

# VERTICAL AND HORIZONTAL DISTRIBUTION OF FREE-LIVING MARINE NEMATODES FROM STRANGFORD LOUGH, NORTHERN IRELAND.

by

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## Résumé

Répartition verticale et horizontale de Nématodes libres marins  
de Strangford Lough, Irlande du Nord.

L'auteur analyse la faune de Nématodes trouvée en trois stations différentes d'une plage intercotidale à Strangford Lough, Irlande du Nord, pour déterminer la répartition verticale et horizontale des espèces. La population étudiée se tient très près de la surface du sédiment, pendant toute l'année, avec la plus grande partie de la population totale, au niveau du premier centimètre de sédiment. La fluctuation saisonnière de la répartition verticale est rapportée à la variation de profondeur de la couche anaérobic, au-dessous de la surface du sable. La répartition horizontale est déterminée par la résistance des Nématodes aux conditions fluctuantes de l'environnement, par leur affinité pour un sable riche en vase et en détritux et par la nourriture disponible.

Les variations des caractères morphologiques des Nématodes sont discutées, en fonction de l'habitat.

## Introduction

Previous reviews of the meiofauna inhabiting marine sediments have drawn attention to the importance of these animals to a full understanding of the energy budget of the sea (McIntyre, 1969). Although the free-living nematodes are the major constituent of the meiofauna (Wieser, 1960; McIntyre, 1964), there is not a great deal of detailed information available concerning their ecology. Some primarily taxonomic papers provide ecological information as a secondary product but frequently the characterisation of the habitat is poor. Most of the recent ecological studies on marine nematodes from Europe deal with exposed sandy beaches (Gray and Rieger, 1971; Harris, 1972 a, 1972 b; McIntyre and Murison, 1973) or subtidal communities (Boucher, 1972, 1973; Lorenzen, 1974; Ward, 1973; Warwick and Buchanon, 1970, 1971). Capstick (1959) studied nematode-salinity relationships in the mud and muddy sand of the Blyth

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Estuary and Warwick (1971) discussed nematode associations in sheltered beaches of the Exe Estuary.

In another paper (Platt, in press) data was reported on the population densities and species composition of nematode populations from a sheltered intertidal sandflat in Strangford Lough, Northern Ireland. Platt (1973) gives descriptions of new species from the area. This paper presents further data on the vertical and horizontal distribution of these populations.

#### Methods and environmental features

The three stations, Station A (at approximately neap high tide level), Station B (at approximately mid-tide level) and Station C (at approximately neap low tide level), were sampled during low tide at monthly intervals. The general features of the sediments may be summarised as follows. The deposits consisted of very fine sand, with a median grain size of 125  $\mu\text{m}$  at Station A, 146  $\mu\text{m}$  at Station B and 196  $\mu\text{m}$  at Station C, which were well sorted and contained much detritus at Stations A and B, with more at Station A than B. The water table and hydrogen sulphide layer were close to the surface throughout the year. There was a fluctuating salinity and temperature regime. The range of salinity values recorded was 27.9 ppt to 38.1 ppt and the range of temperature values recorded was 2.1° to 23.7° C. The organic carbon content ranged from 0.08 to 0.31 percent («Walkey and Black values»). The pH ranged from 6.9 to 7.9 units. *Zostera nana* was abundant at Stations A and B but absent from Station C.

Three replicate sediment cores were taken to obtain samples of the fauna to a depth of 5 cm. They were divided into five one-centimetre layers and the nematodes extracted by a decantation technique. Based on trial samples the extraction efficiency was determined to be 90-95 percent.

For a fuller description of the sampling methods and environmental features refer to Platt (in press).

#### VERTICAL DISTRIBUTION

The vertical distribution of the nematode population for each month is shown in Table 1. From the data, it can be seen that for most samples, over half of the total population was found within the upper one-centimetre layer and that a greater percentage was found in the upper layers during the summer months.

Analysis of variance indicated a significant correlation (at the 5 percent level at Station A and B, and the 10 percent level at Station C) between the percentage of the fauna in the various sediment layers and the depth below the surface of the hydrogen sulphide deposits. The seasonal variation in the depth to which a proportion

of the nematodes penetrated clearly follows the fluctuations in the depth of the hydrogen sulphide layer (Fig. 1). However, since the vertical distribution data are only for one-centimetre cuts, it was not possible to determine just how close to the surface the majority of the animals may have been confined, especially during the summer months.

TABLE 1  
Percentage of total nematode populations present in each depth zone throughout the year.

Depth	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Station A</i>												
0-1 cm	44.7	62.7	73.4	98.4	87.2	81.0	85.9	96.4	69.8	66.3	68.1	52.2
1-2 cm	34.7	23.0	21.4	1.2	4.6	16.1	13.5	2.4	22.4	28.7	20.5	34.7
2-3 cm	13.4	13.1	4.7	0.2	1.1	2.6	0.6	1.2	5.3	4.0	5.9	10.6
3-4 cm	4.8	1.2	0.5	0.2	1.6	0.2	0.0	0.0	2.5	1.0	4.4	1.5
4-5 cm	2.4	0.0	0.0	0.0	5.5	0.1	0.0	0.0	0.0	0.0	1.1	1.0
<i>Station B</i>												
0-1 cm	45.4	59.8	71.3	77.1	72.7	98.1	86.5	89.1	58.1	78.3	83.4	52.2
1-2 cm	27.7	17.2	19.2	10.7	7.7	1.9	5.4	6.9	24.1	13.7	9.9	15.9
2-3 cm	15.3	12.6	7.1	2.9	5.4	0.0	3.5	3.2	10.9	3.6	4.3	19.2
3-4 cm	8.0	3.5	1.2	5.5	7.3	0.0	1.5	0.8	3.7	1.9	1.6	7.4
4-5 cm	3.6	6.9	1.2	3.8	6.9	0.0	3.1	0.0	3.2	2.5	0.8	5.3
<i>Station C</i>												
0-1 cm	51.5	61.5	64.8	88.2	86.8	83.4	86.3	75.0	88.9	84.5	65.3	65.8
1-2 cm	30.8	8.6	16.1	7.1	5.8	7.4	6.9	13.7	6.6	8.2	14.3	8.5
2-3 cm	7.1	14.2	4.7	2.2	4.5	3.8	3.1	4.9	2.2	4.2	11.4	6.2
3-4 cm	6.5	8.6	8.4	0.5	2.1	2.6	2.0	3.5	0.5	1.9	5.7	9.8
4-5 cm	4.1	7.1	6.0	2.0	0.8	2.8	1.7	2.9	1.8	1.2	3.3	9.7

The annual vertical distribution figures for the selected species (Table 2) show that they fall into three groups, corresponding to those described by Boucher (1972). Some were virtually restricted to the upper 0-1 cm layer (Group 1), with over 80 percent of their total numbers at this level, e.g. *Axonolaimus paraspinosus* and *Neochromadora poecilosoma*. Other species decreased in numbers more gradually (Group 2), with less than 80 percent but more than 20 percent of their total numbers present in the top layer, e.g. *Spirinia parasitifera* and *Metalinhomoeus filiformis*. Relatively few species had their greatest density below the 0-1 cm depth layer (Group 3), with less than 20 percent of their total numbers in the top layer, e.g. *Microlaimus cuanensis*. The commoner species comprising 90 percent of the population at each station have been separated into these three groups (Appendix Table). Of these species 53 percent belong to Group 1, 40 percent to Group 2 and only 7 percent to Group 3. The species comprising the remaining 10 percent of the population at each station are considered too rare to be assigned to a group with confidence.

TABLE 2  
Percentage vertical distribution for selected species  
from all three sampling stations for the whole year.

Species	Depth (cm)					Total numbers
	0-1	1-2	2-3	3-4	4-5	
<i>Axonolaimus paraspinosus</i> Stekhoven and Adam	93.0	6.0	1.0	0.0	0.0	186
<i>Metalinhomoeus filiformis</i> (De Man)	58.2	34.5	4.5	1.4	1.4	368
<i>Theristus pertenuis</i> Bresslau and Stekhoven	44.2	22.5	10.8	15.6	6.9	231
<i>Theristus riemanni</i> Platt	29.8	36.2	17.0	4.8	12.2	188
<i>Theristus setosus</i> (Bütschli)	97.5	2.1	0.2	0.0	0.2	474
<i>Theristus normandicus</i> (De Man)	93.6	4.9	1.1	0.0	0.4	264
<i>Cobbia trefusiaeformis</i> (De Man)	21.2	40.0	22.3	11.8	4.7	85
<i>Metachromadora suecica</i> (Allgen)	92.6	4.6	1.7	0.4	0.7	543
<i>Spirinia parasitifera</i> (Bastian)	58.0	28.7	9.1	2.8	1.4	2,959
<i>Microlaimus cuanensis</i> Platt	11.9	26.1	23.2	14.9	23.9	134
<i>Monoposthia mirabilis</i> Schulz	72.2	13.4	6.4	4.9	3.1	327
<i>Nudora bipapillata</i> Platt	97.2	2.6	0.2	0.0	0.0	471
<i>Neochromadora poecilosoma</i> (De Man)	98.7	0.5	0.4	0.2	0.2	1,098

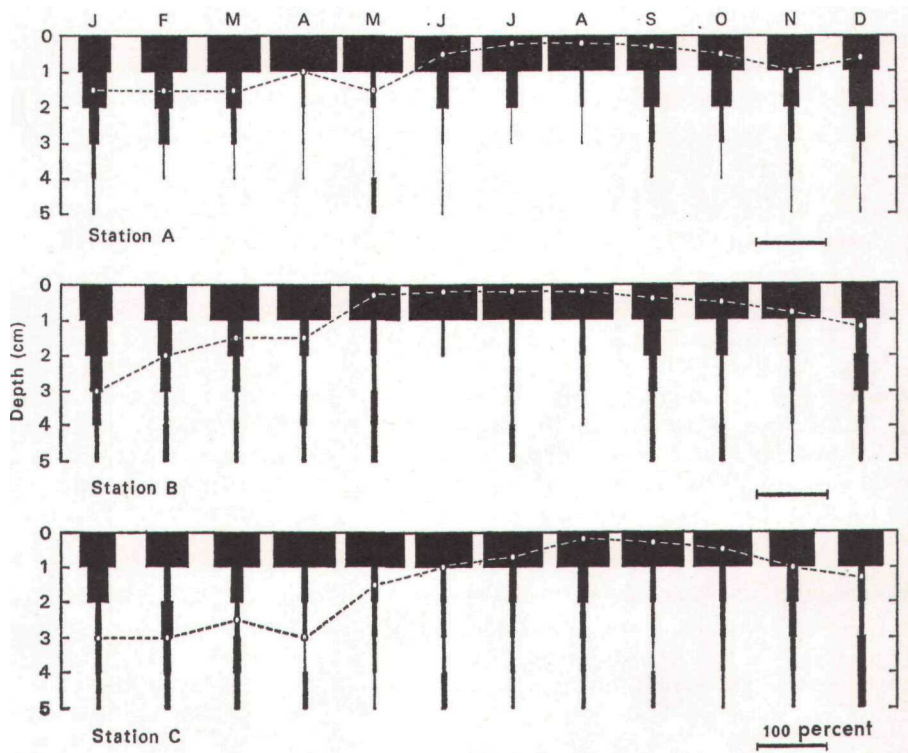


FIG. 1.

The percentage distribution of the monthly nematode populations from each station. Depth of the blackened hydrogen sulphide layer beneath the sediment surface is indicated by the white circles and hatched line.

The data relating to the seasonal variation in the depth distribution for individual species is too voluminous to be reported here. However, the majority of species for which sufficient data is available generally followed the trend exhibited by the total population. Species in Group 1 had their population concentrated in the top 0-1 cm layer throughout the year but with some slightly deeper penetration in the winter months. Group 2 species tended to have their population centres at higher levels during the summer months. Species in Group 3 had their population centres below the 0-1 cm layer throughout the year.

On the basis of the form of the buccal cavity, Wieser (1953) separated the free-living marine nematodes into four feeding groups: selective and non-selective deposit feeders, epigrowth feeders (i.e. feeding on material attached to particles) and predator/omnivores. Combining the individual numbers of those species comprising 90 percent of the total population in each layer, in the upper 0-1 cm layer, 30.0 percent were epigrowth feeders, 54.4 percent were deposit feeders (both selective and non-selective) and 15.6 percent were predator/omnivores. In the next layer (1-2 cm), the proportion of epigrowth feeders was less at 16.6 percent, while 73.1 percent were deposit feeders and 10.3 percent were predator/omnivores. In the next three layers, the percentage of deposit feeders decreased progressively with increasing depth, from 65.9 percent, through 52.0 percent to 47.8 percent. The percentage of epigrowth feeders increased from 25.1 percent, through 32.3 to 39.8 percent for each 1 cm depth increase. The percentage of the predator/omnivores for these layers were 9.0, 15.7 and 12.4 percent.

### HORIZONTAL DISTRIBUTION

When the numbers of individual species from each of the three stations are compared (see Appendix Table), a number of interesting horizontal distribution patterns are revealed. The explanation for each distribution pattern appears to depend on a combination of an ability to withstand fluctuating environmental conditions and an affinity for sediments with a high percentage of silt and detritus, possibly associated with the presence of food material for certain species.

Some species were eurytopic, being found at substantial population densities at all stations; *Axonolaimus paraspinosus*, *Desmolaimus fennicus*, *Eleutheroilaimus stenosoma*, *Southernia zosterae*, *Neochromadora poecilosoma*, *Chromadora nudicapitata*, *Enoploides spiculohamatus*, *Viscosia glabra* and *Viscosia viscosia*. Some species showed a degree of preference for the more stable conditions found lower on the shore or an affinity for slightly coarser sediments (i.e. recorded in greatest numbers at Station C); *Theristus normandicus*, *Metachromadora snecica*, *Microlaimus marinus*, *Innocuanema tentabundum*, *Viscosia* sp.1 and *Oncholaimellus mediterraneus*. Other

species were able to withstand the unstable environmental conditions higher on the shore and exhibited a preference for finer sediments (i.e. found predominately at Station A); *Odontophora setosa*, *Sphaerolaimus balticus*, *Theristus setosus*, *Spirinia parasitifera*, *Nudora bipapillata*, *Sabatieria cupida* and *Chromadora macrolaimus*. Fewer species had their largest numbers at the mid-tide station, presumably as a result of an affinity for finer sediments but an inability to withstand the more extreme conditions higher on the shore; *Ascolaimus elongatus*, *Leptolaimus septempapillatus*, *Theristus pette-*

TABLE 3  
Percentage occurrence of morphological characters of the species from each station.

Character	Station		
	A	B	C
<i>Body length (mm)</i>			
0.5 - 1.0	7	17	13
1.0 - 1.5	25	26	55
1.5 - 2.0	15	26	14
2.0 - 5.0	53	31	18
<i>Somatic setae (µm)</i>			
0 - 5	74	71	45
5 - 10	10	14	33
10 - 20	12	8	19
20+	4	7	3
<i>Feeding type</i>			
1A - selective deposit	40	23	8
1B - non-selective deposit	28	33	17
2A - epigrowth	24	30	53
2B - omnivores/predators	8	14	22
<i>Posterior oesophagus structure</i>			
Bulb (Bu)	80	58	57
Posterior thickening (T)	5	10	13
Cylindrical throughout (abs.)	15	32	30

*nuis*, *Microlaimus zosterae*, *Microlaimus cuanensis* and *Desmodora communis*.

The other species were truly stenotopic. Some had an affinity for the conditions found higher on the shore; *Bathylaimus assimilis*, *Metalinhomoeus filiformis*, *Paralinhomoeus tenuicaudata*, *Theristus longus*, *Theristus riemanni*, *Cobbia trefusiaeformis*, *Metachromadora vivipera*, *Hypodontolaimus balticus*, *Hypodontolaimus* sp. 1, *Atrochromadora microlaima* and *Anoplostoma viviparum*. Other species showed a preference for conditions found at Station C; *Theristus mirabilis*, *Theristus invagiferous*, *Theristus biggi*, *Chromaspirina* sp. 1, *Chromaspirina* sp. 2, *Spirinia laevis*, *Leptonemella* sp. 1, *Monoposthia costata*, *Monoposthia mirabilis*, *Richtersia inaequalis*, *Prochromadorella septempapillata*, *Pomponema sedecima*, *Paracan-*

*thonchus caecus*, *Paracanthochus longus*, *Paracanthochus tyrrenicus*, *Enoplolaimus propinquus*, *Chaetonema riemanni*, *Viscosia lan-grunensis* and *Viscosia* sp. 1.

Differences in the species composition between the three stations were also examined by a consideration of various morphological characters of the fauna in relation to features of the habitats. The percentage occurrence of the morphological characters discussed here is shown in Table 3; the classes correspond to those of Wieser (1959). The characters of each species recorded from Strangford Lough are given in the Appendix Table.

### 1. Body length.

Habitats with larger interstitial spaces, primarily a result of a greater size of particles in the sediment, may be expected to possess larger animals. However, in this study, the greatest percentage of larger animals was found at Station A, the habitat with the smallest mean grain size. Most of the sediment at all the stations was below the suggested 'critical grain size' of 200  $\mu\text{m}$  (Wieser, 1959) which may restrict the distribution of certain animals. At Station A and to a lesser degree at Station B, many nematodes probably move by pushing aside the sand grains rather than moving between them, so a larger size may be an advantage. At Station C, there is a larger fraction of the sediment with particle sizes larger than 200  $\mu\text{m}$  and there is less detritus to block the interstitial spaces so that more animals may be truly interstitial. At this site, the majority of the animals were in the 1.0-1.5 mm size category.

### 2. Somatic setae.

The distribution of setal length classes between the three stations (based on the length of the longest somatic setae, including cervical setae but not the cephalic, labial or terminal setae) showed Station C to be less dominated by animals with short (0.5  $\mu\text{m}$ ) setae than Station A or B. However, the situation may be confused by the large numbers of the dominant species *Spirinia parasitifera* (with short setae) occurring at Stations A and B. The presence of this species at these two localities can be explained adequately by factors other than setal length, such as its large size and feeding habits, which are more important in influencing its distribution. When this species is not included in the analysis, the difference observed between the three areas is less marked.

Greater setal length has often been associated with unstable sandy habitats (Wieser, 1959; Warwick, 1971) where increased anchorage prevents the animals from being removed from the sediment. The overall dominance in the areas studied here of forms with short setae is thus a result of the prevailing calm conditions.

### 3. Feeding type and oesophagus structure.

The four feeding-type groups described by Wieser (1953), based primarily on morphology, are defined as: 1A, selective deposit feeders, buccal cavity absent or greatly reduced and unarmed; 1B, non-selective deposit feeders, large conical or cup-shaped buccal cavity, unarmed; 2A, epigrowth feeders, buccal cavity present armed with small to medium, hollow or solid teeth; 2B, omnivorous with capacity for predation and predators, buccal cavity heavily armed with well cuticularised teeth and/or mandibles.

The feeding group to which the genus *Spirinia* is designated is worthy of special note since it is such a dominant animal in the Strangford Lough samples. Wieser (1953) originally referred this taxon erroneously to group 2A but subsequently rectified this in Wieser and Kanwisher (1961), placing it in group 1A. However, some authors have since maintained the genus in group 2A, possibly because of the minute teeth. The distribution of *Spirinia parasitifera* from Strangford Lough supports it as a deposit feeder since it was most numerous where detritus was abundant and was not restricted to the upper one-centimetre depth zone as were many 'true' epigrowth feeders.

Deposit feeders dominated the fauna at Stations A and B, while epigrowth feeders dominated at Station C. The greater percentage abundance of group 1A (selective deposit feeders) at Station A compared with Station B is associated with the finer grain size and higher detritus content of the deposits. The proportion of epigrowth feeders increased from high to low tide in accordance with the expected distribution of the microflora (Meadows and Anderson, 1966, 1968). Likewise, the proportion of the omnivore/carnivore group 2B increased from high to low tide reflecting increasing scarcity of fine deposits for groups 1A and 1B.

A comparison of the oesophagus structures possessed by species of the four feeding groups suggests an association between oesophagus type and assumed feeding activity. Nematodes require a valve and pumping mechanism to fill the intestine against the higher turgor pressure of the body cavity; it is the oesophagus which provides this mechanism. As shown in Table 3, the majority of nematodes from the Strangford Lough habitats possess a modification of the simple cylindrical oesophagus; either a posterior thickening or a muscular bulb is present, which acts as a combined accessory valve and pump. The association between feeding type and oesophagus structure appears to be related to the number of times the buccal cavity may be expected to come into contact with the external environment during feeding activity. In group 2B (omnivore/predators) 71 percent of the species had a simple oesophagus with no modifications and only 29 percent had a bulb. These animals feed either by swallowing whole or by holding on to the prey and sucking out the body contents. It may be expected, as is common in predatory animals, that feeding activity may be a relatively infrequent occurrence and that, when the lips and buccal cavity are fixed on to the



prey during feeding, the lumen of the buccal cavity will not be in contact with the external environment.

On the other hand, species of the group 1A (selective deposit feeders) must rely more continually on the sucking power of their oesophageal structures to obtain their food. In this group, only 33 percent lacked a modified oesophagus, 22 percent had a posterior thickening and 45 percent possessed a true bulb. Non-selective deposit feeders (group 1B) have a buccal cavity, so that once a sample of 'food' has been taken, the lips can close and the material subsequently pumped into the intestine. In this group, only 22 percent had a bulb, 26 percent possessed a posterior thickening and 52 percent had a cylindrical oesophagus. The epigrowth feeders (group 2A) scrape food material off surfaces and munch of their food can be expected to be microflora of relatively low calorific value. Thus, although possessing a buccal cavity, they must feed frequently in order to consume sufficient food material for their needs so that the buccal cavity is liable to be open to the external environment for longer periods of time. In this group, only 7 percent lacked any oesophageal modification, 23 percent had a posterior thickening and 70 percent possessed an oesophageal bulb.

## DISCUSSION

Several authors have shown that nematode populations reduce in density with increasing depth below the sediment surface (Wieser and Kanwisher, 1961; Teal and Wieser, 1966; Tietjen, 1969; Grey and Rieger, 1971) and suggested vertical gradients in various physical and biotic factors as possible causes. In Strangford Lough sites, vertical gradients in salinity, temperature and grain size were probably too slight to account for the sharp reduction in nematode numbers with depth. The quantity of potential food, as represented by the carbon content values and the presence of detritus, varied little with depth. Interstitial water content was not studied in detail but, in the sediments studied, it was unlikely to vary sufficiently with depth to exert much influence on the nematode densities. The most probable explanation is the reduced amount of available oxygen below the surface layers, associated with the presence of reducing conditions in the hydrogen sulphide layer. Oxygen diffusion rate measurements (Platt, in press) indicated that there was a reduction in the order of 25-50 percent in the availability of oxygen between the surface and the 1 cm depth level during periods of tidal emersion. Clearly, many species must possess some ability to withstand the periods of low oxygen availability during low tide in view of the proximity of the R.P.D. layer to the surface, especially in the summer months. The importance of the R.P.D. layer was pointed out by Ott and Machan (1971). However, in a saltmarsh, Teal and Wieser (1966) found large numbers of nematodes living in the presence of high concentrations of hydrogen sulphide and Wieser and Kanwisher (1961) indicated that species differ in their ability

to survive anaerobic conditions. The absence of substantial numbers of nematodes able to survive in the deeper layers of the hydrogen sulphide deposits indicates some other factor, perhaps the quality of the available food, may be playing a part in limiting the presence of such species.

The few species that had their population centred below the upper layer (i.e. vertical distribution Group 3), may be representatives of the thibios (Boaden and Platt, 1971), the meiofaunal group normally associated with reducing conditions found deep in marine sediments.

The initial reduction in the percentage abundance of epigrowth feeders between the 0-1 cm layer and the 1-2 cm was probably due to the reduction with increasing depth of the numbers of micro-organisms attached to sand grains (Meadows and Anderson, 1966). Certain species, especially those belonging to the family Chromadoridae, were almost entirely restricted to the upper one-centimetre layer. However, below the 2 cm level, the percentage of assumed epigrowth feeders in the population increased again, due mainly to the distribution patterns of the genera *Microlaimus*, *Monoposthia*, *Paracanthochus* and *Pomponema*. It may be that these animals are not utilising the same food material as other epigrowth feeders. *Paracanthochus*, *Pomponema* and *Monoposthia* species, with their well developed buccal armature, may be able to feed as omnivores or predators, while the relatively small buccal cavities of the *Microlaimus* species may enable them to be successful deposit feeders. Clearly, more detailed information on the feeding biology of the marine nematodes is needed to clarify the situation.

The horizontal distribution of the nematodes indicates that a number of physical and biotic factors were involved in determining the specific faunal assemblage of each habitat. The grain size composition of the sediment played a large part in dictating the general morphological form of the animals. Thus, at Station A, large species with short somatic setae predominated, while at Station C there was a greater percentage of smaller forms with slightly longer somatic setae. The nature of the available food also played a part in determining species composition; deposit feeders predominated higher on the shore and epigrowth feeders predominated lower on the shore. A further important factor was the physiological adaptation of certain species to short and long term fluctuations in the physical factors of the habitat; species at Station A must be able to tolerate wide ranges in salinity and temperature while species of Station C were exposed to less extreme conditions.

Little data is available from comparable areas for a discussion of the horizontal distribution of species found in Strangford Lough. From Buzzards Bay, Wieser (1960) recorded the genera *Pomponema* and *Ondotophora* as characteristic of sandy sediments; the distribution of *Pomponema sedecima* in Strangford Lough supports this, being found in greatest numbers at Station C, but does not agree for the *Ondotophora* species found in this study. Wieser also recorded *Sabatieria*, *Sphaerolaimus* and *Metalinhomoeus* as characteristic of silt or mud fauna; the distribution of allied forms from Strangford Lough was similar. Hopper and Meyers (1967) recorded

*Spirinia parasitifera* as a dominant species in a turtle grass flat with a sediment of 'fine, loose, sandy silt'; in Strangford Lough, this species was found at the station with the finest sediments.

Warwick and Buchanan (1970) recorded a number of species from off the Northumberland coast as being eurytopic or displaying an affinity for silt or sand. The Strangford Lough data agrees with their designation of *Sabatieria cupida* as having an affinity for silt; but, in Strangford Lough, *Theristus setosus* also showed a marked affinity for finer sediments, whereas in the Northumberland populations this species was more typical of sandy habitats. However, all these localities are sublittoral and thus more stable than the intertidal environments studied here.

In a study of the distribution of intertidal marine nematodes from the Exe estuary (Warwick, 1971) the species typical of each of six habitats were listed and their distribution was related to salinity, grain size composition and the amount of water retained by the sediment. In general, for those species common to both the Exe estuary and Strangford Lough, their distribution showed similar trends in relation to environment stability (as expressed by salinity and water table characteristics) and grain size composition. For example, in the Exe estuary, *Monoposthia mirabilis* was described as typical of habitats with coarser sediments and a permanent high salinity water table: in Strangford Lough, this species was typical of Station C, with the largest grain size and relatively stable conditions. *Anoplostoma viviparum* was typical of fine mud with low interstitial salinity in the Exe estuary; in Strangford Lough, it was predominant at Station A, with the finest sediments and the widest range of environmental conditions.

In summary, whereas the vertical distribution of the intertidal nematodes from Strangford Lough may be related primarily to the depth below the surface of the anaerobic layer, the horizontal distribution is seen to be the result of a specific combination of the degree of environmental stability, the nature of the available food and the particle size composition of the sediment. A more detailed elucidation of the role played by these various factors is difficult without experimental evidence.

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#### Summary

The nematode fauna from three stations on an intertidal sandflat in Strangford Lough, Northern Ireland, has been analysed for the vertical and horizontal species distribution. The nematode populations were close to the sediment surface throughout the year, with the majority of the total population in the upper one-centimetre layer of the sediment. Seasonal fluctuations in the vertical distribution is related to variation in the depth of the anaerobic layer beneath the sand surface. Horizontal distribution of the nematode fauna is determined by the ability of the nematodes to withstand fluctuating environmental conditions, on their affinity for sediments with a high silt and detritus content and the nature of the available food material. An examination is also made of the morphological characters of the nematode species in relation to habitat characteristics.

## REFERENCES

- BOADEN, P.J.S. and PLATT, H.M., 1971. — Daily migration patterns in an intertidal meiobenthic community. *Thalassia Jugosl.*, 7 (1), pp. 1-12.
- BOUCHER, G., 1972. — Distribution quantitative et qualitative des Nématodes d'une station de vase terrigène côtière de Banyuls-sur-Mer. *Cah. Biol. Mar.*, 13, pp. 457-474.
- BOUCHER, G., 1973. — Premières données écologiques sur les nématodes libres marins d'une station de vase côtière de Banyuls. *Vie Milieu*, 23 (1B), pp. 69-100.
- CAPSTICK, C.K., 1959. — The distribution of free-living nematodes in relation to salinity in the middle and upper reaches of the River Blyth estuary. *J. Anim. Ecol.*, 28, pp. 189-210.
- GRAY, J.S. and RIEGER, R.M., 1971. — A quantitative study of the meiofauna of an exposed sandy beach, at Robin Hood's Bay, Yorkshire. *J. mar. biol. Ass. U.K.*, 51, pp. 1-19.
- HARRIS, R.P., 1972 a. — The distribution and ecology of the interstitial meiofauna of a sandy beach at Whitsand Bay, East Cornwall. *J. mar. biol. Ass. U.K.*, 52, pp. 1-18.
- HARRIS, R.P., 1972 b. — Seasonal changes in the meiofauna population of an intertidal sandy beach. *J. mar. biol. Ass. U.K.*, 52, pp. 389-403.
- HOPPER, B.E. and MEYERS, S.P., 1967. — Population studies on benthic nematodes within a subtropical seagrass community. *Mar. Biol.*, 1, pp. 85-96.
- LORENZEN, S., 1974. — Die Nematodenfauna der sublittoralen regim der Deutschen Bucht, Insbesondere im Titan. Abwassergebiet bei Helgoland. *Veröff. Inst. Meeresforsch. Bremerh.*, 14, pp. 305-327.
- MCINTYRE, A.D., 1964. — Meiobenthos of sub-littoral muds. *J. mar. biol. Ass. U.K.*, 44, pp. 665-674.
- MCINTYRE, A.D., 1969. — Ecology of marine meiobenthos. *Biol. Rev.*, 44, pp. 245-290.
- MCINTYRE, A.D. and MURISON, D.J., 1973. — The meiofauna of a flatfish nursery ground. *J. mar. biol. Ass. U.K.*, 53, pp. 93-118.
- MEADOWS, P.S. and ANDERSON, J.G., 1966. — Micro-organisms attached to marine and freshwater sand grains. *Nature*, 212, pp. 1059-1060.
- MEADOWS, P.S. and ANDERSON, J.G., 1968. — Micro-organisms attached to marine sand grains. *J. mar. biol. Ass. U.K.*, 48, pp. 161-175.
- OTT, J.A. and MACHAN, N., 1971. — Dynamics of climatic parameters in intertidal sediments. *Thalassia Jugosl.*, 7 (1), pp. 219-229.
- PLATT, H.M., 1973. — Freelifving marine Nematodes from Strangford Lough, Northern Ireland. *Cah. Biol. Mar.*, 14, pp. 295-321.
- PLATT, H.M. — Ecology of free-living marine nematodes from an intertidal sandflat in Strangford Lough, Northern Ireland—physical factors, population densities and species composition. *Estuar. and Coast. Mar. Sci.* (in press).
- TEAL, J.M. and WIESER, W., 1966. — The distribution and ecology of nematodes in a Georgia salt-marsh. *Limnol. Oceanogr.*, 11, pp. 217-222.
- TIETJEN, J.H., 1969. — The ecology of shallow water meiofauna in two New England estuaries. *Oecologia*, 2, pp. 251-291.
- WARD, A.R., 1973. — Studies on the sublittoral free-living nematodes of Liverpool Bay. 1. The structure and distribution of the nematode populations. *Mar. Biol.*, 22, pp. 53-66.
- WARWICK, R.M., 1971. — Nematode associations in the Exe estuary. *J. mar. biol. Ass. U.K.*, 51, pp. 439-454.
- WARWICK, R.M. and BUCHANAN, J.B., 1971. — The meiofauna off the coast of Northumberland. II. Seasonal stability of the nematode population. *J. mar. biol. Ass. U.K.*, 51, pp. 355-362.
- WIESER, W., 1953. — Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. *Ark. Zool. Ser.* 2, 4, 26, pp. 439-484.
- WIESER, W., 1959. — Free-living nematodes. IV. General part. Reports of Lund University Chile Expedition, 1948-9. *Acta Univ. Lund, N.F.*, Adv. 2, Bd. 55, pp. 1-111.
- WIESER, W., 1960. — Benthic studies in Buzzards Bay. II. The meiofauna. *Limnol. Oceanogr.*, 5, pp. 121-137.
- WIESER, W. and KANWISHER, J., 1961. — Ecological and physiological studies on marine nematodes from a small salt marsh near Woods Hole, Massachusetts. *Limnol. Oceanogr.*, 6, pp. 262-270.

## APPENDIX TABLE

Morphological characterisation, vertical distribution group (VDG - see text) and total numbers of the commoner species comprising 90 percent of the total population at each station.

Species	Body length (mm)	Somatic setae ( $\mu\text{m}$ )	Feeding type (see text)	V D B	Total numbers		
					Sta. A	Sta. B	Sta. C
<i>Ascolaimus elongatus</i> (Bütschli)	2.0-5.0	5-10	1B	1	1	59	9
<i>Axonolaimus paraspinosus</i> Stekhoven and Adam	1.5-2.0	0-5	1B	1	32	112	42
<i>Odontophora setosa</i> (Allgen)	2.0-5.0	5-10	1B	2	73	49	5
<i>Leptolaimus septempapillatus</i> Platt	0.5-1.0	0-5	1B	2	19	32	6
<i>Bathylaimus assimilis</i> De Man	2.0-5.0	0-5	1B	1	43	15	0
<i>Desmolaimus fennicus</i> Schneider	1.0-1.5	0-5	1B	1	131	23	22
<i>Metalinhomoeus filiformis</i> (De Man)	2.0-5.0	0-5	1B	2	355	13	0
<i>Paralinhomoeus tenuicaudatus</i> (Bütschli)	2.0-5.0	0-5	2A	2	36	26	0
<i>Eleutherolaimus stenosoma</i> (De Man)	1.5-2.0	0-5	1B	1	59	67	20
<i>Sphaerolaimus balticus</i> Schneider	1.5-2.0	10-20	2B	1	55	12	8
<i>Theristus pertenuis</i> Bresslau and Stekhoven	1.0-1.5	0-5	1B	2	48	176	7
<i>Theristus longus</i> Platt	1.0-1.5	5-10	1B	3	6	35	0
<i>Theristus riemanni</i> Platt	1.0-1.5	0-5	1B	2	185	3	1
<i>Theristus mirabilis</i> Stekhoven and De Coninck	1.0-1.5	20+	1B	1	0	0	37
<i>Theristus invagiferous</i> Platt	1.0-1.5	20+	1B	2	0	1	60
<i>Theristus setosus</i> (Bütschli)	1.5-2.0	20+	1B	1	237	217	20
<i>Theristus biggi</i> Gerlach	0.5-1.0	0-5	1B	1	1	0	18
<i>Theristus normandicus</i> (De Man)	1.0-1.5	0-5	1B	1	2	31	231
<i>Cobbia trefusiaeformis</i> De Man	1.5-2.0	5-10	2A	2	16	69	0
<i>Southernia zosteræ</i> Allgen	1.0-1.5	0-5	1A	1	14	33	46
<i>Chromaspirina</i> sp. 1	2.0-5.0	10-20	2B	2	0	0	47
<i>Chromaspirina</i> sp. 2	2.0-5.0	10-20	2B	2	0	0	22
<i>Metachromadora suecica</i> (Allgen)	1.0-1.5	0-5	2B	1	12	88	443
<i>Metachromadora vivipera</i> (De Man)	1.5-2.0	0-5	2B	1	190	5	0
<i>Spirinia parasitifera</i> (Bastian)	2.0-5.0	0-5	1A	2	2,315	607	37
<i>Spirinia laevis</i> (Bastian)	2.0-5.0	10-20	1A	2	0	9	248
<i>Leptonemella</i> sp. 1	2.0-5.0	0-5	1A	3	0	0	33
<i>Microlaimus marinus</i> (Schulz)	1.0-1.5	0-5	2A	2	5	42	197
<i>Microlaimus zosteræ</i> Allgen	0.5-1.0	0-5	2A	1	5	268	68
<i>Microlaimus cuanensis</i> Platt	1.0-1.5	0-5	2A	3	37	92	5
<i>Desmodora communis</i> (Bütschli)	1.5-2.0	0-5	2A	1	37	55	1
<i>Monoposthia costata</i> (Bastian)	2.0-5.0	5-10	2A	1	2	5	27
<i>Monoposthia mirabilis</i> Schulz	1.0-1.5	5-10	2A	2	0	3	324
<i>Nudora bipapillata</i> Platt	1.0-1.5	5-10	2A	1	452	13	6
<i>Richtersia inaequalis</i> Riemann	0.5-1.0	5-10	2A	2	0	7	92
<i>Sabatieria cupida</i> Bresslau and Stekhoven	2.0-5.0	0-5	1B	2	153	5	27
<i>Innocuonema tentabundum</i> (De Man)	0.5-1.0	5-10	2A	1	42	130	303
<i>Hypodontolaimus balticus</i> Schneider	1.0-1.5	0-5	2A	1	25	33	2
<i>Hypodontolaimus</i> sp. 1	1.0-1.5	0-5	2A	1	0	15	3
<i>Neochromadora poecilosoma</i> (De Man)	1.0-1.5	10-20	2A	1	501	122	475
<i>Atrochromadora microlaima</i> (De Man)	0.5-1.0	10-20	2A	1	43	24	1
<i>Chromadora nudicapitata</i> Bastian	0.5-1.0	0-5	2A	1	26	26	45
<i>Chromadora macrolaima</i> De Man	0.5-1.0	0-5	2A	1	258	12	27
<i>Prochromadorella septempapillata</i> Platt	1.0-1.5	0-5	2A	2	0	3	44
<i>Choniolaimus</i> sp. 1	2.0-5.0	0-5	2A	3	0	0	24
<i>Pomponema sedecima</i> Platt	1.0-1.5	5-10	2A	2	0	5	291
<i>Paracanthonchus caecus</i> (Bastian)	1.5-2.0	0-5	2A	1	6	0	135
<i>Paracanthonchus longus</i> Allgen	1.5-2.0	5-10	2A	2	0	1	30
<i>Paracanthonchus tyrrhenicus</i> (Brunetti)	1.5-2.0	5-10	2A	2	0	0	203
<i>Enoploides spiculohamatus</i> Schulz	2.0-5.0	10-20	2B	1	79	71	27
<i>Enoplolaimus propinquus</i> De Man	1.5-2.0	5-10	2B	2	0	0	84
<i>Chaetonema riemanni</i> Platt	1.0-1.5	0-5	1B	1	0	0	27
<i>Viscosia glabra</i> (Bastian)	1.5-2.0	0-5	2B	1	32	15	13
<i>Viscosia langrunensis</i> De Man	2.0-5.0	0-5	2B	2	0	1	49
<i>Viscosia viscosia</i> (Bastian)	1.5-2.0	0-5	2B	1	72	155	20
<i>Viscosia</i> sp. 1	2.0-5.0	0-5	2B	1	3	7	170
<i>Oncholaimellus mediterraneus</i> Stekhoven	1.0-1.5	0-5	2B	2	8	15	140
<i>Anoplostoma viviparum</i> (Bastian)	1.5-2.0	0-5	1B	1	161	55	0