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NEMATODE ASSOCIATIONS IN THE EXE ESTUARY

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(Text-fig. 1)

Sampling of the free-living nematode fauna in the Exe estuary has been conducted along four transects over an annual cycle, and measurements of the fluctuations in physico-chemical conditions in the sediments have been made. The transects were at Topsham, near the head of the estuary, Lympstone, about half way down the length of the estuary, Shelly Bank, in a sheltered position just inside the mouth of the estuary at Exmouth, and the exposed beach near Orcombe Point, just outside the mouth. The main factors governing distribution in the estuary appear to be salinity, the granulometric composition of the substrate with its associated variation in organic content, and the degree to which the sediment retains water during low tide. Salinity differences were the main cause of zonation at Topsham, but were only influential at the top and bottom of the Lympstone transect and the top of the Shelly Bank transect. Grain composition and drainage provide the main distribution barriers at Lympstone, Shelly Bank and Orcombe Point. Species confined to the bottom of the shore at Shelly Bank, where the sand at the upper levels is well drained, were found much higher up the shore at Orcombe Point. This is attributed to the fact that the water table remains permanent at Orcombe Point, drainage being restricted by a sandstone ledge which runs beneath the beach. Six major habitats are distinguished in the estuary. Each has its own characteristic association of nematode species, although there is some overlap between them. The species composition of these habitats is determined in part by the morphological adaptations which the nematodes exhibit, and these are discussed.

INTRODUCTION

The problems involved in the identification of freeliving marine nematodes have stood in the way of ecologists for some time. Although considerable advances are now being made on the continent (particularly in Kiel Bay and the Mediterranean) and in North America, our lack of knowledge of the British species is still lamentable. In order to rectify this state of affairs to some extent, a study of the distribution of nematodes in the Exe estuary was planned to cover as wide a spectrum of physical and chemical conditions as possible, ranging from fine muds with a low interstitial salinity at the head of the estuary to coarse sands with a high salinity at the mouth. It is hoped that the characterization of the fauna of various habitats in the estuary will form a basis for further ecological studies in other areas. Not surprisingly, a large proportion of the species found were new British records, and some new to science. The fourteen species of this latter group discussed in this paper are described elsewhere (Warwick, 1970).

DESCRIPTION OF STUDY AREA

A descriptive account of the estuary has been given by Holme (1949), to which little can be added. Four transects along the eastern shore were selected for quantitative sampling, two across the muddy shores at Topsham (To) and Lympstone (Ly), and two across the sands at Shelly Bank (Sh) and Orcombe Point (Op). The positions of these transects are shown in Fig. 1. The transects were sampled at five stations corresponding with M.H.W.S.T., M.H.W.N.T., M.T.L., M.L.W.N.T. and M.L.W.S.T., except at Topsham where at high tide water reaches the sea wall well above the mud surface and the M.H.W.S.T.

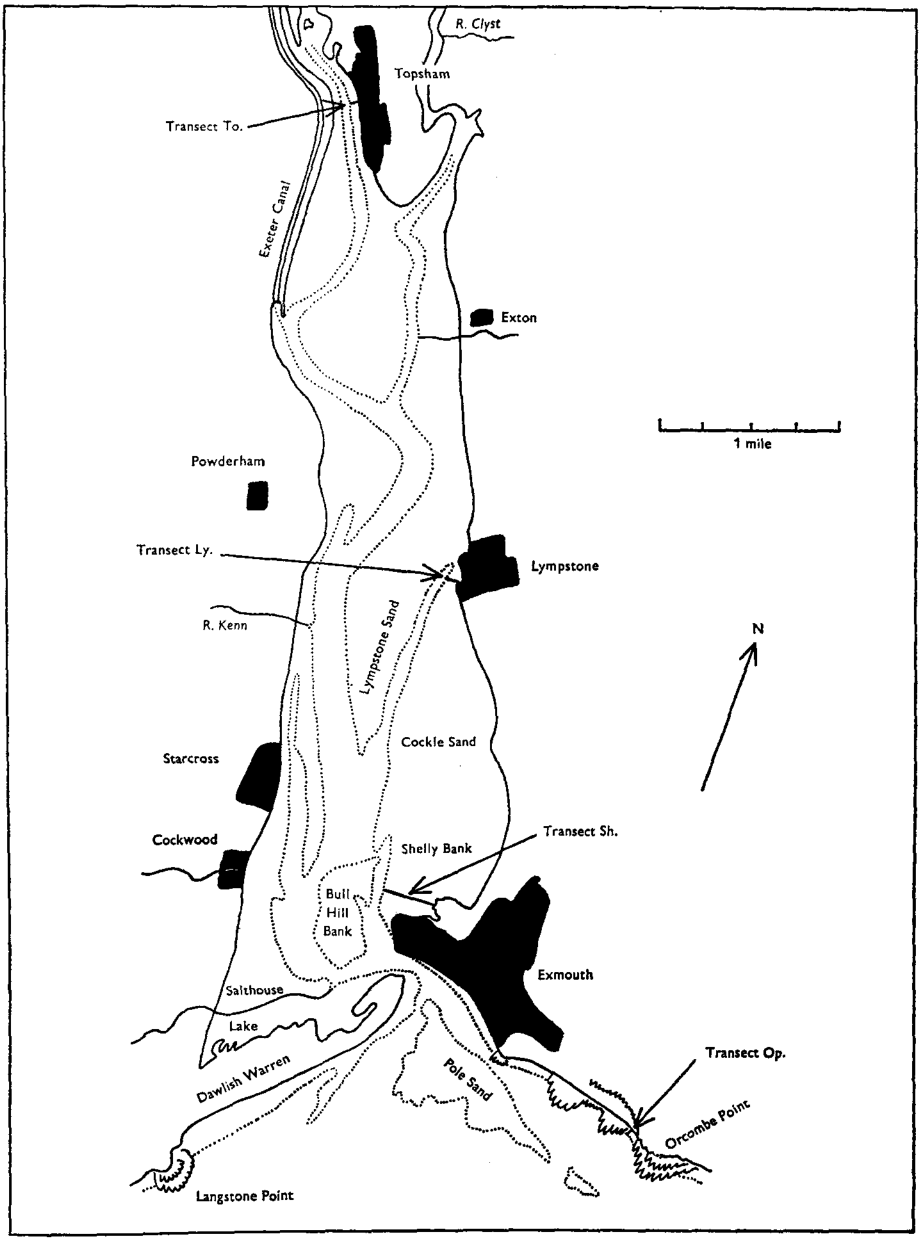

Fig. 1. Map of Exe estuary showing locations of transects.

level could not be sampled. Sampling was conducted at each station bimonthly between October 1966 and September 1967 at the time of the lowest monthly spring tides. Three cores of sediment, each of 3·5 cm internal diameter, were collected at each station for analysis of the nematode populations. A summary of the range of physical and chemical conditions along the transects is given in Table 1. All factors have been measured on each sampling day, except for the organic content of the sediments which was only estimated once. The Walkley and Black values have been multiplied by 2·4, and thus represent 'the percentage of available organic matter' (Morgans, 1956). Salinity is expressed as a percentage of standard seawater (Copenhagen), and thus represents the percentage 'dilution'.

TABLE 1. THE PHYSICAL AND CHEMICAL CONDITIONS ALONG THE FOUR TRANSECTS

See text for details of organic content and salinity measurements

		Median particle diameter (mm)	Organic content (%)	Interstitial salinity (% of standard s.w.)	H_2S depth (cm)	Water table depth (cm)
To	M.H.W.N.T.	< 0·063	6·43	1·1–44·6	0·2–7·0	0
	M.T.L.	< 0·063	7·06	1·7–42·6	0·1–10·0	0
	M.L.W.N.T.	< 0·063	7·99	0·6–38·1	0–5·5	0
	M.L.W.S.T.	< 0·063	7·15	0·3–27·1	0–2·5	0
Ly	M.H.W.S.T.	0·70–2·30	0·24	—	absent	absent
	M.H.W.N.T.	0·33–0·38	0·37	48·5–101·2	2·0–4·0	0–5·0
	M.T.L.	< 0·063	1·98	37·9–98·0	1·5–3·0	0
	M.L.W.N.T.	0·16–0·21	2·22	16·1–95·1	1·8–3·5	0
	M.L.W.S.T.	< 0·063	5·88	10·9–90·8	1·0–5·0	0
Sh	M.H.W.S.T.	0·27–0·76	0·09	—	absent	absent
	M.H.W.N.T.	0·17–0·27	0·39	80·1–100·6	3·0–7·5	0–4·0
	M.T.L.	0·23–1·20	0·09	—	absent	absent
	M.L.W.N.T.	0·33–1·15	0·06	—	absent	absent
	M.L.W.S.T.	0·28–2·30	0·09	80·4–96·8	absent	0
Op	M.H.W.S.T.	0·34–1·00	0·06	84·3–94·0	absent	3·0–absent
	M.H.W.N.T.	0·36–2·8	0·04	82·9–94·8	absent	0–16·2
	M.T.L.	0·38–1·75	0·06	81·1–98·9	absent	0–15·0
	M.L.W.N.T.	0·26–3·6	0·07	77·9–96·4	absent	0–11·0
	M.L.W.S.T.	0·21–0·27	0·09	79·3–98·6	absent	0

The Topsham transect was some 40 m long, and was situated 1 m seawards from the 'Victoria Jubilee Pier'. The sediment was of uniformly soft silt. During winter spates of the river the interstitial salinity is very reduced, and even in summer at M.H.W.N.T. a maximum of only 44 % sea water is reached, the concentration falling off towards the bottom of the shore. The mud is highly organic. The depth of the blackened H_2S layer depends largely on the scouring effect of the current, and during a sudden winter spate may be exposed on the surface of the mud.

The Lympstone transect extended 300 m across the gently sloping mud flats between the shore-line and the edge of a brackish water run-off channel which traverses the flats. The top 20 m of shore are more steeply shelving and the sediment is coarser than at the lower levels. The lower shore consists of fine mud, but there is some admixture of sand around M.L.W.N.T. Conditions are more marine in character than at Topsham, but the spate of the river still affects the interstitial salinity in winter. At M.H.W.S.T. the interstitial salinity could not be measured because the water table sinks below the sampling level during low tide. However, the presence of fresh water and terrestrial Dorylaimids, Rhabditids and a species of *Tripyla* in the sediment indicate that the film of water round the sand grains must be of a very reduced salinity. The organic content of the sediment is lower than at Topsham, but increases towards the bottom of the shore.

The Shelly Bank transect was 480 m long and passed across the sand flats from the base of a grassy bank on the edge of King George's Field, Exmouth, to the edge of the narrow channel dividing Shelly Bank from Bull Hill Bank.

At the three lower levels the sand varied considerably in grain composition from month to month, indicating a considerable degree of instability. The spate of the river only has a slight effect on the interstitial salinity, and there is no indication of a decrease in salinity down the shore. At M.H.W.S.T., however, similar salinity conditions exist as at the corresponding Lympstone station. The organic content of the sediment is very low, reaching a maximum in the finer sand at M.H.W.N.T.

The Orcombe Point transect stretched some 140 m seawards from the cliff face across Exmouth beach, and was situated at the eastern termination of the coast road to the western side of Orcombe Point. The beach is quite exposed, and the sand is highly mobile, particularly at the middle three tide levels. At M.L.W.S.T., however, the sand is always fine and relatively stable. A sandstone ledge runs beneath the beach and, being less permeable than the sands above it, restricts the drainage of the beach considerably. This causes the water table to remain relatively permanent. Interstitial salinities below 80% sea water are often recorded, and may be attributed to run-off from the land seeping under the beach and being prevented from sinking to deeper levels by the ledge. The organic content of the sediment is very low.

HORIZONTAL DISTRIBUTION OF THE NEMATODE SPECIES

No marked seasonal variation in the species composition or density of the populations could be detected, these being more affected by short term environmental vicissitudes. The relative abundances of species calculated below have therefore been taken as the mean over the sampling period. Species which occurred in less than 50% of the sampling months are not regarded as being characteristic of a station, and will in general be omitted from future discussion.

Topsham

The distribution of the characteristic species along the Topsham transect is given in Table 2. This shows that several species decrease markedly in dominance from M.H.W.N.T. to M.L.W.S.T., namely *Anoplostoma viviparum*, *Hypodontolaimus geophilus*, *Sabatieria vulgaris* and to a lesser degree *Theristus oxycercus*. It is suggested that these species are intolerant of the very low and fluctuating salinities which occur towards the bottom of the shore, since all other factors remain fairly uniform along the transect. Four other species are distributed fairly uniformly along the transect; *Theristus setosus*, *Desmolaimus fennicus*, *Adoncholaimus thalassophygas* and *Leptolaimus papilliger*. It is suggested that these species are very euryhaline. *Axonolaimus spinosus* shows a very marked increase in dominance towards the bottom of the transect and it may be that this species actually prefers very low salinities.

Little information is available for comparison with these results. The upper transect in the Blyth estuary (Capstick, 1959) most nearly resembles the Topsham transect, but only two species are common to both, namely *Anoplostoma viviparum* and *Adoncholaimus thalassophygas*. The latter was only present in small numbers in the Blyth, so that valid comparisons cannot be made. *Anoplostoma viviparum* showed a maximum population density in the Blyth around M.H.W.N.T., and its numbers fell off towards the top and bottom of the transect. This is in agreement with the present findings at Topsham where, however, levels above M.H.W.N.T. could not be sampled. In the Elbe estuary Riemann (1966) reports that *Theristus setosus* and *Axonolaimus spinosus* are both characteristic of the brackish water region. *Theristus setosus* commonly extended into the fresh water zone, whilst *Axonolaimus spinosus* was only a sporadic invader of this zone.

TABLE 2. DOMINANCE PERCENTAGES AND FREQUENCY OF OCCURRENCE OF CHARACTERISTIC SPECIES ON THE TOPSHAM TRANSECT

n/c = not a characteristic species (found on less than 50 % of occasions).
A = absent.

	Tide level			
Species	M.H.W.N.T.	M.T.L.	M.L.W.N.T.	M.L.W.S.T.
Anoplostoma viviparum (Bastian, 1865)	31·3 (6/6)	26·5 (4/6)	26·9 (6/6)	n/c
Hypodontolaimus geophilus (de Man, 1876)	21·4 (6/6)	n/c	2·2 (3/6)	n/c
Theristus setosus (Bütschli, 1874)	15·5 (6/6)	29·2 (6/6)	21·9 (6/6)	28·2 (4/5)
Sabatieria vulgaris (de Man, 1907)	13·6 (5/6)	9·9 (4/6)	6·6 (3/6)	6·0 (3/5)
Desmolaimus fennicus Schneider, 1926	5·5 (6/6)	n/c	4·5 (4/6)	n/c
Axonolaimus spinosus (Bütschli, 1874)	3·9 (4/6)	19·4 (5/6)	23·6 (5/6)	47·7 (5/5)
Theristus oxycercus (de Man, 1890)	0·8 (3/6)	n/c	n/c	n/c
Adoncholaimus thalassophygas (de Man, 1876)	n/c	3·5 (5/6)	4·1 (3/6)	n/c
Leptolaimus papilliger de Man, 1876	n/c	n/c	1·9 (4/6)	n/c
Rhabditid sp. 1	n/c	n/c	0·5 (3/6)	A

Lympstone

At Lympstone the substrate is less uniform in character, so that salinity is unlikely to be the only factor of importance in governing the pattern of distribution summarized in Table 3.

At M.H.W.S.T., where the sand is coarse and well drained, a characteristic fauna is found. *Bathylaimus stenolaimus*, *Eurystomina terricola* and *Tripyla* sp. are confined to this station, whilst *Oncholaimus brachycercus* has its maximum dominance here, but is also present in smaller numbers at M.H.W.N.T. These species must be tolerant of low salinity as well as considerable drying out of the sediment.

The presence of several other species shows a marked correlation with the occurrence of muddy-sand at M.H.W.N.T. and M.L.W.N.T. Species confined to M.H.W.N.T. are *Ascolaimus elongatus*, *Adoncholaimus fuscus*, *Theristus acer*, *Paracanthonchus tyrrhenicus*, *Metachromadora remanei* and *Enoploides spiculohamatus*. These species probably prefer

TABLE 3. DOMINANCE PERCENTAGES AND FREQUENCY OF OCCURRENCE OF CHARACTERISTIC SPECIES ON THE LYMPSTONE TRANSECT

Notation as in Table 2

Species	Tide level				
	M.H.W.S.T.	M.H.W.N.T.	M.T.L.	M.L.W.N.T.	M.L.W.S.T.
Oncholaimus brachycercus de Man, 1889	32·1 (6/6)	1·8 (4/6)	A	A	A
Bathylaimus stenolaimus Stekhoven & De Coninck, 1933	16·4 (3/6)	A	A	A	A
Eurystomina terricola (de Man, 1907)	8·7 (3/6)	A	A	A	A
Tripyla sp.	8·4 (3/6)	A	A	A	A
Ascolaimus elongatus (Bütschli, 1874)	n/c	52·2 (6/6)	A	A	A
Adoncholaimus fuscus (Bastian, 1865)	A	12·2 (6/6)	A	A	A
Theristus acer (Bastian, 1865)	A	7·1 (6/6)	n/c	A	n/c
Tripyloides gracilis (Ditlevsen, 1919)	A	7·0 (6/6)	n/c	1·7 (4/6)	n/c
Paracanthonchus tyrrhenicus (Brunetti, 1949)	n/c	5·2 (5/6)	A	A	n/c
Theristus setosus	A	2·6 (3/6)	n/c	n/c	4·1 (5/5)
Metachromadora remanei Gerlach, 1951	A	2·3 (3/6)	n/c	n/c	A
Axonolaimus paraspinosus Stekhoven & Adam, 1931	n/c	1·8 (3/6)	12·1 (6/6)	4·7 (6/6)	1·2 (3/5)
Viscosia viscosa (Bastian, 1865)	A	0·8 (3/6)	5·6 (6/6)	15·7 (6/6)	8·8 (5/5)
Enoploides spiculohamatus Schulz, 1932	A	0·7 (4/6)	A	A	A
Theristus oxycercus	A	0·6 (3/6)	14·7 (6/6)	8·5 (6/6)	8·0 (5/5)
Odontophora setosa (Allgén, 1929)	A	0·3 (3/6)	n/c	7·3 (6/6)	n/c
Sabatieria vulgaris	A	n/c	18·6 (6/6)	4·2 (5/6)	24·4 (5/5)
Hypodontolaimus ponticus (Filipjev, 1922)	A	n/c	13·2 (6/6)	20·2 (6/6)	2·5 (4/5)
Praeacanthonchus punctatus (Bastian, 1865)	A	n/c	12·1 (5/6)	3·9 (5/6)	A
Sphaerolaimus hirsutus Bastian, 1865	A	n/c	11·5 (5/6)	7·6 (6/6)	1·6 (5/5)
Anoplostoma viviparum	A	A	1·4 (4/6)	2·8 (4/6)	A
Dichromadora cephalata (Steiner, 1916)	A	A	1·4 (3/6)	A	n/c
Metachromadora vivipara (de Man, 1907)	A	n/c	0·6 (3·6)	0·5 (3/6)	A
Terschellingia longicaudata de Man, 1907	A	A	0·6 (3/6)	A	n/c
Atrochromadora microlaima (de Man, 1889)	A	A	n/c	6·2 (3/6)	4·7 (3/5)
Desmolaimus fennicus	A	A	n/c	1·5 (4/6)	n/c
Paralinhomoeus tenuicaudatus (Bütschli, 1874)	A	n/c	n/c	1·4 (3/6)	A
Calyptronema maxweberi (de Man, 1922)	A	n/c	n/c	1·1 (3/6)	A
Hypodontolaimus balticus (Schneider, 1906)	A	A	n/c	1·0 (3/6)	A
Terschellingia communis de Man, 1888	A	A	A	n/c	39·7 (5/5)

a greater admixture of sand than is found at M.L.W.N.T. *Tripyloides gracilis* and *Odontophora setosa* are common to both the muddy-sand stations, the former showing its maximum dominance at M.H.W.N.T. and the latter at M.L.W.N.T. *Desmolaimus fennicus*, *Paralinhomoeus tenuicaudatus*, *Calyptronema maxweberi* and *Hypodontolaimus balticus* are virtually confined to M.L.W.N.T., indicating their preference for the greater mud content. *Sabatieria vulgaris* shows a marked preference for pure mud, its maximum population density occurring at M.T.L. and M.L.W.S.T., with a reduction in density at M.L.W.N.T. and only the occasional specimen occurring at M.H.W.N.T. Several species appear to be less affected by substrate composition and show a maximum concentration near the middle of the transect, falling off in numbers towards the top and bottom. These include *Axonolaimus paraspinosus*, *Viscosia viscosa*, *Theristus oxycercus*, *Hypodontolaimus ponticus*, *Sphaerolaimus hirsutus*, *Anoplostoma viviparum*, *Dichromadora cephalata*, *Metachromadora vivipara* and *Terschellingia longicaudata*. A similar intertidal distribution was recorded by Capstick (1959) in the Blyth estuary for *Spirinia parasitifera*, *Anoplostoma viviparum* and *Hypodontolaimus balticus* on the lower transect, *Spirinia parasitifera*, *Anoplostoma viviparum* and *Paralinhomoeus lepturus* on the middle transect, and *Anoplostoma viviparum* and *Sabatieria* spp. on the upper transect. Interstitial salinities at the time of low spring tides were, as on the Lympstone transect, not considered sufficient to reduce the numbers of these species at the upper and lower ends of the transect. However, Capstick suggests that the lower salinity of the tidal water at neap tides, particularly when the river is in spate, may result in greater decreases in interstitial salinity at the lower end of the transect than the spring tide samples would indicate. A similar explanation probably applies in the Exe. Salinity stratification in the Blyth would result in a depression of the interstitial salinity at high water mark, since the less saline water is on the surface. In the Exe it is unlikely that salinity stratification occurs (Holme, 1949) and the causal factor may be the effect of substrate composition or a short term reduction of the interstitial salinity by rain. Such an explanation would account for the distribution of *Theristus setosus* on the transect, since it shows maximum population densities at M.H.W.N.T. and M.L.W.S.T. Capstick found similar concentrations of this species at the upper and lower ends of the upper transect in the Blyth, and suggests that it can tolerate, or may actually prefer, habitats subject to varying salinity. *Terschellingia communis* is markedly concentrated at M.L.W.S.T., possibly for similar reasons. It may be excluded from the upper shore because of its dependence on a pure mud substrate.

The zonation of species at Lympstone is therefore probably the result of the complex interaction of factors, mainly salinity, grain composition and the degree of water retention of the sediment. The suggested reasons for the zonation of individual species are necessarily only tentative, since no experimental evidence has been obtained to substantiate them.

Shelly Bank

The conditions prevailing at M.H.W.S.T. and M.H.W.N.T. are similar, but not identical, to those found at the corresponding levels at Lympstone. The fauna shows a like similarity (Table 4), and the same factors are probably responsible for governing distribution. *Bathylaimus stenolaimus* and *Eurystomina terricola* are again confined to M.H.W.S.T., as

TABLE 4. DOMINANCE PERCENTAGES AND FREQUENCY OF OCCURRENCE OF CHARACTERISTIC SPECIES ON THE SHELLY BANK TRANSECT

Notation as in Table 2

	Tide level				
Species	M.H.W.S.T.	M.H.W.N.T.	M.T.L.	M.L.W.N.T.	M.L.W.S.T.
Bathylaimus stenolaimus	55·8 (6/6)	n/c	A	n/c	n/c
Dorylaimid sp. 4	9·4 (4/6)	A	A	A	A
Oncholaimus brachycercus	8·0 (3/6)	1·4 (3/6)	n/c	0·4 (3/6)	0·6 (3/6)
Trefusia longicaudata de Man, 1893	6·2 (4/6)	13·4 (5/6)	n/c	A	A
Paracyatholaimus intermedius de Man, 1880	5·6 (5/6)	A	A	A	A
Eurystomia terricola	2·2 (4/6)	A	n/c	A	A
Enoplus schulzi Gerlach, 1952	1·6 (3/6)	A	A	A	A
Ascolaimus elongatus	n/c	17·7 (6/6)	A	n/c	n/c
Adoncholaimus fuscus	A	13·0 (5/6)	A	n/c	n/c
Bathylaimus assimilis de Man, 1922	A	10·0 (6/6)	A	A	A
Microlaimus honestus de Man, 1922	n/c	6·0 (4/6)	0·8 (3/6)	0·6 (3/6)	2·6 (5/6)
Microlaimus robustidens Stekhoven & De Coninck, 1933	A	5·0 (5/6)	A	A	n/c
Triplyoides gracilis	A	4·1 (5/6)	A	A	n/c
Paracanthonchus tyrrhenicus	A	3·9 (4/6)	9·9 (6/6)	6·0 (6/6)	1·4 (4/6)
Theristus normandicus (de Man, 1890)	n/c	3·5 (4/6)	n/c	3·5 (3/6)	5·4 (6/6)
Theristus acer	n/c	3·5 (5/6)	A	n/c	A
Metachromadora remanei	A	2·3 (3/6)	A	A	n/c
Desmodora communis (Bütschli, 1874)	A	2·3 (4/6)	A	n/c	n/c
Camacolaimus barbatus Warwick, 1970	A	0·7 (3/6)	n/c	A	0·4 (3/6)
Calyptronema maxweberi	n/c	0·4 (3/6)	A	A	A
Enoplolaimus litoralis Schulz, 1936	A	A	14·0 (6/6)	11·0 (5/6)	0·7 (4/6)
Mesacanthion africanthiforme Warwick, 1970	A	A	13·8 (6/6)	4·1 (5/6)	1·7 (6/6)
Dolicholaimus benepapillosus (Schulz, 1935)	A	A	13·8 (6/6)	5·8 (5/6)	n/c
Enoploides brunettii Gerlach, 1952	A	A	11·2 (6/6)	16·9 (6/6)	3·9 (6/6)
Bathepsilonema pustulatum Gerlach, 1952	A	A	4·4 (6/6)	n/c	A
Theristus psammoides Warwick, 1970	A	A	3·2 (6/6)	0·5 (3/6)	n/c
Spilophorella paradoxa (de Man, 1888)	A	A	2·8 (6/6)	n/c	n/c
Chromadora nudicapitata (Bastian, 1865)	A	n/c	2·1 (4/6)	5·1 (5/6)	2·7 (6/6)
Chromadorita tenuis (Schneider, 1906)	A	A	2·0 (3/6)	n/c	n/c
Monoposthia mirabilis (Schulz, 1932)	A	A	1·8 (4/6)	n/c	2·1 (5/6)
Enoplolaimus propinquus de Man, 1922	A	A	1·6 (3/6)	2·2 (4/6)	7·7 (5/6)
Hypodontolaimus schuurmans-stekhoveni Gerlach, 1951	A	A	1·6 (4/6)	2·0 (3/6)	0·6 (3/6)
Microlaimus parhonestus Gerlach, 1950	A	n/c	1·4 (4/6)	n/c	1·0 (4/6)
Theristus denticulatus Warwick, 1970	A	A	1·2 (3/6)	n/c	1·1 (3/6)

TABLE 4 *cont.*

Species	Tide level M.H.W.S.T.	M.H.W.N.T.	M.T.L.	M.L.W.N.T.	M.L.W.S.T.
Chromadorina germanica (Bütschli, 1874)	A	A	1·2 (5/6)	A	A
Enoplus brevis Bastian, 1865	A	A	1·2 (4/6)	3·5 (6/6)	A
Leptolaimus ampullaceus Warwick, 1970	A	A	0·8 (4/6)	1·2 (4/6)	0·6 (3/6)
Monoposthia costata (Bastian, 1865)	A	A	0·7 (4/6)	n/c	0·7 (3/6)
Diplopeltis incisus (Southern, 1914)	A	A	0·3 (3/6)	2·0 (5/6)	n/c
Oncholaimus campylocercoides De Coninck & Stekhoven, 1933	A	A	A	1·5 (4/6)	0·5 (5/6)
Chromadorita tentabunda (de Man, 1890)	A	A	n/c	0·8 (3/6)	n/c
Desmodora pontica Filipjev, 1922	A	n/c	n/c	0·7 (4/6)	1·3 (4/6)
Mesacanthion hirsutum Gerlach, 1952	A	A	n/c	0·6 (3·6)	2·0 (6/6)
Dichromadora hyalocheile Stekhoven & De Coninck, 1933	A	A	n/c	0·6 (3/6)	3·4 (6/6)
Sigmophora litoralis (Schulz, 1938)	A	A	A	0·3 (3/6)	2·7 (5/6)
Paracanthonchus opheliae Warwick, 1970	A	A	n/c	n/c	20·1 (6/6)
Sigmophora rufum Cobb, 1933	A	A	A	n/c	9·4 (6/6)
Viscosia cobbi Filipjev, 1918	A	A	n/c	n/c	5·5 (6/6)
Epacanthion gorgonocephalum Warwick, 1970	A	A	A	n/c	3·3 (5/6)
Sabatieria celtica Southern, 1914	A	A	n/c	n/c	0·9 (4/6)
Xyala striata Cobb, 1920	A	A	n/c	n/c	0·9 (3/6)
Microlaimus spirifer Warwick, 1970	A	A	n/c	n/c	0·9 (3/6)
Stephanolaimus elegans Ditlevsen, 1919	A	A	A	A	0·7 (4/6)
Odontophora villoti Luc & De Coninck, 1959	A	A	A	A	0·7 (4/6)
Spirinia laevis (Bastian, 1865)	A	A	n/c	n/c	0·6 (3/6)
Euchromadora vulgaris (Bastian, 1865)	A	A	A	n/c	0·5 (3/6)
Anticoma acuminata (Eberth, 1863)	A	A	A	A	0·5 (4/6)
Chromaspirina parapontica Luc & De Coninck, 1959	A	A	A	A	0·5 (3/6)
Paralinhomoeus uniovarium Warwick, 1970	A	A	A	A	0·4 (3/6)
Convexolaimus teissieri Vitiello, 1967	A	A	A	A	0·3 (3/6)
Theristus mirabilis (Stekhoven & De Coninck, 1933)	A	A	A	A	0·3 (3/6)
Pomponema reducta Warwick, 1970	A	A	A	A	0·3 (3/6)
Eumorpholaimus sabulicolus Schulz, 1932	A	A	A	A	0·2 (3/6)
Enoplolaimus denticulatus Warwick, 1970	A	A	A	A	0·2 (3/6)

are three additional species, Dorylaimid sp. 4, *Paracyatholaimus intermedius* and *Enoplus schulzi*. *Oncholaimus brachycercus* shows a maximum at this level, but is found occasionally down the remainder of the transect. *Ascolaimus elongatus*, *Adoncholaimus fuscus*, *Theristus acer* and *Metachromadora remanei* once more show a maximum at M.H.W.N.T., as do the additional species *Bathylaimus assimilis*, *Microlaimus robustidens*, *Tripyloides gracilis*, *Desmodora communis* and *Calyptronema maxweberi*. *Trefusia longicaudata* has its maximum population at this level, but is also common at M.H.W.S.T.

The zonation between M.T.L. and M.L.W.S.T. is probably the most interesting. The sand at these three stations is variable in grain composition, and the only constant difference between them is their degree of water retention. At M.L.W.S.T. the water table is permanently on the surface, and at M.T.L. it sinks well below the sampling level (20 cm). At M.L.W.N.T. the sand also dries out, but is uncovered for shorter periods than M.T.L., and thus probably retains a thicker film of water round its particles. Thus we find a gradation from typically littoral species which do not require a permanent water table at M.T.L. to more typically sublittoral species requiring a permanent water table at M.L.W.S.T. Species belonging to the former group, decreasing in abundance from M.T.L. to M.L.W.S.T. include *Enoplolaimus litoralis*, *Mesacanthion africanthiforme*, *Dolicholaimus benepapillosus*, *Bathepsilonema pustulatum*, *Theristus psammoides*, *Spilophorella paradoxa*, *Chromadorita tenuis* and *Chromadorina germanica*. Species increasing in abundance towards M.L.W.S.T. include *Enoplolaimus propinquus*, *Desmodora pontica*, *Mesacanthion hirsutum*, *Dichromadora hyalocheile*, *Sigmophora litoralis*, *Paracanthonchus opheliae*, *Sigmophora rufum*, *Viscosia cobbi*, *Epacanthion gorgonocephalum*, *Sabatieria celtica*, *Xyala striata*, *Microlaimus spirifer*, *Stephanolaimus elegans*, *Odontophora villoti*, *Spirinia laevis*, *Euchromadora vulgaris*, *Anticoma acuminata*, *Chromaspirina parapontica*, *Paralinhomoeus uniovarium*, *Convexolaimus teissieri*, *Theristus mirabilis*, *Pomponema reducta*, *Eumorpholaimus sabulicolus*, *Enoplolaimus denticulatus*, *Microlaimus honestus* and *Theristus normandicus*. The remaining species appear to be independent of the water content of the sediment, and their distribution is somewhat sporadic. These include *Enoploides brunettii*, *Chromadora nudicapitata*, *Monoposthia mirabilis*, *Hypodontolaimus schuurmansstekhoveni*, *Microlaimus parhonestus*, *Theristus denticulatus*, *Enoplus brevis*, *Leptolaimus ampullaceus*, *Monoposthia costata*, *Diplopeltis incisus*, *Oncholaimus campylocercoides* and *Chromadorita tentabunda*.

Orcombe Point

Being an exposed shore, wave action causes the M.H.W.S.T. level to be washed with saline water at almost every tide, and the fauna typical of this level at Lympstone and Shelly Bank is absent. Because of the permanent water table, many species confined to the bottom of the shore at Shelly Bank are found much higher up the beach at Orcombe Point. At M.L.W.S.T., where the sediment is much finer and more stable, a different fauna altogether is found.

Of the typically littoral species found at Shelly Bank only *Enoplolaimus litoralis* is present at Orcombe Point, where it is confined to M.H.W.S.T. (Table 5). Species which apparently depend on a permanent water table are found at all tide levels. *Enoplolaimus propinquus* has its maximum dominance at M.H.W.S.T., *Epacanthion gorgonocephalum* and

Enoplolaimus denticulatus are present in varying abundance between M.H.W.N.T. and M.L.W.N.T., and *Mesacanthion hirsutum* between M.H.W.N.T. and M.L.W.S.T. *Microlaimus spirifer* is concentrated at M.H.W.N.T. and *Sigmophora rufum* at M.T.L. and M.L.W.S.T. *Enoploides brunettii* is again rather evenly distributed, but is absent from M.H.W.S.T. *Axonolaimus hexapilus*, concentrated at M.T.L., was not found at Shelly Bank, and may be

TABLE 5. DOMINANCE PERCENTAGES AND FREQUENCY OF OCCURRENCE OF CHARACTERISTIC SPECIES ON THE ORCOMBE POINT TRANSECT

Notation as in Table 2

Species	Tide level M.H.W.S.T.	M.H.W.N.T.	M.T.L.	M.L.W.N.T.	M.L.W.S.T.
Enoplolaimus propinquus	27·3 (4/6)	n/c	2·4 (3/6)	n/c	11·3 (3/4)
Enoplolaimus litoralis	24·7 (4/6)	n/c	n/c	A	n/c
Epacanthion gorgonocephalum	n/c	31·4 (6/6)	38·5 (6/6)	11·0 (3/5)	n/c
Ascolaimus elongatus	A	20·4 (6/6)	2·8 (3/6)	A	n/c
Enoplolaimus denticulatus	A	19·1 (6/6)	6·1 (5/6)	7·1 (3/5)	A
Enoploides brunettii	A	4·9 (5/6)	8·4 (4/6)	n/c	1·8 (3/4)
Microlaimus spirifer	A	3·9 (3/6)	n/c	A	A
Bathylaimus paralongisetosus Stekhoven & De Coninck, 1933	n/c	2·8 (3/6)	n/c	n/c	3·9 (4/4)
Mesacanthion hirsutum	n/c	2·5 (3/6)	6·8 (3/6)	8·7 (3/5)	9·0 (4/4)
Axonolaimus hexapilus Wieser & Hopper, 1967	n/c	n/c	5·2 (3/6)	n/c	A
Sigmophora rufum	A	n/c	5·1 (4/6)	n/c	7·2 (3/4)
Viscosia cobbi	A	A	n/c	n/c	11·5 (3/4)
Chromaspirina inglisi Warwick, 1970	A	A	A	A	8·5 (4/4)
Axonolaimus orcombensis Warwick, 1970	A	A	A	n/c	6·6 (4/4)
Pomponema reducta	A	n/c	A	A	6·6 (4/4)
Sigmophora litoralis	A	A	n/c	n/c	5·8 (3/4)
Oncholaimellus calvadosicus de Man, 1890	A	A	A	A	4·0 (3/4)
Gammanema conicaudata Gerlach, 1952	A	A	A	A	3·9 (4/4)
Theristus interstitialis Warwick, 1970	A	A	A	A	3·4 (3/4)
Theristus normandicus	A	A	A	A	2·4 (2/4)
Spirinia laevis	A	A	A	n/c	2·3 (4/4)
Theristus mirabilis	A	A	A	A	1·5 (2/4)
Leptonemella aphanothecae Gerlach, 1950	A	A	A	A	1·1 (2/4)
Dichromadora hyalocheile	A	A	n/c	n/c	1·1 (2/4)
Xyala striata	A	A	A	n/c	0·8 (2/4)
Neochromadora tecta Gerlach, 1951	A	A	n/c	n/c	0·8 (2/4)
Leptolaimus ampullaceus	A	A	A	A	0·7 (2/4)

characteristic of exposed shores. Its only other known locality is clean sand at M.T.L. on a beach at Virginia Key, Florida, U.S.A. (Wieser & Hopper, 1967), but the degree of exposure here is not noted. The fauna at M.L.W.S.T. is probably determined by the fine and stable nature of the sediment. Whilst *Bathylaimus paralongisetosus* is also a characteristic species at M.H.W.N.T., the remainder of the species is confined to M.L.W.S.T. only. Included in this group are *Viscosia cobbi*, *Chromaspirina inglisi*, *Axonolaimus orcombensis*, *Pomponema reducta*, *Sigmophora litoralis*, *Oncholaimellus calvadosicus*, *Gammanema coni-*

caudata, Theristus interstitialis, T. normandicus, Spirinia laevis, Theristus mirabilis, Leptonemella aphanothecae, Dichromadora hyalocheile, Xyala striata, Neochromadora tecta and *Leptolaimus ampullaceus*.

CHARACTERIZATION OF HABITATS

The three main factors governing distribution within the estuary appear to be salinity, grain composition and the degree to which the sediment retains water. The shore of the estuary can be divided into six fairly well defined habitats with respect to these three major factors, although some overlap exists between them. Each habitat is characterized by a typical association of nematode species. The habitats are as follows.

(1) Fine mud, usually with a low interstitial salinity, retaining a permanent water table (To all stations, Ly M.T.L. and M.L.W.S.T.).
(2) Muddy-sand retaining a permanent water table, salinity sometimes slightly reduced (Ly M.H.W.N.T. and M.L.W.N.T., Sh M.H.W.N.T.).
(3) Coarse sand at M.H.W.S.T. drying out between spring tides, interstitial salinity very low due to seepage of coastal subsoil water – Küstengrundwasser of German literature (Ly M.H.W.S.T., Sh M.H.W.S.T.).
(4) Coarse littoral sands drying out at low tide, not subject to lowering of interstitial salinity (Sh M.T.L. and M.L.W.N.T.).
(5) Coarse sands with a more or less permanent high salinity water table (Sh M.L.W.S.T., Op M.H.W.S.T., M.H.W.N.T., M.T.L. and M.L.W.N.T.).
(6) Fine stable sand retaining a permanent high salinity water table (Op M.L.W.S.T.).

The M.L.W.N.T. level at Lympstone, although included in group 2, is in many respects intermediate between 1 and 2. Sh M.L.W.N.T. and Op M.H.W.S.T. are similarly intermediate between 4 and 5, both in physico-chemical properties and faunal composition. Several species are shared between two or more habitats, particularly between 4 and 5. The species typical of these habitats are listed in Table 6.

The reason why each habitat is characterized by a typical association of species is made clearer if the morphological and physiological adaptations of the animals are considered. Salinity tolerance is governed by physiological adaptations which are not investigated here. Distribution in relation to grain composition and drainage is more likely to be affected by morphological adaptations. As Wieser (1959) points out, the correlation between morphological character and habitat type can either be proved definitely by experiment or inferred by establishing a co-existence in the field between habitat type and morphological organization. Only the latter approach is adopted here. The main morphological features which have drawn attention are the feeding types (as deduced from the structure of the buccal cavity), the length of the cephalic and body setae, the body length, the cuticular pattern and the presence or absence of ocellar pigments. For comparative purposes these have been divided into the class intervals delimited by Wieser (1959). The percentage occurrence of each feature for the species characteristic of the six habitats is given in Table 7.

Feeding types

Marine nematodes have been divided into four feeding types by Wieser (1953). These divisions have been adhered to, with some reservations, in the later works of Wieser (1959, 1960), King (1962), Hopper & Meyers (1967*a*, *b*), Tietjen (1969) and Warwick &

Buchanan (1970). They are: Group 1A, selective deposit feeders; Group 1B, non-selective deposit feeders; Group 2A, epigrowth feeders and Group 2B, capable of predation but probably omnivores.

TABLE 6. LISTS OF SPECIES TYPICAL OF THE SIX HABITATS

Habitat 1		
Anoplostoma viviparum	*Hypodontolaimus geophilus*	*Theristus setosus*
Sabatieria vulgaris	*Desmolaimus fennicus*	*Axonolaimus spinosus*
Theristus oxycercus	*Adoncholaimus thalassophygas*	*Leptolaimus papilliger*
Rhabditid sp. 1	*Hypodontolaimus ponticus*	*Axonolaimus paraspinosus*
Praeacanthonchus punctatus	*Sphaerolaimus hirsutus*	*Viscosia viscosa*
Dichromadora cephalata	*Metachromadora vivipara*	*Terschellingia longicaudata*
Tershellingia communis	*Atrochromadora microlaima*	
Habitat 2		
Ascolaimus elongatus	*Adoncholaimus fuscus*	*Theristus acer*
Triploides gracilis	*Paracanthonchus tyrrhenicus*	*Theristus setosus*
Metachromadora remanei	*Axonolaimus paraspinosus*	*Oncholaimus brachycercus*
Viscosia viscosa	*Enoploides spiculohamatus*	*Theristus oxycercus*
Odontophora setosa	*Trefusia longicaudata*	*Bathylaimus assimilis*
Microlaimus honestus	*Microlaimus robustidens*	*Theristus normandicus*
Desmodora communis	*Camacolaimus barbatus*	*Calyptronema maxweberi*
Habitat 3		
Oncholaimus brachycercus	*Bathylaimus stenolaimus*	*Eurystomina terricola*
Tripyla sp.	Dorylaimid sp. 4	*Trefusia longicaudata*
Paracyatholaimus intermedius	*Enoplus schulzi*	
Habitat 4		
Enoplaimus litoralis	*Mesacanthion africanthiforme*	*Dolicholaimus benepapillosus*
Enoploides brunettii	*Paracanthonchus tyrrhenicus*	*Bathepsilonema pustulatum*
Theristus psammoides	*Spilophorella paradoxa*	*Chromadora nudicapitata*
Chromadorita tenuis	*Monoposthia mirabilis*	*Hypodontolaimus schuurmans-stekhoveni*
Enoplolaimus propinquus	*Microlaimus parhonestus*	*Theristus denticulatus*
Chromadorina germanica	*Enoplus brevis*	*Microlaimus honestus*
Leptolaimus ampullaceus	*Monoposthia costata*	*Diplopeltis incisus*
Habitat 5		
Paracanthonchus opheliae	*Sigmophora rufum*	*Enoplaimus propinquus*
Viscosia cobbi	*Theristus normandicus*	*Enoploides brunettii*
Dichromadora hyalocheile	*Epacanthion gorgonocephalum*	*Chromadora nudicapitata*
Sigmophora litoralis	*Microlaimus honestus*	*Monoposthia mirabilis*
Mesacanthion hirsutum	*Mesacanthion africanthiforme*	*Paracanthonchus tyrrhenicus*
Desmodora pontica	*Theristus denticulatus*	*Microlaimus parhonestus*
Sabatieria celtica	*Xyala striata*	*Microlaimus spirifer*
Monoposthia costata	*Enoplolaimus litoralis*	*Stephanolaimus elegans*
Odontophora villoti	*Spirinia laevis*	*Oncholaimus brachycercus*
Leptolaimus ampullaceus	*Euchromadora vulgaris*	*Hypodontolaimus schuurmans-stekhoveni*
Anticoma acuminata	*Oncholaimus campylocercoides*	*Chromaspirina parapontica*
Paralinhomoeus uniovarium	*Camacolaimus barbatus*	*Convexolaimus teissieri*
Theristus mirabilis	*Pomponema reducta*	*Eumorpholaimus sabulicolus*
Enoplolaimus denticulatus	*Ascolaimus elongatus*	*Bathylaimus paralongisetosus*
Axonolaimus hexapilus		
Habitat 6		
Viscosia cobbi	*Enoplolaimus propinquus*	*Mesacanthion hirsutum*
Chromaspirina inglisi	*Sigmophora rufum*	*Axonolaimus orcombensis*
Pomponema reducta	*Sigmophora litoralis*	*Oncholaimellus calvadosicus*
Bathylaimus paralongisetosus	*Gammanema conicaudata*	*Theristus interstitialis*
Theristus normandicus	*Spirinia laevis*	*Enoploides brunettii*
Theristus mirabilis	*Leptonemella aphanothecae*	*Dichromadora hyalocheile*
Xyala striata	*Neochromadora tecta*	*Leptolaimus ampullaceus*

The distribution of feeding types in the six habitats agrees broadly with the findings of Wieser (1959) and King (1962). There is an increase in the dominance of predatory (or omnivorous) species in sandy sediments and greater numbers of deposit feeders in mud. This is clearly a reflection of the amount and type of food present. In habitat 1, pure mud, group 1 B (non-selective deposit feeders) is dominant as expected, and the

TABLE 7. PERCENTAGE OCCURRENCE OF SELECTED MORPHOLOGICAL CHARACTERS IN THE SIX HABITATS

	Habitat					
	1	2	3	4	5	6
Feeding types						
1 A	20	5	12	10	5	10
1 B	35	48	12	14	26	29
2 A	25	24	25	48	35	14
2 B	20	24	50	29	35	48
Setal length (μ)						
0–5	47	29	17	10	5	0
5–10	37	38	33	38	30	19
10–20	5	24	33	19	33	29
20–40	11	5	17	19	19	33
> 40	0	5	0	14	14	19
Body length (mm)						
0·5–1	26	0	17	33	14	5
1·1–1·5	37	38	17	38	21	33
1·6–2	26	29	33	10	19	24
2·1–5	11	33	33	14	47	38
> 5	0	0	0	5	0	0
Cuticular pattern						
Smooth	35	43	88	33	30	29
Striated	35	52	12	33	44	48
Punctuated	30	5	0	33	26	24
Visual pigments						
Concentrated	0	0	0	10	7	0
Scattered	0	0	0	10	2	0
None	100	100	100	81	91	100

other groups are present in roughly equal proportions. In muddy-sand group 1 B shows an even greater dominance and the reduction in numbers of 1 A (selective deposit feeders) is marked. This group feeds by sucking in fine deposits and it is evident that such deposits are scarce. Epigrowth feeders and carnivores are present in roughly equal proportions as in the fine muds. In habitat 3 (sand bathed in coastal subsoil water) food in the form of fine deposits is scarce. Carnivores predominate and groups 1 A and 1 B are uncommon, the epigrowth feeders occupying an intermediate position. In well drained sands (habitat 4), water at low tide is confined to a thin film round the sand grains. The fauna must live in this film and consequently group 2 A predominate, browsing epigrowths off the surface of the grains. Active carnivores are restricted in their movements and are consequently not quite so abundant as in other sandy habitats. Both types of deposit feeder are scarce. In coarse sand retaining a water table (habitat 5) groups 1 B and 2 B are not so restricted in their movements. The carnivores are now equal in dominance with the epigrowth feeders and the non-selective deposit feeders also increase in proportion. The absence of fine soft deposits still precludes group 1A. In habitat 6 the sediment is fine enough for non-selective deposit feeders, and these now become second in importance to the carnivores.

Setal length

Lengths recorded in Table 7 represent the longest setae, either cephalic or somatic. It has long been established that the length of setae is greater in sandy habitats than in all others (Cobb, 1893; Gerlach, 1953; Wieser, 1959). Long setae have generally been considered to provide an anchorage for the nematodes in this highly dynamic habitat. In the present study the 0–5 μ class predominate in fine mud and the 5–10 μ class in muddy-sands. The 5–10 and 10–20 μ classes co-dominate in habitat 3, the 5–10 μ class dominates in habitat 4, the 10–20 μ in habitat 5 and the 20–40 μ in habitat 6. The shorter length of setae in habitat 4 reflects the fact that the animals are confined at low tide to a thin film of water round the sand grains and do not lie freely in the interstitial spaces.

Body length

The size of the animals inhabiting a sediment is related to the size of the interstitial spaces. Mud-dwelling species are generally small, although large species are also present which are capable of active burrowing by displacement of the substratum. In sand the nematodes are truly interstitial, and a more direct relationship is found between their size and the nature of the interstitial space. In habitats 1 and 2 the dominant size class is 1·1–1·5 mm, and in habitat 3 the 1·6–2·0 and 2·1–5·0 mm classes co-dominate. Small species predominate again in habitat 4 although the sediment is coarse, and this again can be attributed to the fact that during low tide their living space is much smaller than is superficially apparent. Habitat 5, as expected, shows a marked dominance of the 2·1–5 mm class, and in habitat 6 where the substrate is finer this dominance is not so marked and the smaller species are almost equally numerous.

Cuticular pattern

Wieser (1959) concludes from the available data from several geographic regions that there is no close correlation between habitat and cuticular pattern. The present investigation bears this out. The complexity of the cuticular pattern can probably be attributed solely to the mechanics of the body (Inglis, 1964) and has little ecological significance.

Visual pigmentation

Few nematodes with true ocelli were encountered, these being more typical of algal habitats. The only species with any concentration of pigment at all were found in coarse sandy habitats, but this is probably a function of the greater faunal diversity of this habitat and of little ecological significance.

To summarize, species from muddy sediments tend to be small with short setae and mainly deposit feeders, whilst species from sand tend to be predators or epigrowth feeders with long bodies and setae. When sands are well drained the living space is effectively reduced, with a consequent reduction in body and setal length.

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