J. mar. biol. Ass. U.K. (1982) 62, 535–548
Printed in Great Britain

MEIOBENTHOS OF A SUBLITTORAL SANDBANK IN THE SOUTHERN BIGHT OF THE NORTH SEA

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(Figs. 1–2)

The meiofauna of a subtidal linear sandbank, the Kwinte Bank, in the Belgian coastal waters of the North Sea was analysed, with particular reference to the nematodes and harpacticoids. Nematodes are evenly spread over the whole sandbank but species differ. Diversity is very high (on average 3·8 bits/ind.) and 136 species were identified. Density on the contrary is low (on average 384 ind./10 cm²). Three species groups can be distinguished which are correlated with sediment characteristics. All trophic groups of nematodes are equally distributed within the sediment.

Copepods are both more numerous and more diverse in the coarser sediments of the northern side of the sandbank. One cyclopoid and 65 harpacticoid species were identified with an average diversity of 2·3 bits/ind. and an average density of 162 ind./10 cm². Two species groups can be distinguished, again correlated with sediment characteristics. It is suggested that stable fine and coarse sand associations occur in the North Sea, similar to other coastal and offshore sublittoral sand associations in the European seas.

INTRODUCTION

The background and aims of this study are outlined in the introductory section of the preceding paper (Vanosmael *et al.* 1982).

MATERIALS AND METHODS

Description of the study area, sampling methods and methods used for grain size, chemical and statistical analysis are described by Vanosmael *et al.*

The meiofauna was subsampled from a Reineck box-corer to a depth of 10 cm using acrylic cores with a surface area of 10·17 cm². The cores were immediately extruded and fixed with heated (70 °C) 7 % formalin. Fixation with warm formalin causes relaxation and stretching of the nematodes, thus facilitating later identification (Seinhorst, 1966). To elutriate the meiofauna from the sediment, decantation on a 38 μm sieve was used, since all stations consisted of clean sand.

Densities of the meiofauna are based on counting of two replicates. However, nematodes were identified in only one replicate. Furthermore, in rich samples only 100 individuals picked out of a counting chamber at random were identified.

RESULTS

Density (Table 1)

Nematodes represent more than 50 % of the meiofauna in stations SB 1, 2, 4, 6, 7 and 8 whereas in stations SB 3, 5, 9 and 10 copepods predominate. The mean density of nematodes and harpacticoids over all stations is 366 ± 77 ind./10 cm² and 161 ± 26

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Table 1. *Density* (*N*/10 *cm*^{2}) *and relative abundance* (A) *on ten stations*

Mean and standard error of two observations; +, < one individual.

	SB 1		SB 2		SB 3		SB 4		SB 5		SB 6	
	N	A	N	A	N	A	N	A	N	A	N	A
Nematoda	1095±234	88·7	596±126	75·0	58±8	21·7	796±4	80·8	196±10	33·6	134±62	69·9
Copepoda	116±28	9·3	146±6	18·9	164±31	61·4	84±12	8·5	342±2	58·8	52±20	26·9
Annelida	21±8	1·7	22±4	2·8	5±1	1·9	54±9	5·5	11±2	1·9	4±1	2·3
Ostracoda	+	0·1	14±2	1·9	19±8	7·2	32±8	3·2	20±2	3·4	0	0
Halacarida	+	0·1	6±1	0·8	19±1	7·2	18±4	1·8	11±4	1·9	+	0·2
Hydrozoa	0	0	4±4	0·5	2±2	0·8	+	0·1	2±1	0·3	+	0·2
Total	1234±272		771±126		266±29		983±35		581±22		192±43	

	SB 7		SB 8		SB 9		SB 10		Mean	
	N	A	N	A	N	A	N	A	N	A
Nematoda	280±6	77·9	155±3	83·3	214±7	39·2	150±16	29·8	366±77	65·1
Copepoda	64±10	17·8	25±6	13·4	294±6	54·0	327±67	64·9	161±26	28·6
Annelida	11±3	3·1	4±2	2·4	30±6	5·5	14±2	2·8	17±3	3·0
Ostracoda	0	0	0	0	0	0	0	0	9±3	1·6
Halacarida	0	0	0	0	0	0	6±3	1·2	6±2	1·1
Hydrozoa	4±4	1·1	2±2	1·1	6±6	1·3	7±2	1·4	3±1	0·5
Total	358±17		186±9		544±12		503±86		562±77	

ind./10 cm^2 respectively. On average nematodes account for 60·0 % (range 21·7–88·7 %), harpacticoids for 33·4 % (range 9·3–64·9 %) and other taxa for 6·6 % (range 1·9–17·1 %). The other taxa consist mainly of interstitial Annelida, followed by Ostracoda, Halacarida and Hydrozoa.

Ostracoda and Halacarida are more abundant in the northern part but Hydrozoa are more abundant in the southern part.

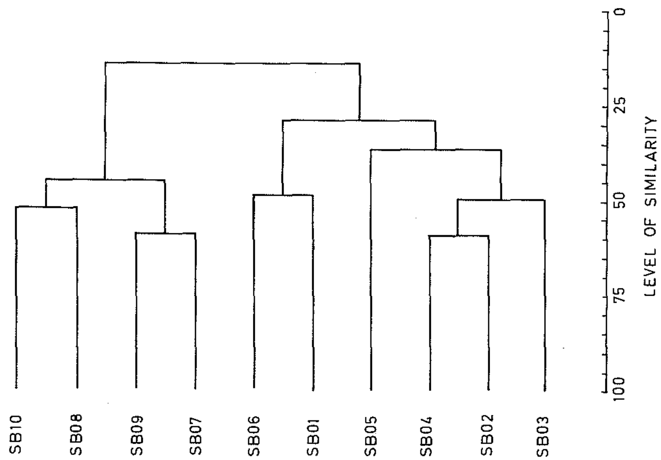
Nematoda

In the ten sampling stations 1550 nematodes were identified. (A complete species list including relative abundance per station is available on request.) A list of the species with a relative abundance greater than 2 % is given in Fig. 1. Several individuals could not be identified to species level, because of the paucity of the material (mostly juveniles). In all, 136 species were found, belonging to 28 families. Faunal affinities among the stations are illustrated in a dendrogram in Fig. 1. Species occurring only once were eliminated.

The ten stations are arranged into three clusters. The first group comprises stations SB 2, 3, 4 and 5. The nematode taxocene shows a low amount of dominance by one or a few species. Species with a mean relative abundance larger than 1 % over these four stations belong mainly to the Desmodorida: *Chromaspirina pellita*, *Desmodora schulzi*, *Desmodorella tenuispiculum*, *Dracognomus tinae*, *Epsilonema* sp. A, *Ixonema sordidum*, *Metepsilonema hagmeireri*, *Microlaimus annelisae*, *Microlaimus marinus*, *Onyx perfectus* and *Prochaetosoma mediterranicum*. Other abundant (more than 1 %) species are: *Stephanolaimus elegans*, *Tricoma* sp. A, *Rhynchonema quemer*, *Theristus roscoffiensis*, *Theristus* sp. A, *Actinonema celtica*, *Chromadorita* aff. *mucrocaudata*. Thirty-three species out of 76 are restricted to this station group I; members of the Epsilonematidae and Draconematidae are the most characteristic. These animals (*Dracognomus tinae*, *Epsilonema pustulatum*, *E. serrulatum*, *Epsilonema* sp. *A*. *Metepsilonema emersum*, *M. hagmeieri*, *Perepsilonema crassum*, *Prochaetosoma mediterranicum*) have a very aberrant habitus within the nematodes and a different way of locomotion ('leech-like' movement).

The second group contains the stations SB 1 and SB 6, and is characterized by a high percentage of Chromadorida, essentially Cyatholaimidae. Among these, the following species have a mean relative abundance > 1 %: *Choniolaimus* sp. A, *Chromadorita* aff. *mucrocaudata*, *Dichromadora cucullata*, *Gammanema rapax*, *Latronema aberrans*, *Pomponema* sp. A, *Prochromadorella ditlevseni*, *Prochromadorella septempapillata*, *Sabatieria celtica*.The Enoplidae also are rather abundant: *Enoploides spiculohamatus*, *Oxyonchus* sp. A, *Rhabdocoma reimanni*, *Rhabdodemainia* sp. A, *Trefusia* sp. A and *Viscosia* sp. A. Other abundant species are *Daptonema* sp. A, *Gonionchus villosus*, *Theristus* sp. A, *Trichotheristus mirabilis*, *Calomicrolaimus honestus*, *Chromaspirina pellita*, *Desmodora schulzi*, *Microlaimus marinus*, *Onyx perfectus* and *Richtersia deconincki*. Fifteen species out of 52 are restricted to these two stations, but none of them shows a distinct dominance.

The third group contains the southern stations SB 7, 8, 9 and 10. When compared with the two other station groups, more Areaolaimida and Monhysterida are present. There is no dominance of any species: the following nematodes have a mean relative abundance > 1 %: *Axonolaimus* sp. A, *Odontophora* sp. A, *Stephanolaimus elegans*,



	Group III	Group II	Group I
Median particle diameter (μm)	188–230	234–281	375–654
Mud < 63 μm (%)	0·00–0·26	0·14–1·61	0·00–0·30
Gravel > 2000 μm (%)	0·00–0·00	2·21–6·84	0·24–10·62
Density (N/10 cm^2; S.E.)	200 ± 20	615 ± 295	407 ± 114
Total species number	78	52	76

Species composition (relative dominance > 2 %)

Group III

	D (%)	F (%)	FT (%)
Leptonemella sp. A	6·6	75	50
Microlaimus marinus	5·8	100	100
Dasynemella albaensis	5·5	100	50
**Bathylaimus* sp. A.	5·3	100	40
Microlaimus ostracion	4·6	75	40
**Xyala* sp. A	4·5	75	30
Calomicrolaimus sp. A	4·3	50	30
Chromaspirina parapontica	3·6	75	60
Theristus sp. A	3·6	100	90
**Daptonema stylosum*	3·2	25	10
Rhynchonema quemer	3·2	100	90
**Tubolaimoides tenuicaudatus*	2·9	75	30
Odontophora sp. A	2·5	100	50
Viscosia sp. A	2·5	100	100
**Gonionchus longicaudatus*	2·1	75	30
Stephanolaimus elegans	2·1	100	80
Xyala rienmanni	2·0	25	20

Group II

	D (%)	F (%)	FT (%)
Microlaimus marinus	23·0	100	100
**Gonionchus villosus*	7·0	50	10
**Pomponema* sp. A	7·0	50	10
Trichotheristus mirabilis	4·9	100	60
**Daptonema* sp. A	3·5	50	10
**Gammanema rapax*	3·5	50	10
**Rhabdodemania* sp. A	3·5	50	20
Dichromadora cucullata	2·8	100	30
**Trefusia* sp. A	2·6	50	20
Prochromadorella septempapillata	2·5	100	30
Rhabdocoma riemanni	2·4	50	10
**Prochromadorella ditlevseni*	2·2	50	10
**Latronema aberrans*	2·0	50	10

Group I

	D (%)	F (%)	FT (%)
Desmodora schulzi	15·6	100	60
Onyx perfectus	13·1	100	90
Microlaimus marinus	7·9	100	100
Rhynchonema quemer	6·2	100	90
Actinonema celtica	3·7	75	50
Chromadorita aff. *mucrocaudata*	3·7	50	30
**Desmodorella tenuispiculum*	3·5	100	40
**Metepsilonema hagmeireri*	3·0	75	30
**Tricoma* sp. A	2·9	75	30
**Dracognomus tinae*	2·1	50	20
**Theristus roscoffiensis*	2·1	50	20

Fig. 1. Dendrogram resulting from clustering based on Czekanowski index applied to nematode species from ten stations of the Kwinte Bank; main sediment characteristics, density, species number and species composition according to the clusters; *D*, relative abundance (> 2 %); *F*, frequency within the clusters; *FT*, frequency based on all stations of the sandbank; species marked with an asterisk are exclusive for each group.

Daptonema stylosum, *Gonionchus longicaudatus*, *Rhynchonema quemer*, *Rhynchonema scutatum*, *Theristus* sp. A, *Trichotheristus mirabilis*, *Tubolaimoides tenuicaudatus*, *Xyala riemanni*, *Xyala* sp. A, *Bolbolaimus* sp. A, *Calomicrolaimus* sp. A, *Chromaspirina inglisi*, *Chromaspirina pellita*, *Dasynemella albaensis*, *Leptonemella granulosa*, *Leptonemella* sp.A, *Microlaimus monstrosus*, *Microlaimus ostracion*, *Microlaimus marinus*, *Onyx perfectus*, *Gammanema* sp. A, *Bathylaimus* sp. A, *Enoploides spiculohamatus* and *Viscosia* sp. A. Twenty-seven species out of 78 are restricted to these four stations.

Table 2. *Relative importance of the feeding types of nematodes in ten stations of the Kwinte Bank*

1 A, Selective deposit feeders; 1 B, non-selective deposit feeders; 2 A, epistratum feeders; 2 B, omnivores and carnivores.

	SB 1	SB 2	SB 3	SB 4	SB 5	SB 6	SB 7	SB 8	SB 9	SB 10
1A	6·0	22·4	43·7	10·6	25·3	23·1	21·8	17·0	16·4	12·9
1B	17·2	14·2	10·4	12·3	15·2	19·1	30·2	51·6	24·8	36·4
2A	50·5	44·9	24·5	56·2	28·5	30·7	31·2	12·6	37·3	32·4
2B	26·1	19·9	21·7	20·2	31·5	29·4	15·5	18·9	24·2	13·8

Table 3. *Diversity, evenness and number of species in ten stations of the Kwinte Bank*

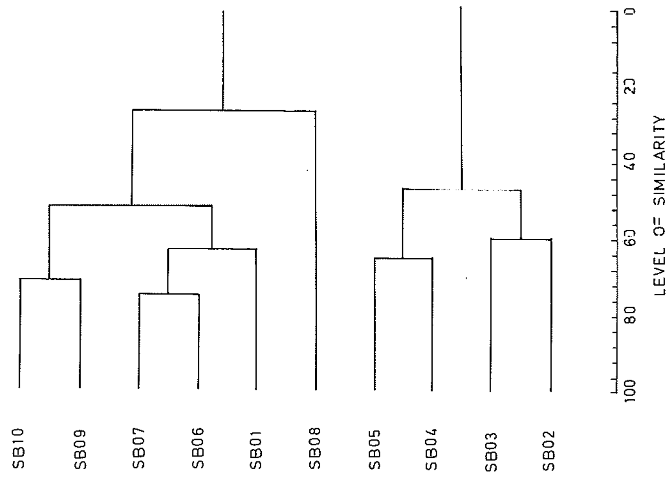
	Nematoda			Copepoda		
	H	*J'*	*S*	*H*	*J'*	*S*
SB 1	3·60	0·84	34	1·96	0·58	13
SB 2	4·55	0·88	49	2·74	0·74	17
SB 3	3·29	0·82	25	2·58	0·66	19
SB 4	3·96	0·75	47	3·15	0·86	22
SB 5	3·36	0·83	25	3·08	0·63	37
SB 6	3·68	0·84	33	1·98	0·65	11
SB 7	3·51	0·92	30	2·06	0·64	15
SB 8	3·39	0·88	20	1·24	0·63	5
SB 9	4·58	0·87	54	1·92	0·49	17
SB 10	3·91	0·92	31	2·62	0·72	14

The division of these three groups corresponds to the decrease in the median particle size of the sand fraction. Station group I has a median grain size larger than 300 μm and large amounts of gravel. The sand fraction of group II stations has a median grain size between 230 and 300 μm, without gravel. According to this classification, three different types of sediment on the crest of the Kwinte Bank are reflected in three different nematode associations.

Wieser (1953) divided the free-living marine nematodes into four feeding type groups, based primarily on the morphology of the buccal cavity and on gut contents. These groups are 1A: selective deposit feeders; 1B: non-selective deposit feeders; 2A: epigrowth feeders and 2B: omnivorous, with capacity for predation and predators.

Table 2 gives the percentage compositions of the four feeding types per station. There is no clear dominance of one feeding type.

Species diversity *H* and evenness *J'* are given in Table 3. Both values are very high and no large differences among the stations are observed.



	Group II	Group I
Median particle diameter (μm)	188–281	375–654
Mud < 63 μm (%)	0–1·61	0–0·30
Gravel > 2000 μm (%)	0–6·84	0·24–10·62
Density (N/10 cm^2; S.E.)	146±37	184±37
Total species number	29	52

Species composition (relative dominance > 1 %)	*D* (%)	*F* (%)	*FT* (%)		*D* (%)	*F* (%)	*FT* (%)
Leptastacus laticaudatus intermedius	43·1	100	100	*Interleptomesochra eulittoralis*	15·0	75	40
Paraleptastacus espinulatus	8·3	100	70	*Leptastacus laticaudatus intermedius*	13·6	100	100
Apodopsyllus sp. A	7·8	50	50	*Metacyclopina brevisetosa*	12·8	75	30
**Kliopsyllus constrictus* s.str.	5·5	67	40	**Ectinosoma reductum*	10·1	50	20
Sarsameira sp. A.	5·4	50	40	**Ameira brevipes*	6·9	75	30
Kliopsyllus sp. A	5·3	50	70	*Kliopsyllus* sp. A.	5·3	100	70
Evansula pygmaea	4·6	83	60	*Diarthrodella secunda*	5·0	100	60
Kliopsyllus holsaticus s.str.	4·6	83	70	**Robertgurneya ilievecensis*	4·7	100	40
Arenocaris bifida	3·0	83	60	*Ectinosomatidae sp. A	3·8	50	20
Kliopsyllus sp. B	2·3	67	50	*Leptastacus minutus*	2·8	25	20
**Stenocaris* sp. A	1·3	17	10	*Psammotopa phyllosetosa*	2·5	75	50
**Stenocaris* sp. B	1·3	17	10	**Leptomesochra confluens*	2·1	25	10
**Psammastacus remanei*	1·3	33	20	*Sarsameira* sp. A.	1·8	25	40
Halectinosoma herdmani	1·2	50	40	**Halectinosoma erythrops*	1·7	75	30
				**Paramesochra helgolandica*	1·3	50	20
				**Arenopontia* sp. A	1·3	50	20
				Kliopsyllus holsaticus s.str.	1·2	50	70

Fig. 2. Dendrogram resulting from clustering based on Czekanowski index applied to copepod species from ten stations of the Kwinte Bank; main sediment characteristics, density, species number and species composition according to the clusters; *D*, relative abundance (> 1 %); *F*, frequency within the clusters; *FT*, frequency based on all stations of the sandbank; species marked with an asterisk are exclusive for each group.

Copepoda

On the Kwinte Bank one cyclopoid and 65 harpacticoid copepod species were found. The latter belong to eight families: Cylindropsyllidae (16), Ectinosomatidae (14), Paramesochridae (13), Ameiridae (13), Diosaccidae (5), Tachidiidae (2), Tetragonicipitidae (1) and Cletodidae (1).

Generally, the Kwinte Bank harbours a very rich and diverse copepod fauna which is essentially characterized by mesopsammic forms. Species occurring with a frequency greater than 10% were used for cluster analysis. The normal (Q) analysis of all stations reveals two groups (Fig. 2). Group I clusters SB 2, 3, 4 and 5; group II clusters SB 1, 6, 7, 8, 9 and 10. The relative abundance of the species with a relative abundance greater than 1% arranged according to these clusters is given in Fig. 2. In group I the coarser sediment stations are clustered; they represent deposits with a mixture of sand (375–654 μm), gravel and shell. The fauna of this station group is the most diverse, with 52 species of which 35 are restricted to this group. Three harpacticoid and one cyclopoid species predominate. In descending order of dominance they are *Interleptomesochra eulittoralis*, *Leptastacus laticaudatus intermedius*, *Metacyclopina brevisetosa* and *Ectinosoma reductum*. They are associated with the following important (4–10% species: *Kliopsyllus* sp. A, *Diarthrodella secunda* and *Robertgurneya ilievecensis*. Species restricted (dom. > 1%; freq. > 10%) to this group are *Ectinosoma reductum*, *Ameira brevipes*, *Robertgurneya ilievecensis*, Ectinosomatidae sp. A, *Sarsameira* sp. A, *Halectinosoma erythrops*, *Arenopontia* sp. A, *Paramesochra helgolandica*, *Intermedopsyllus intermedius*. All other characteristic species (freq. > 10%) occur with a dominance < 1%, except *Leptomesochra confluens*, which is quantitatively important in SB 5.

In the second station group only finer (188–288 μm) sands are found. The fauna is less diverse, and consists of 29 species, twelve of which are exclusive to this group. One strongly dominant species (43%), *Leptastacus laticaudatus intermedius*, is associated with the following important (4–10%) species: *Paraleptastacus espinulatus*, *Apodopsyllus* sp. A, *Kliopsyllus* sp. A, *Kliopsyllus holsaticus* s.str., *Evansula pygmaea*. Species restricted to group II (dom. > 1%) are: *Kliopsyllus constrictus* s. str., *Psammastacus remanei*, *Stenocaris* sp. A and *Stenocaris* sp. B. *Leptastacus laticaudatus intermedius* is abundant in all stations, but as *Halectinosoma herdmani* and *Arenocaris bifida* it shows a preference for finer deposits.

Diversity values (Table 3) range between 1·24 bits/ind. and 3·16 bits/ind., with the highest values in station group I. Diversity H and the number of species are significantly higher in the northern stations, which have a fauna which is essentially comparable to that of the open sea zone, the more stressed nature of the habitat being clearly reflected in a lower diversity of the community.

DISCUSSION

Density

The relative abundance of the major meiofaunal taxa from the Kwinte Bank is very similar to those recorded from other sublittoral coarse sands (Moore, 1979*a*; Scheibel, 1973). The meiofauna is characterized by low densities of nematodes and high densities of copepods, annelids and halacarid mites. Nematode and copepod densities are consistent with those found in similar offshore and subtidal biotypes (McIntyre & Murison, 1973; Ward, 1973; Scheibel, 1973; Lorenzen, 1974; Platt, 1977; Moore, 1979*a*; Tietjen, 1980).

Nematode densities are low when compared with the surrounding regions. For the Southern Bight of the North Sea values are given by Govaere *et al.* (1980) of 1178 ind./10 cm^2 for the coastal zone, 1423 ind./10 cm^2 for the transition zone and 998 ind./10 cm^2

for the open sea zone. These values are averages over the period 1972–4 and are too low due to sampling errors. Somewhat higher values have been reported for the coastal zone in 1977–8, with between 1400 and 2860 ind./10 cm^2 over all stations and extremes of 80 and 8750 ind./10 cm^2 for single stations and an overall mean of 1650 ind./10 cm^2 over all seasons and stations (Heip *et al.* 1979).

Average copepod densities are 244 ind./10 cm^2 in the open sea zone of the Southern Bight (Govaere *et al.* 1980), 151 ind./10 cm^2 for the Irish Sea (Moore, 1979*a*) and 153 ind./10 cm^2 for the Kieler Bucht (Scheibel & Noodt, 1975).

Values found for the Kwinte Bank (384 ind./10 cm^2 for nematodes and 162 ind./10 cm^2 for copepods) are to be considered too low, especially for the coarser deposits and the nematodes, as in very well-aerated deposits meiofauna can live deeper than 10 cm (Heip, Willems & Goosens, 1977; McLachlan, Winter & Botha, 1977). Cores taken by SCUBA diving to a depth of 20 cm in July 1978 indicate that our cores contain approximately 65% of the total meiofauna.

Species composition of nematodes

The generic composition of the nematode communities of the Kwinte Bank is similar to those of other clean sandy biotopes, as far as genera are concerned (Wieser, 1959; Warwick, 1971; McIntyre & Murison, 1973; Ward, 1973; Tietjen, 1980 and our continuing study of the Southern Bight). Most ecological studies of marine nematodes describe biotopes which are very different in their sediment composition, so that different nematode associations are easily recognizable. Problems arise with the analysis of one sediment type, e.g. clean sand.

The three station groups determined by clustering reflect three faunal units, among which the cluster of the coarser sand stations SB 2, 3, 4 and 5 is the most remarkable one: the large amount of Epsilonematidae and Draconematoidea (8 species) is exceptional for offshore communities. Until now only *Metepsilonema hagmeieri* and *Perepsilonema crassum* have been found in European offshore communities (Lorenzen, 1974); *Epsilonema pustulatum* occurs in the sandy sediment of the Shelly Bank in the Exe Estuary (Warwick, 1971). *Metepsilonema callosum* and *Perepsilonema papulosum* have been found in a sublittoral region off the coast of Chile (Lorenzen, 1973). Nicholls (1980) mentions a *Metepsilonema* species in sublittoral sand off the coast of Peru. Offshore Draconematoidea are also scarce: only five species from a total of 48 were recorded from offshore habitats (Allen & Noffsinger, 1978). All the other species are reported from sandy beaches, algae and animal Aufwuchs.

Epsilonematidae and Draconematoidea are adapted to the extreme instability of the substrate of the sandbanks and are confined to such biotopes. Most records from these nematodes are from beaches, which are also subjected to strong hydrodynamical stress.

Wieser (1959) describes a number of interesting species which occur on sublittoral coarse bottoms as well as on littoral sand on the coast of Chile. Nevertheless, he was unable to define a stenotypic fauna for the coarse sediments. The genera that Wieser considers to be characteristic for the sublittoral coarse bottoms are the same as many genera restricted, in our study, to the fine sands, e.g. *Trefusia* (compared with *Rhabdocoma*), *Latronema*, *Campylaimus*, *Oxyonchus*, *Pomponema*, *Nudora* (compared with

Monoposthia), *Bathylaimus* and *Xyala*. The investigated sediment of Chile is probably not coarse enough for Epsilonematidae and Draconematoidea, or else less subjected to hydrodynamical stress.

Comparison of the nematode community of sublittoral coarse bottoms with data of littoral sand in Europe is difficult, since no quantitative data are available about nematodes of coarse beaches. *Desmodora* is characteristic of clean, coarse substrate, where *Graphonema*, *Dichromadora* and *Microlaimus* are also common (Ward, 1973). The following genera are also abundant in these biotopes: *Enoploides*, *Ixonema*, *Rhynchonema*, *Monhystera*, *Chromaspirina*, *Hypodontolaimus*, *Metachromadora*, *Neochromadora*, *Richtersia*, *Bradylaimus*, *Camacolaimoides*, *Halaphanolaimus*, *Latronema* and *Sabatieria* (*hilarula*). This composition is similar to the nematode associations of the Kwinte Bank, with only one exception: no Epsilonematidae and no Draconematoidea.

The following species are characteristic for medium-coarse sand stations in the New York Bight (Tietjen, 1980): *Neochromadora poecilosoma*, *Neochromadora pectinata*, *Prochromadorella neapolitana*, *P. paramucrodonta*, *Microlaimus* spp. and *Chromaspirina* spp.

Of special interest is 'habitat 5' in the study of Warwick (1971), defined as 'coarse sands with a more or less permanent high salinity water table'. The species of this biotope belong to the same genera as those on the Kwinte Bank (not restricted to the coarse sediments only).

It is too early to define nematode communities for the Kwinte Bank – if they ever exist in such a high-energy environment. Wieser (1959) states that the fauna of unstable biotopes consists largely of erratic 'guests' brought in by water movements, and partly of eurytopic and resistant species, which though sometimes typical, are distributed in irregular patches. This is reflected in the unusually low frequency of most of the species.

Station group II is more closely related to group I than to group III. The large amount of Chromadoridae species is responsible for this. Nevertheless, for comparison with the literature, groups II and III should be discussed together. The large number of Araeolaimida and Monhysterida is typical of fine sands with a small amount of silt. McIntyre & Murison (1973), Ward (1973) and Lorenzen (1974) obtain comparable results in their studies of fine–medium sand biotopes. The species composition is nearly the same, but the relative abundance differs considerably. At present, we are unable to offer a definite explanation for these observations, since it is dangerous to interpret quantitative data based on only one sampling date.

Feeding types

The absence of a dominant feeding type indicates that this sandy biotype is indeed very heterogeneous and that nematodes occupy many niches. The correlation between sediment composition and trophic structure of the community is studied by (among others) Wieser (1953, 1959), Hopper & Meyers (1967), Tietjen (1969), Warwick & Buchanan (1970), Coull (1970), Boucher (1972, 1974), Vitiello (1972, 1975) and Juario (1975). In general they state that muddy sediments are dominated by 1B types (50–60%) and that sandy bottoms are more dominated by 2A types (50–60%); in most biotopes, 1A and 2B types are numerically less important. On the Kwinte Bank, only the fine stations of group III have more than 20% of the 1B type. The large amount of the 1A-type feeders is remarkable and has up to now only been found by Boucher (1980) in the sublittoral fine sands of the Bay of Morlaix. This high percentage of the 1A type in the Kwinte Bank is mostly due to the presence of Epsilonematidae and Draconematoidea, which are truly interstitial forms. In the study of Boucher (1980) the 1A feeding group was represented by the Stilbonematidae.

Species diversity of the nematodes

The nematode diversities on the Kwinte Bank are generally higher (range 3·29–4·58 bits/ind., mean 3·78 bits/ind.) than those recorded elsewhere in the Southern Bight of the North Sea (unpublished results). This is certainly influenced by the high number of microhabitats present in the sediments of the Kwinte Bank. Warwick & Buchanan (1970), Heip & Decraemer (1974) and Juario (1975) found a correlation between diversity and sedimentological characteristics (silt–clay fraction and median grain size of the sand fraction). This correlation was not found here, and indeed the nematodes appear to be the only major group in which it is absent (Table 3). The reason for this finding may be that the number of different biotopes is not sufficiently high and that, more specifically, no muddy stations are present.

Species composition of the copepods

Most data on copepods, and more especially Harpacticoida, of off-shore sandy deposits are provided by Soyer (1970), Bodiou & Chardy (1973) and Bodiou (1975) for the French Catalonian coast and by Moore (1979*a*) and Govaere *et al.* (1980) for the North European seas.

Clean sands are characterized by the dominance of Cylindropsillidae, Paramesochridae, Ectinosomatidae and Tetragonicipitidae, the latter particularly in very coarse sands. This is also found on the Kwinte Bank. However, the species composition of the Kwinte Bank differs in the high number of Ameiridae. Based on the harpacticoid associations, Govaere *et al.* (1980) distinguished three zones for the Southern Bight which correspond roughly with the zones defined for the macrobenthos. They are: (1) a coastal zone characterized by a *Microarthridion littorale–Halectinosoma herdmani* community, (2) an open sea zone with a *Leptastacus laticaudatus–Paramesochra helgolandica* community and (3) a transition zone with a *Leptastacus laticaudatus–Halectinosoma herdmani* community. Although the Kwinte Bank is geographically located within the transition zone, the harpacticoid association clearly resembles the open sea zone community, where a total number of 54 species is recorded from fourteen stations. The most common species are *Leptastacus laticaudatus*, *Paramesochra helgolandica*, *Arenosetella germanica*, *Kliopsyllus paraholsaticus*, *Psammotopa phyllosetosa*, *Intermedopsyllus intermedius* and *Evansula incerta*.

The resemblance between the harpacticoid associations from the Kwinte Bank and that of the open sea zone is probably best explained by the fact that food input in both systems is low though the reasons are different: strong turbulence in the sandbank and nutrient poor waters in the open sea.

Clustering of two station groups reflects the existence of a coarse sand and a fine sand association. The species composition of group I strongly resembles the mesopsammic assemblage of the coarse sands of the French Catalonian coast (Soyer, 1970) and the coarse sand association of the Irish Sea (Moore, 1979*a*). Comparison with these studies suggests that the copepod faunas of medium and coarse (> 300 μm) offshore deposits are similar. Here, the following species are common and/or characteristic: *Ectinosoma reductum*, *Amphiascus varians*, *Ameira brevipes*, *Interleptomesochra attenuata*, *Paramesochra similis*, *P. helgolandica*, *Kliopsyllus coelebs*, *K. paraholsaticus*, *Cylindropsyllus laevis*, *C. remanei*, *Intermedopsyllus intermedius*, *Leptastacus laticaudatus* in addition to different members of the genera *Hastigerella*, *Arenosetella* and *Apodopsyllus*. Only one member of the Tetragonicipitidae has been found, although they are characteristic of gravels (Bodiou & Soyer, 1973).

All deposits of group II have a median grain size larger than 160 μm, which explains the dominance of interstitial forms (McLachlan *et al.* 1977; Moore, 1979*b*). The harpacticoid association of group II is similar to the *Kliopsyllus holsaticus* association described by Scheibel & Noodt (1975). This association is characteristic for the clean well-sorted fine sands (200–300 μm) of the Kieler Bight and includes typical representatives such as *Scottopsyllus minor*, *Evansula pygmaea*, *Paraleptastacus espinulatus*, *Leptastacus laticaudatus intermedius*, *Rhizothrix minuta* and *Hastigerella tenuissima* (Scheibel & Noodt, 1975; Scheibel, 1976). A comparison with fine sand associations characterized by a median grain size smaller than 160 μm (Soyer, 1970; Bodiou & Chardy, 1973; Bodiou, 1975; Moore, 1979*a*) reveals a marked faunal change, reflecting the importance of the interstitial copepod barrier 160 μm in determining the composition of harpacticoid associations. Many species of the Kwinte Bank are also found in the intertidal of many clean sandy beaches in Europe (Noodt, 1957; Renaud-Debyser, 1963; Renaud-Debyser & Salvat, 1963; Wells & Clark, 1965; Fenchel, Jansson & Thun, 1967; Jansson, 1968; Moore, 1979*b*; Mielke, 1976; Harris, 1972). In particular, the fauna of Whitsand Bay in Cornwall (Harris, 1972) is very similar. The sand of this beach (300–350 μm) has a harpacticoid fauna dominated by *Leptastacus laticaudatus* (25%) associated with *Intermedopsyllus intermedius* (15%) *Kliopsyllus constrictus* (14%) and *Psammotopa phyllosetosa* (10%).

From the present study and that of Govaere *et al.* (1980) it is suggested that a stable *Leptastacus laticaudatus* community can be described for well-sorted clean, fine to medium sands of the Southern Bight of the North Sea. In the open sea zone *L. laticaudatus* is associated with *Paramesochra helgolandica* but on the Kwinte Bank this species is replaced by *Paraleptastacus espinulatus*. Whether this difference in associated species is due to seasonal influence or to substrate composition cannot be decided. In the coarse sands of the Kwinte Bank this *Leptastacus* community gradually changes towards a community dominated by *Interleptomesochra eulittoralis* associated with the cyclopoid *Metacyclopina brevisetosa*. The latter association is characterized by higher diversity and contains many coarse sand indicator species previously described from *Amphioxus* sand (Monard, 1935; Por, 1964*a*, *b*; Soyer, 1970).

Species diversity of the copepods

Diversities recorded in this study (range 1·24–3·15 bits/ind.; mean 2·33 bits/ind.) are higher than those recorded from sandy beaches of the Isle of Man (Moore, 1979*b*) and are lower than those found for the deeper, more stable coarse and offshore fine sand stations of the Irish Sea (Moore, 1979*a*). Hulings & Gray (1976) state that meiofauna densities are mainly controlled by wave, tide and current action. The same is concluded by Hartzband & Hummon (1974) for copepod diversity. For high-energy environments, usually with grain size larger than 200 μm, the increasing diversity values when one goes from exposed littoral habitats to shallow and deeper sublittoral habitats suggest a correlation with a decrease in hydrodynamical stress.

We are grateful to the Management Team of the Mathematical Model North Sea (Ministry of Public Health, Belgium) who have always assisted us with much competence.

We thank the crew of the Research Vessel 'Mechelen' for assistance at sea; Alex Braeckman, Mark De Keere, Rudi Herman, Anita Van Bost and Dirk Van Gansbeke for very helpful technical assistance (sampling survey, sedimentological analysis and other laboratory work); Professor Dr A. Coomans and J. Sharma for their critical reading of the manuscript; Dr J. Govaere for support and intellectual stimulation during the course of this study and for valuable comments on the manuscript.

C. Heip and M. Vincx acknowledge a grant from the Belgian National Science Foundation (NFWO). D. Claeys and C. Vanosmael acknowledge a grant from the Belgian Institute for the Encouragement of Scientific Research in Industry and Agriculture (IWONL).

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