- Jones, N. S.: Marine bottom communities. *Biol. Rev.* **25**, 283—313 (1950).
- Lloyd, M. and R. J. Ghelardi: A table for calculating the "equitability" component of species diversity. *J. Anim. Ecol.* **33**, 217—225 (1964).
- MacArthur, R. H.: On the relative abundance of bird species. *Proc. natn. Acad. Sci. U.S.A.* **43**, 293—295 (1957).
- Margalef, R.: La teoria de la información en ecología. *Mems R. Acad. Cienc. Artes Barcelona* **33**, 373—449 (1957).
- McIntyre, A. D.: Quantitative differences in the fauna of boreal mud associations. *J. mar. biol. Ass. U.K.* **41**, 599—616 (1961).
- Mountford, M. D.: An index of similarity and its application to classificatory problems. *In: Progress in soil zoology*, pp 43—50. Ed. by P. W. Murphy. Butterworth 1962.
- Preston, F. W.: The commonness and rarity of species. *Ecology* **29**, 254—283 (1948).
- Raabe, E. W.: Über den 'Affinitätswert' in der Pflanzensoziologie. *Vegetatio* **4**, 53—68 (1952).
- Rees, E. I. S., A. J. M. Walker and A. R. Ward: Benthic fauna in relation to sludge disposal. *In: Out of sight out of mind; report of a working party on sludge disposal in Liverpool Bay*, Vol. 2. Appendix 14. pp 297—343. London: Her Majesty's Stationary Office 1972.
- Sanders, H. L.: Marine benthic diversity: a comparative study. *Am. Nat.* **102**, 243—282 (1968).
- Simpson, E. H.: Measurement of diversity. *Nature, Lond.* **163**, p. 688 (1949).
- Sly, P. G.: Marine geological studies in the eastern Irish Sea and adjacent estuaries, with special reference to sedimentation in Liverpool Bay and River Mersey. Thesis to University of Liverpool (UK) 1966.
- Warwick, R. M. and J. B. Buchanan: The meiofauna off the coast of Northumberland. I. The structure of the nematode population. *J. mar. biol. Ass. U.K.* **50**, 129—146 (1970).
- Whittaker, R. H.: Dominance and diversity in land plant communities. *Science, N.Y.* **147**, 250—260 (1965).
- Wieser, W.: Free-living marine nematodes. IV. General Part. *Chile Reports 34. Acta Univ. lund (N.F. Avd. 2)* **55** (5), 1—111 (1959a).
- Free-living nematodes and other small invertebrates of Puget Sound beaches. *Univ. Wash. Publs Biol.* **19**, 1—179 (1959 b).
- Benthic studies in Buzzards Bay II. The meiofauna. *Limnol. Oceanogr.* **5**, 121—137 (1960).
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