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Macro- and meiobenthos of a sublittoral sandbank in the Southern Bight  
of the North Sea

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## ABSTRACT

The benthic fauna of a linear-sandbank, the Kwinte Bank, in the Belgian coastal waters of the North Sea has been sampled on ten stations in September 1978. Density and species composition of the macro- and meiofauna and sediment characteristics have been studied. The Kwinte Bank shows a gradient from finer sediments in the south to coarser sediments in the north resulting from the tidal current pattern in the region and can be considered as a biogeographical island, as the bank is surrounded by a region of much finer sediments.

The macrofauna consists of 73 identified species and has an average density of 4910 ind./m<sup>2</sup> and an average diversity of 2.5 bits/ind. Interstitial polychaetes predominate and among those Hesionura augeneri is the most abundant species. Two species groups can be distinguished and can be correlated with sediment characteristics. Both species number and density of the macrofauna increase with increasing grain size whereas diversity decreases due to the predominance of H. augeneri in coarser sediments.

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 cm<sup>2</sup>). Three species groups can be distinguished which are correlated with sediment characteristics.

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 cm<sup>2</sup>. As in the macrofauna, two species groups can be distinguished, again correlated with sediment characteristics.

The benthic fauna of the Kwinte Bank is clearly related to the fauna of the open sea zone of the Southern Bight, in spite of the fact that the bank is situated in the transition zone between open and coastal waters. The fauna is also related to the interstitial fauna of exposed sandy beaches.

## INTRODUCTION

In the Southern Bight of the North Sea, off the Belgian coast, exists a series of parallel sublittoral sandbanks, the Flemish Banks, situated in a southwest-northeastern direction, 15 to 25 km long and 3 to 6 km wide. They are separated by channels, 4 to 6 km wide, and rise about 25 m above the surrounding sea floor (fig. 1). These sandbanks resulted from the accumulation of sandy deposits of glacial origin sedimented by the giant stream draining the waters from the present Rhine, Meuse, Scheldt and Thames before the Flandrian marine transgression about 12,000 years ago. When from boreal times onwards the North Sea became slowly inundated, a connection with the English Channel was finally established about 8,700 years ago, first as a small channel but then extending until the very strong tidal currents resulted, which are responsible for the present geomorphology of the region.

The system of the Flemish Banks is to be considered as an island of coarser sediments in a region characterized by finer grained and silty sediments (see Govaere et al., 1980, for a further description of the Southern Bight area). The benthic fauna of that region and of the sediments further off-shore has been the subject of ongoing research that is part of a comprehensive study initiated by the Belgian Government in 1970. Data have been published by Heip & Decraemer (1974), Jensen (1976), Govaere (1976), Heip et al. (1979), Govaere et al. (1980), Willems & Claeys (in press) and Vincx (in press). A large amount of unpublished data has been assembled in Government Reports (Van Damme & Heip, 1977; Govaere et al., 1977) and thesises (Jensen, 1974; Degadt, 1976; Bisschop, 1977; Vanosmael, 1977; Govaere, 1978; Rappé, 1978; Van Steen, 1978; Claeys, 1979; Kerckhof, 1980).

In spite of this intense research, the sandbanks themselves had never been investigated until commercial interest in sand and gravel exploitation started. This made necessary an assessment of the impact of large-scale human interference through the exploitation of several million tons of sediment annually. Therefore baseline data were collected from 1977 onwards. Apart from their use in management, these data are useful in an ecological context as the sandbanks are extremely interesting ecological habitats. They can be considered as islands and their fauna can

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be compared to that of the surrounding region, which is well known. Furthermore, the sandbanks are stressed, high-energy environments in the sublittoral and subject to extreme physical disturbance through the very strong tidal currents.

This paper and an accompanying paper by Rappé & Govaere (in preparation) are the first reports on the fauna of two of the Flemish Banks, the Buiten Ratel and the Kwinte Bank. It presents a comprehensive picture of the total benthic fauna of the Kwinte Bank in September 1978.

## MATERIAL AND METHODS

### Description of the study area

The Kwinte Bank is located about 12 km off the Belgian coast, between Nieuwpoort and Oostende (fig. 1). It is bordered by two channels, the Kwinte on its western and the Negenvaam on its eastern side.

The following description is based on observations by Bastin (1974). In cross-section, the Kwinte Bank is asymmetric with a steep north-western and a gentle south-eastern slope. The upper sediment layer is characterized by sandwaves, megaripples and small sand ripples, occurring on different scales (fig. 2). The sandwaves are most developed in the north-eastern part and reach an amplitude of up to 8 metres. The top of these sandwaves as well as the megaripples and the small sandripples are continuously broken down and rebuilt by strong currents and this process is visible at the water surface by the appearance of suspended patches of sediment. Particularly during storms, the whole top of the sandbank is completely destroyed and rebuilt afterwards as a result of the current pattern typical for the sandbank system, which has been described by Houbolt (1968) and Bastin (1974).

The sediment of the bank consists of fine to coarse sands and shows a gradient from fine sediments in the south to coarser sediments in the north. However, the distribution of the sediments can be very patchy locally. Many small patches, with a mixture of coarse sand and shell, occur on the slopes of the sandwaves and are due to strong erosion. The bottom of the depressions (-20 m) between the sandwaves of the north-eastern part consists of finer sediments enriched with some mud and they are characterized by an abundant fauna.

### Sampling

Samples were collected on 5 September 1978 at ten stations (SB 1 to SB 10) covering the whole length of the sandbank (fig. 1). The stations were located using a Decca-navigator; the coordinates are given in table 1.

Macrofauna sampling was carried out by means of a Van Veen grab (0.1 m<sup>2</sup>); samples were immediately fixed with formalin 7%. The meiofauna was subsampled from a Reineck box-corer to a depth of

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10 cm using acrylic cores with a surface area of 10.17 cm<sup>2</sup>. 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).

The macrofauna was elutriated in the laboratory using an adaptation of the Barnett-technique used in meiofauna research (Heip, unpublished). The samples are placed at the closed end of an horizontal trough (L: 6 m, W: 15 cm, H: 15 cm) open at the other end and washed out with a water current over a 250 µm sieve. The heaviest organisms (mollusks) are left behind on the trough after elutriation and were picked out by hand. The use of a 250 µm sieve instead of the usual 0.5 or 1 mm sieves was decided after preliminary investigation had demonstrated the importance of interstitial polychaetes in the sandbank fauna.

To elutriate the meiofauna from the sediment, decantation on a 38 µm sieve was used since all the stations consist of clean sand.

For the macrofauna, the harpacticoids and nematodes three, two and one replicate were examined respectively. All the animals in the replicates were identified and counted, except the nematodes for which in rich samples only 100 individuals picked out of a counting chamber at random were identified. All densities of meiofauna however are based on counting of two replicates (table 2).

Approximately 20 g of homogenized substrate was used for grain size analysis of the sand fraction according to Buchanan & Kain (1971). The wet sieved fraction smaller than 62 µm was used as a measure of mud content. The amount of organic material was determined by loss of weight on ignition at 550 °C.

Faunal affinities among the stations were examined by use of the Czekanowski qualitative similarity coefficient (Sørensen, 1948):

$$S = \frac{2a}{2a + b + c}$$

where a is the number of species present in both stations, b and c are the number of species present in station 1 and 2 only. The stations were clustered by flexible sorting ( $\beta = -0.25$ ) (Clifford & Stephenson, 1975) and arranged in an affinity dendrogram (Ordana program of Bloom et al., 1977, as adapted by Govaere, 1978).

Species diversity was measured by the Brillouin index  $H = \frac{1}{N} \log_2 \frac{N!}{N_1! N_2! \dots N_n!}$  proposed by Margalev (1958). Evenness  $J = H/H_{\max}$ , where  $H_{\max} = \log_2 S$  was calculated after Pielou (1966).

### Statistical tests

As the data concern only one sampling date it was decided to compare them only internally. Especially the relationship with sediment composition was investigated. For this purpose only simple non-parametrical tests were used, as non-normality of the data is important. These tests are all described in e.g. Siegel (1956).

Firstly it was tested whether the parameter has a clumped distribution, i.e. whether higher or lower values tend to be grouped. This was done using the one-sample runs test. Then it was investigated whether there was a linear trend, as the stations are linearly arranged and a gradient was thought to exist in sediment characteristics. These was done by correlating the data with the series of natural numbers 1 to 10 using Spearman's rank correlation coefficient. The third test consisted in looking for differences between the northern end (stations 1-5) and the southern end (stations 6-10) of the sandbank. This was done using Wilcoxon's U-test. For the individual species the significance of density differences between clusters was also tested using Wilcoxon's U-test. Finally the correlation with median grain size of the sand fraction was tested using again Spearman's rank correlation coefficient.

The results for general parameters are given in table 3. For the individual species the results have not been reproduced in toto but are discussed in the text.

RESULTS

Sediment analysis

Depth, grain size analysis and organic material content are given in table 1.

Insert table 1 here

The median particle diameter of the sand fraction varies between 184  $\mu\text{m}$  and 654  $\mu\text{m}$ . According to the Wentworth-scale (Buchanan & Kain, 1971) the stations can be arranged as follows: coarse sand: SB 3, SB 5; medium sand: SB 2, SB 4, SB 6; fine sand: SB 1, SB 7, SB 8, SB 9 and SB 10. All the sediments are very well sorted except for SB 3, which is well sorted. The median particle diameter shows a significant linear trend and increases towards the northern end of the sandbank. This is reflected by a very significant difference between both halves of the sandbank.

The mud content and organic material content are generally low (<2 %) and the gravel content varies between 0 and 6 %. The gravel content also shows a very significant linear trend of increasing values towards the northern end of the Kwinte Bank.

Macrofauna

Density: densities of the macrofauna range from 500 ind./m<sup>2</sup> (SB 8) to 15330 ind./m<sup>2</sup> (SB 4). The mean value is 4910 ind./m<sup>2</sup> (table 2). The lowest values are recorded in the fine sediment stations, whereas higher values are found in the coarser deposits, mainly due to the large number of interstitial Polychaeta and Archiannelida. On the Kwintebank, Polychaeta are dominant and make up between 44 % (SB 7) and 83 % (SB 5) of the macrofauna. Only at SB 8 they are less important (28 %); in this station Crustacea show a relative abundance of 64 %. The high density of macrobenthic organisms in station SB 4 is striking. Not only Polychaeta are well represented (10470 ind./m<sup>2</sup>), but also the Archiannelida (870 ind./m<sup>2</sup>), Oligochaeta (800 ind./m<sup>2</sup>), Nemertinea (620 ind./m<sup>2</sup>), Mollusca (1650 ind./m<sup>2</sup>) and Echinodermata (860 ind./m<sup>2</sup>) are abundant in comparison with the other stations.

Insert table 2 here

Total macrofauna density shows a significant linear trend and increases towards the north. This is very significantly correlated with median grain size and is mainly due to the dominance of the Polychaeta which repeat both trends. Among the other macrofauna

Insert table 3 here



groups only the Oligochaeta and Echinodermata show no linear trend but all groups including those two are clumped and all except the Echinodermata show significant or very significant correlations with median grain size (table 3). However, for the Crustacea the trend is opposite to that of the other macrofauna groups as they are more abundant in the finer grained sediments on the south end of the bank.

Insert table 4 here

Species composition: in this study, 37 species of Polychaeta, 4 species of Archiannelida, 12 species of Mollusca, 17 species of Crustacea and 3 species of Echinodermata have been found (table 4).

In all stations Hesionura augeneri is the most dominant species, representing almost 55 % of the macrofauna. In stations SB 1, SB 2, SB 3, SB 4 and SB 5 this species reaches numbers of 2000 (SB 1) to 7700 (SB 4) ind./m<sup>2</sup>, whereas in the southern area it is less abundant: between 20 (SB 8) and 790 (SB 10) ind./m<sup>2</sup>. Other dominant species on the Kwinte Bank are, in descending order: Protodriloides sp., Nemertinea spp., Oligochaeta spp., Protodriloides chaetifer, Macrochaeta helgolandica, Spisula spp., Microphthalmus listensis, Glycera capitata, Nephtys cirrosa, Bathyporeia elegans, Polygordius appendiculatus, Spio filicornis, Tanaissus lilljeborgi and Ophelia borealis.

Insert fig. 3 here

Fig. 3 represents the dendrogram resulting from the normal (Q) analysis, applied to all stations using all species except the Oligochaeta, Nemertinea and those recorded in one station only (with a frequency smaller than 10 %). Two major station groups can be distinguished. Group I contains three stations: SB 2, 3 and 4 (coarse to medium sand), group II contains the other stations: SB 1, 5, 6, 7, 8, 9 and 10. These stations, except SB 5 and SB 6, are characterized by fine sand. The same groupings are obtained using Polychaeta only. Group I included 53 species and group II has 48 species. In group I 14 species out of 28 Polychaeta, 6 species out of 11 Mollusca and 3 species out of 8 Crustacea are restricted to this group. The dominant species in group I are: Glycera capitata, Goniadella bobretzkii, Macrochaeta helgolandica, Polygordius appendiculatus, Protodrilus sp., Mytilus edulis and Spisula spp. The species restricted to this group and occurring with high density are Sphaerosyllis bulbosa, S. hystrix, Protodorvillea kefersteini, Ophryotrocha gracilis, Aonides paucibranchiata and Polycirrus medusa.

In group II 9 species out of 23 Polychaeta, 1 species out of 6 Mollusca and 9 species out of 14 Crustacea are restricted to that group. Species which are numerically dominant are Nephtys cirrosa, Spio filicornis, Ophelia borealis, Protodriloides chaetifer, Gastrosaccus spinifer, Tanaissus lilljeborgi and Bathyporeia elegans. Species exclusive to group II and with high frequency are Scoloplos armiger, Spiophanes bombyx and Scoelepis bonnieri. The increasing importance of Crustacea in group II is remarkable ( $\bar{N}_I = 20 \text{ ind./m}^2$  and  $\bar{N}_{II} = 131 \text{ ind./m}^2$ ) (table 4).

Many macrofauna species show clumping along the sandbank, but linear trends are not so frequent. They occur in Hesionura augeneri, Microphthalmus similis, both Streptosyllis species, Glycera capitata, Goniadella bobretzkii, Macrochaeta helgolandica, Polygordius appendiculatus, Protodrilus sp., Mytilus edulis and Spisula spp., with increasing density towards the coarser northern sediments, and in Scoelepis bonnieri, Tanaissus lilljeborgi and Bathyporeia elegans with increasing density towards the finer, southern sediments. Correlations with median grain size are uncommon and were only found for Hesionura augeneri, Goniadella bobretzkii and Macrochaeta helgolandica among the polychaetes, Protodrilus sp. among the archiannelids and Mytilus edulis and Spisula spp. among the mollusks, where they are positive, and Abra alba among the mollusks and Tanaissus lilljeborgi and Bathyporeia elegans among the crustaceans where they are negative.

Many of the commoner species show significant differences in density between the clusters. The exceptions are the Microphthalmus spp., Nephtys longosetosa, Scoloplos armiger, Scoelepis bonnieri and Ophelia borealis among the polychaetes, Protodriloides chaetifer among the archiannelids, Caecum glabrum and Abra alba among the mollusks, Pseudocuma longicornis, Tanaissus lilljeborgi and Megaluropus agilis among the crustaceans.

Species diversity: diversity of the macrofauna does not show any trends but is on average significantly higher in the northern part of the sandbank. Diversity is low at stations SB 1, 2, 3, 4, 5 and 10 and this can be explained by the dominance of Hesionura augeneri. In fact, diversity is negatively correlated with median grain size because of this. In station SB 8 Bathyporeia elegans is dominant.

Contrary to species diversity, the number of species shows a very significant linear trend and increases with increasing median grain size (table 3).

Meiofauna

Density: 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  $366 \pm 77 \text{ ind}/10\text{cm}^2$  and  $161 \pm 26 \text{ ind}/10 \text{ cm}^2$  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.

Nematodes and copepods show no trends in density and are not clumped along the sandbank (table 4). Ostracoda and Halacarida are more abundant in the northern part but Hydrozoa are more abundant in the southern part. Density of Ostracoda and Hydrozoa is correlated with median grain size, in an opposite way.

Nematoda:

In the ten sampling stations 1550 nematodes were identified. A list of the species with their relative abundance in each sample is given in table 6. 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. 4. Species occurring only once were eliminated (see table 6).

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 hagmeieri, Microlaimus annelisiae, Microlaimus sp. A., 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 and Cyatholaimidae sp. 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

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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, Chromadoridae sp. A and Cyatholaimidae sp. A. The Enoplidae also are rather abundant: Enoploides spiculohamatus, Oxyonchus sp. A, Rhabdocoma riemanni, Rhabdodemia 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 sp. A, 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, Daptonema stylosum, Gonionchus longicaudatus, Rhynchonema quemer, Rhynchonema scutatatum, 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 sp. A, Onyx perfectus, Gammenema sp. A Cyatholaimidae sp., Bathylaimus sp. A, Enoploides spiculohamatus and Viscosia sp. A. Twenty-seven species out of 78 are restricted to these four stations.

The division of these three groups corresponds to the decrease in the median particle size of the sand fraction. Stationgroup I has a median grain size larger than  $300\ \mu\text{m}$  and large amounts of gravel. The sand fraction of group II stations has a median grain size between  $230$  and  $300\ \mu\text{m}$ , with 2-7 % gravel. Group III contains the fine sandy stations whose median grain size is less than  $230\ \mu\text{m}$ , 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.

Significant clumping is frequent among nematode species, but linear trends are rare. In species occurring in three or more stations trends were only observed in the following cases: Odontophora sp., Gonionchus longicaudatus, Siphonolaimus sp.A, Bolbolaimus sp. A, Dasynemella albaensis, Leptonemella granulosa, Microilaimus monstrosus and M. ostracion, Monoposthia mirabilis, Pseudonchus sp.A, Ptycholaimellus sp.A and Bathylaimus sp. A; in these species density is significantly lower when median grain size is larger. Only in Desmodora schulzi, Actinosoma celtica and Chromadoridae sp. occurs the opposite phenomenon. Differences between north and south and between clusters are also rare, as are correlations with median grain size. Significant correlations were found for Odontophora sp., Daptonema stylosum, Gonionchus longicaudatus, Tubolaimoides tenuicadudatus, Xyala sp. A, Dasynemella albaensis, Microilaimus monstrosus, Microilaimus ostracion, Pseudonchus sp.A, Nannolaimus aff. guttatus and Bathylaimus sp. A where they are negative and in Desmodora schulzi, Desmodorella tenuispiculum and Ixonema sordidum where they are positive.

#### Nematode diversity:

Species diversity H and evenness J' are given in table 5. Both values are very high and no large differences among the stations are observed. Neither species diversity, nor number of nematode species show any clumping, trends or correlation with median grain size (table 4).

#### Copepoda

On the Kwinte Bank 1 cyclopoid and 65 harpacticoid copepod species were found. The latter belong to 8 families: Cylindropsyllidae (16), Ectinosomatidae (14), Paramesochridae (13), Ameiridae (13), Diosaccidae (5), Tachidiidae (2), Tetragonicipitidae (1) and Cleto-  
didae (1).

Generally, the Kwinte Bank harbors 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 station reveals two groups (fig.5). Group I clusters SB 2, 3, 4 and 5; group II clusters SB 1, 6, 7, 8, 9 and 10. The relative abundance of each species per station arranged according to these clusters is given in table 7. In group I the coarser sediment stations are clustered; they represent deposits with a mixture of sand (375-654  $\mu\text{m}$ ), gravel and shell. The fauna of

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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 eulitoralis, Leptastacus laticaudatus intermedius, Metacyclopsina 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 erythroptus, 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  $\mu\text{m}$ ) sands are found. The fauna is less diverse, and consists of 29 species, 12 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 herdmanni and Arenocaris bifida it shows a preference for finer deposits.

Clumping is very frequent in copepod species, but of the commoner species (dom. > 1%; freq. > 30 %) only a few show linear trends: Arenosetella sp. B, Thompsonula hyaenae, Kliopsyllus constrictus, Evansula pygmaea, Paraleptastacus espinulatus, Psammastacus remanei and Arenocaris bifida and in all these species density is greater in finer grained sediments to the south. A significant correlation with median grain size was found for Halectinosoma sarsi, Kliopsyllus constrictus, Paraleptastacus espinulatus and Arenocaris bifida, where it is negative, and for Diarthrodella secunda, where it is positive.

#### Copepod diversity

Diversity values range between 1.24 bits/ind. and 3.16 bits/ind., with the highest values in station group I. Diversity II and the number of species are significantly higher in the northern stations and both are positively correlated with median grain size (table 5).

## DISCUSSION

Macrofauna

Density: There is little published information on macrobenthos from offshore sandy bottoms, particularly sandbanks (Tyler & Shackley, 1980). Densities of macrofauna from the Kwinte Bank (10400 ind./m<sup>2</sup> in group I and 2400 ind./m<sup>2</sup> in group II) are generally higher than those recorded by other authors from the North Sea. McIntyre (1978) summarized data from sublittoral sediments: between 824 and 1007 ind./m<sup>2</sup> for fine sandy substrates, between 640 and 1557 ind./m<sup>2</sup> for coarse sands and 926 ind./m<sup>2</sup> for gravel. Dicks (1976) found 2719 ind./m<sup>2</sup> for Ekofisk in the western North Sea, Rachor & Gielach (1978) recorded 2716 to 13176 ind./m<sup>2</sup> for September-October samples of the German Bight over several years. Older values are much lower: Hagmeier (1923) recorded 116 ind./m<sup>2</sup> in the German Bight and 173 ind./m<sup>2</sup> in the N Borkum and NNW Eems estuary. Blegvad (1922) found 90 ind./m<sup>2</sup> in the Southern North Sea, Petersen (1918) recorded 284 ind./m<sup>2</sup> in the Kattegat and Stripp (1969) found between 315 ind./m<sup>2</sup> (coarse sand) and 690 ind./m<sup>2</sup> (medium sand) in the Helgolander Bight.

An intensive study of the Southern Bight of the North Sea was made by Govaere (1978) and Govaere et al. (1980). Three major zones were distinguished based on macrofaunal differences: an open sea zone, a transition zone and a coastal zone. Macrofaunal densities found in the open sea zone (2072 ind./m<sup>2</sup>) and transition zone (1613 ind./m<sup>2</sup>) are lower than those found in the Kwinte Bank, which is geographically located in the transition zone, but has a sediment similar to the open sea zone.

Comparison of densities found in the Kwinte Bank with those recorded in literature is difficult because we have used a sieve with a small mesh size (250µm). Small organisms such as interstitial polychaetes will be retained by our sieve, which was especially chosen as interstitial polychaetes proved to be very important in the sandbank system.

Species composition: Difficulties arise also in comparing the composition of the macrofauna of the Kwinte Bank with that of similar biotopes, for the reasons mentioned above. Interstitial polychaetes are generally not recorded or they are considered to belong the meiofauna, although species such as Hesionura augeneri may easily attain a length of 1 cm.

The segregation in two station groups is partially due to the larger number of interstitial polychaete species in group I and partially to Mollusca (more abundant in group I) and Crustacea (more abundant in group II).

The numerically dominant species in the open sea zone, adjacent to the Kwinte Bank, are in descending order: Spiophanes bombyx (constituting more than 50 % of the total fauna), Hesionura augeneri, Nephtys cirrosa, Eteone longa, Bathyporeia guilliamsoniana, Echinocardium cordatum, Scolelepis bonnieri, Glycera capitata, Anaitides subulifera, Spisula elliptica and Echinocyamus pussilus (Govaere et al., 1980). Species found exclusively in the open sea zone are Anaitides subulifera, Ophiura affinis, Tellina pygmaea, Echinocyamus pusillus, Branchiostoma lanceolatum, Exogone hebes, Macrochaeta helgolandica and Streptosyllis arenae. Of these only Branchiostoma lanceolatum and Exogone hebes were not found on the Kwinte Bank in this or previous studies (unpublished). Govaere et al. (1980) note Ophelia borealis as one of the dominant species of the transition zone, but they also found it in the open sea zone. On the Kwinte Bank O. borealis is found in 90 % of all stations but with rather low densities.

The macrofauna of the Kwinte Bank thus resembles that of the open sea zone of the Southern Bight. This is also reflected in the total number of species, which is 23 sp./m<sup>2</sup> for the open sea and 14 sp./m<sup>2</sup> for the transition zone, whereas it is 33 sp/m<sup>2</sup> for group I and 22 sp./m<sup>2</sup> for group II of the Kwinte Bank. Species number is thus nearly identical in group II and the open sea zone which are also very similar in sediment composition. The Kwinte Bank can therefore be considered as a biogeographical island in the transition zone.

Rappé & Govaere (in preparation) make a comparison between the macrofauna of the Kwinte Bank and the Buiten Ratel, another sandbank of the Flemish Banks (fig. 1). Both sandbanks have a similar sediment composition. Three species only were recorded on the Buiten Ratel but not on the Kwintebank.

Hesionura augeneri is the most common interstitial polychaete on the Kwinte Bank and it represents almost 55 % of the total macrofauna. It is known from the European Atlantic coast and the Mediterranean coast (Friedrich, 1937; Laubier, 1965; Hartmann-Schröder & Stripp, 1968; Westheide, 1972; Hartmann-Schröder, 1974; Wolff & Stegenga, 1975; Govaere et al., 1980; Rappé & Govaere, in preparation). Govaere (1978)



found Hesionura augeneri in fine to medium sand, whereas Wolff & Stegenga (1975) recorded it from medium sand only. Rappé & Govaere (in preparation) mention a preference for coarse deposits, Hartmann-Schröder & Stripp (1968) found it on fine sand mixed with shell gravel. On the Kwinte Bank, Hesionura augeneri has its highest densities in the coarser sediments (range 300 ind./m<sup>2</sup> - 710 ind./m<sup>2</sup>).

Another interstitial polychaete, Microphthalmus listensis, is also very common on the Kwinte Bank and shows a preference for fine and medium sands. This species is recorded from different sediments: fine and medium sand (Hartmann-Schröder & Stripp, 1968), medium sand (Govaere, 1978; Wolff, 1973) and coarse sand (Rappé & Govaere, in preparation). Very low densities (max. 35 ind./m<sup>2</sup>) are recorded from the Belgian coastal waters (Govaere, 1978). On the Kwinte Bank highest density was recorded in station SB 9 (330 ind./m<sup>2</sup>).

Nephtys cirrosa is found in all stations with a maximum of 120 ind./m<sup>2</sup> at SB 6. This species prefers fine and medium sand. It has been found by Tyler & Shackley (1980) to be one of the few macrofauna species on a sandbank in Swansea Bay. Many authors (Clark & Haderlie, 1960; Gibbs, 1969; Clark, Alder & McIntyre, 1962; Amoureux, 1968; Hamond, 1966; Wolff, 1973 and Kirkegaard, 1969) mention a strong influence of the sediment type on the distribution of the genus Nephtys. Although very similar in appearance, Nephtys cirrosa and N. hombergii appear to occupy distinct and separate habitats (Clark & Haderlie, op.cit.). The first species is found in clean sand whereas the second is more frequent in fine deposits. Indeed, N. hombergii has never been recorded on the ridge of the Kwinte Bank, nor in this study, neither in previously taken samples. It is only found in grabs from the surrounding channels where silt is present (unpublished results). Nephtys cirrosa seems to prefer a high energy environment, as opposed to N. hombergii, which was also observed by Hamond (1966). Alheit (1978) also mentions oxygen supply correlated with high energy and salinity as important factors determining the distribution of Nephtys species in the North Sea.

Glycera capitata, a widely distributed polychaete, reaches highest densities in the coarser deposits (range 100 - 210 ind./m<sup>2</sup>). Rappé & Govaere (in preparation) also note its preference for coarse and medium sand. Other authors mention its occurrence in different sandy substrata: medium and fine sand (Wolff, 1973; Govaere, 1978); fine sand, gravel and shell deposits (Harris, 1972 and Fauvel, 1923); coarse sand (Kirkegaard, 1969). Hartmann-Schröder (1974) mentions this species as euryoecious.

Spio filicornis, known as a widely distributed species, is found in all stations although with very low densities (range 10 - 80 ind./m<sup>2</sup>). This species occupies all sediment types (Hartmann-Schröder, 1971) with a preference for fine sand (Wolff, 1973).

Macrochaeta helgolandica is represented in group I (medium and coarse sand) with high densities (range: 300 - 710 ind./m<sup>2</sup>). In group II the species is less abundant (range: 3 - 100 ind./m<sup>2</sup>). It was first reported for the Southern North Sea and the Channel by Govaere (1978) and until then was only known from Helgoland (Friedrich, 1937 - type locality) and the Swedish coast (Banse, 1969) in coarse sand and shell deposits respectively.

Ophelia borealis, found in all stations except SB 4, is most abundant in SB 5 (90 ind./m<sup>2</sup>) and SB 6 (60 ind./m<sup>2</sup>). Distributional records suggest that this species is widely spread in the Arctic and the North Atlantic area. Rappé & Govaere (in preparation) found O. borealis on the Buiten Ratel mostly in medium and fine sand. Other authors also note this species from this type of sediment (Eliason, 1962; Hamond, 1966; Kirkegaard, 1969; Wolff, 1973; Govaere, 1978 as O. limacina). On the Kwinte Bank O. borealis inhabits also coarse sand (SB 3: 10 ind./m<sup>2</sup>; SB 5: 90 ind./m<sup>2</sup>)

Three important species of Archiannelida are recorded: Polygordius appendiculatus, Protodriloides chaetifer and a species of the genus Protodrilus. On the Kwinte Bank P. appendiculatus shows a preference for coarse and medium sands (group I) and its highest densities are recorded from SB 2 (130 ind./m<sup>2</sup>) and SB 4 (120 ind./m<sup>2</sup>). Rappé & Govaere (in preparation) did not find the species on the Buiten Ratel Bank. Protodriloides chaetifer reaches densities of 560 ind./m<sup>2</sup> (SB 5 and SB 10) and occurs in fine, medium and coarse sands. It has been recorded for the first time in the Belgian coastal waters (Rappé & Govaere, in preparation).

Spisula elliptica is common in muddy sand, muddy gravel, fine sand and shell gravel, whereas Spisula solida prefers sandy bottoms (Tebble, 1966). Rappé & Govaere (in preparation) note S. solida only from coarse sand and gravel.

Within the Crustacea, Tanaissus lilljeborgi and Bathyporeia elegans are the most common species on the Kwinte Bank. They both show a preference for fine sand. The highest densities are found in station SB 7 and SB 8 with values of 60 ind./m<sup>2</sup> and 80 ind./m<sup>2</sup> for T. lilljeborgi and 100 ind./m<sup>2</sup> and 190 ind./m<sup>2</sup> for B. elegans respectively.

On the Buiten Ratel Bank T. lilljeborgi did not occur in coarse deposits (Rappé & Govaere, in preparation). Wolff (1973) found the species in medium and fine sand. Bathyporeia elegans occurs in fine and medium clean sand on the Buiten Ratel Bank (Rappé & Govaere, in preparation) and at Firemore Bay (McIntyre & Eleftheriou, 1968). Vader (1966) also found a preference for this type of sediment.

The species composition of the Kwinte Bank is roughly comparable to the 'boreal off-shore sand association' described by Jones (1950) or the corresponding 'Venus gallina association' described by Petersen (1914), and also partially to the 'boreal off-shore gravel association' of Jones (1950). As has been indicated by Govaere (1978) for the communities of the Southern Bight, such an association of species is often better characterized by less frequent species than by dominant ones and especially the interstitial polychaetes and archiannelids seem to be very characteristic of the communities described by Petersen (1914) and Jones (1950). In this study we can report Hesionura augeneri, Microphthalmus similis, M. listensis, Streptosyllis arenae, S. websteri, Sphaerosyllis bulbosa, S. hystrix, Protodorvillea kefersteini, Ophryotrocha gracilis and Macrochaeta helgolandica. These species are only rarely recorded in ecological studies.

It is characteristic for the sandbank system that sessile, tube-building polychaetes are represented by a small number of individuals only, whereas the dominant forms are mobile and quickly burrowing organisms such as Hesionura, Microphthalmus and Nephtys which are able to withstand the sometimes extreme physical disturbance of the sediment caused by the strong tidal currents. Withers & Thorp (1978) have already pointed out that the ability of small crustaceans and polychaetes to rapidly re-enter the sediment after having been washed out is of great importance for their persistence in the system.

Species diversity: Govaere et al. (1980) found mean diversity values of 3.28 bits/ind for the open sea and 2.58 bits/ind. for the transition zone. Mean diversity of the macrofauna on the Kwinte Bank in September 1978 was 2.50 bits/ind., which is lower than diversity in the open sea zone, even more so when considering that diversity is near maximum during that month. Rappé & Govaere (in preparation) found values 2.14 bits/ind. in October 1977 and 1.34 bits/ind. in March 1978, after winter. These values were very comparable with those found on the Buiten Ratel Bank, i.e. 2.05 bits/ind. in October 1977 and 1.82 bits/ind. in March 1978. Although these banks

have a fauna which is essentially comparable to that of the open sea zone, the more stressed nature of the habitat is clearly reflected in a lower diversity of the community.

### Meiofauna

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<sup>a</sup>; 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 biotopes (McIntyre & Murison, 1973; Ward, 1973; Scheibel, 1973; Lorenzen, 1974; Platt, 1977; Moore, 1979<sup>a</sup>; 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<sup>2</sup> for the coastal zone, 1423 ind./10 cm<sup>2</sup> for the transition zone and 998 ind./10 cm<sup>2</sup> for the open sea zone. These values are averages over the period 1972-1974 and are too low due to sampling errors. Somewhat higher values have been reported for the coastal zone in 1977-1978, with between 1400 and 2860 ind./10 cm<sup>2</sup> over all stations and extremes of 80 and 8750 ind./10 cm<sup>2</sup> for single stations and an overall mean of 1650 ind./10 cm<sup>2</sup> over all seasons and stations (Heip et al., 1979).

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

Values found for the Kwinte Bank (384 ind./10 cm<sup>2</sup> for nematodes and 162 ind./10 cm<sup>2</sup> 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 et al., 1977; McLachlan et al., 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 SB 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 off-shore 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 unstability 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 substrata, where Graphonema, Dichromadora,

and Microilaimus 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. paramicrodonta, Microilaimus 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 by 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. When compared with the literature, groups II and III should be discussed together. The larger number of Araeolaimida and Monhysterida is typical of fine sands with a small amount of silt. Mc.Intyre & 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 abundances differ 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.

Species diversity: 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) en 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 4). 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 offshore sandy deposits are provided by Soyér (1970), Bodiou & Chardy (1973) and Bodiou (1975) for the French Catalanian coast and by Moore (1979a) 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 14 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 stationgroups 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 Catalanian coast (Soyer, 1970) and the coarse sand association of the Irish Sea (Moore, 1979a). Comparison with these studies suggest that the copepod faunas of medium and coarse ( $> 300 \mu\text{m}$ ) 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. remani, 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  $160 \mu\text{m}$ , which explains the dominance of interstitial forms (McLachlan et al., 1977; Moore, 1979b). 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 ( $200\text{--}300 \mu\text{m}$ ) of the Kieler Bight and includes typical representatives such as Scottopsyllus minor, Evansula pygmaea, Paraleptastacus laticaudatus, 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  $160 \mu\text{m}$  (Soyer, 1970; Bodiou & Chardy, 1973; Bodiou, 1975; Moore, 1979a) reveals a marked faunal change, reflecting the importance of the interstitial copepod barrier  $160 \mu\text{m}$  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, 1952; Renaud-Debyser, 1963; Renaud-Debyser & Salvat, 1963; Wells & Clark, 1965; Fenchel et al., 1967; Jansson, 1968; Moore, 1979b; Mielke, 1976; Harris, 1972). In particular, the fauna of Whitsand Bay in Cornwall (Harris, 1972) is very similar. This beach ( $300\text{--}350 \mu\text{m}$ ) 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 Metacyclops brevisetosa. The latter association is characterized by a higher diversity and contains many coarse sand indicator species previously described from Amphioxus-sands (Monard, 1935; Por, 1964a,b; Soyer, 1970).

Species diversity: 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 1979b) and are lower than those found for the deeper, more stable coarse and offshore fine sand stations of the Irish Sea (Moore 1979a). 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  $\mu\text{m}$ , 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.

General remarks on the benthic communities of the Kwinte Bank

Sublittoral sandbanks are usually high-energy environments dominated by severe hydrodynamical conditions resulting from wave and tidal current action. These determine the large-scale geomorphology and small-scale sedimentology of the sandbanks and thereby influence the composition of the fauna inhabiting them. It is clear that animals have to be adapted to survive in this extreme kind of environment and the morphological characteristics of animals living interstitially or burrowing in the sands have been noted and studied intensively since many years (Swedmark, 1964). Reductions in body size and appendages are common in many groups, as are the development of adhesive glands and sensory organs. The capacity of adaptation to the large variety of interstitial environments depends on the inherent morphological plasticity of each taxon and will be decisive in determining the structure of the community.

Traditionally, the number of niches in a substratum has been considered to depend on median grain size of the sand fraction, the sorting efficiency and the silt content (Wieser, 1959; Warwick & Buchanan, 1970; Heip & Decraemer, 1974; Moore, 1979a). With increasing median grain size the interstitial space becomes larger and more varied, thus providing for more niches for interstitial living species. The silt content determines whether these interstitial spaces will be clogged and therefore unavailable or not. Moreover, an increased silt content indicates a higher food supply and this may increase the number of burrowing macrobenthic species.

On the Kwinte Bank, the silt content is generally low and the number of large macrobenthic species is consequently low as well. On the other hand there is a great diversity of interstitial forms, which can be linked to the north-south gradient of decreasing grain size caused by the diminishing velocity of the tidal currents. The strong 'mesopsammic' character of the Kwinte Bank is due to the fact that all stations have sediments with a median grain size larger than  $200\mu\text{m}$ , a critical limit above which interstitial life can abundantly develop (Wieser, 1959; Fenchel, 1978). The median of  $300\mu\text{m}$  appears to be another distributional barrier for benthic taxa. Interstitial polychaetes become very abundant above this grain size although they occur in finer sediments as well. There are also changes in the copepod taxocene: in the fine sands of the Kwinte Bank most copepods are species of *Cylindropsillidae* and *Paramesochridae*: they are the smallest harpacticoids. In coarser sands, above  $300\mu\text{m}$ , the interstitial fauna is extended with *Ameiridae*, *Ectinosomatidae* and *Diosaccidae*. In gravels the much larger *Tetragonicipitidae* become abundant. In nemato-

des also a number of highly specialized species are present in coarse sands: the Epsilonematidae and Draconematoidea, which are not burrowers and show a very special way of locomotion ('leech-like'), contrasting with nearly all the other nematodes which are gliders.

The Araeolaimida, Desmodorida, Enoplida and Chromadorida all have a slightly higher number of species in coarse sand stations whereas the generally smaller Monhysterida have more species in fine sands.

Overall there is no difference between the number of nematode species from fine and coarse sand station. This indicates the high specialisation within the nematodes and correlates with their high diversity. It is not true for the other groups. There are more polychaete, archiannelid, mollusk and copepod species in coarse than in fine sand, and the converse is true for macro-crustaceans. Overall, macrofauna and copepod diversity and density are higher in coarse sediments. As in the nematodes, there is specialisation within the copepods, with Ectinosomatidae, Diosaccidae, Ameiridae and Paramesochriidae more abundant in coarse sands and Tachidiidae more abundant in fine sands, whereas only the Cylindropsillidae are about evenly spread over different kinds of sediments.

That macrofauna is in general less specialised than meiofauna depends probably on the scale of environmental heterogeneity as experienced by the individual organism; it is also shown by the fact that the number of stations in which a species was found is higher in macrofauna (3.4) than in meiofauna (2.6 for both nematodes and copepods).

The general influence of the substrate on the composition of benthic communities is also reflected in the similarity of the dendrograms based on presence-absence data. They are nearly similar for the three groups, only in nematodes are there three clusters instead of two, indicating again the more specialised nature of this group. This influence of substratum has been studied by e.g. Jones (1950) for the macrofauna, e.g. Soyer (1970) and Moore (1979a,b) for copepods and e.g. Wieser (1959), Warwick (1971), Ward (1973) and Tietjen (1980) for nematodes. A correspondence between macrofaunal and meiofaunal distributions has been observed by Guille & Soyer (1964), Juario (1975), Moore (1979a) and Govare *et al.* (1980). In general, macro- and meiofauna make up a single system of benthic communities (Moore, 1979a) and their distinction is purely a matter of convenience: only the smaller they get, the larger their specialisation and variability.

The correlation between community characteristics such as density and diversity and sediment characteristics such as median grain size is sometimes as high that a significant statistical correlation exists, and the linear north-south gradient in sedimentological characteristics is in many instances statistically correlated with gradients in community parameters but far less with species densities. As this may be due to the low abundance of many species no further explanation is sought here but it has to be pointed out that in abundant species as well linear correlations are relatively rare.

On the community level, the resemblance between the faunal composition of the Kwinte Bank and the open sea zone at the one and exposed sandy beaches at the other hand is also striking. This resemblance can only be correlated with the sediment characteristics and not with hydrodynamical conditions, which could explain the resemblance between sandbanks and beaches, nor with nutrient poor waters, which could explain the resemblance between sandbanks and offshore sediments. It seems as though a number of species is widely adapted and only a fraction of species is eliminated in more stressed environments. This would explain the diversity gradient found from low diversities in beaches, over intermediate diversities on sandbanks to high diversities in the open sea zone.

A last point is to consider the fact that this faunal resemblance occurs in organisms which have no pelagic life stages and whose dispersal must be slow. If the open sea sediments are the source of new colonisation, this diversity gradient could be explained by classical biogeographical theory by the distance between source and island.

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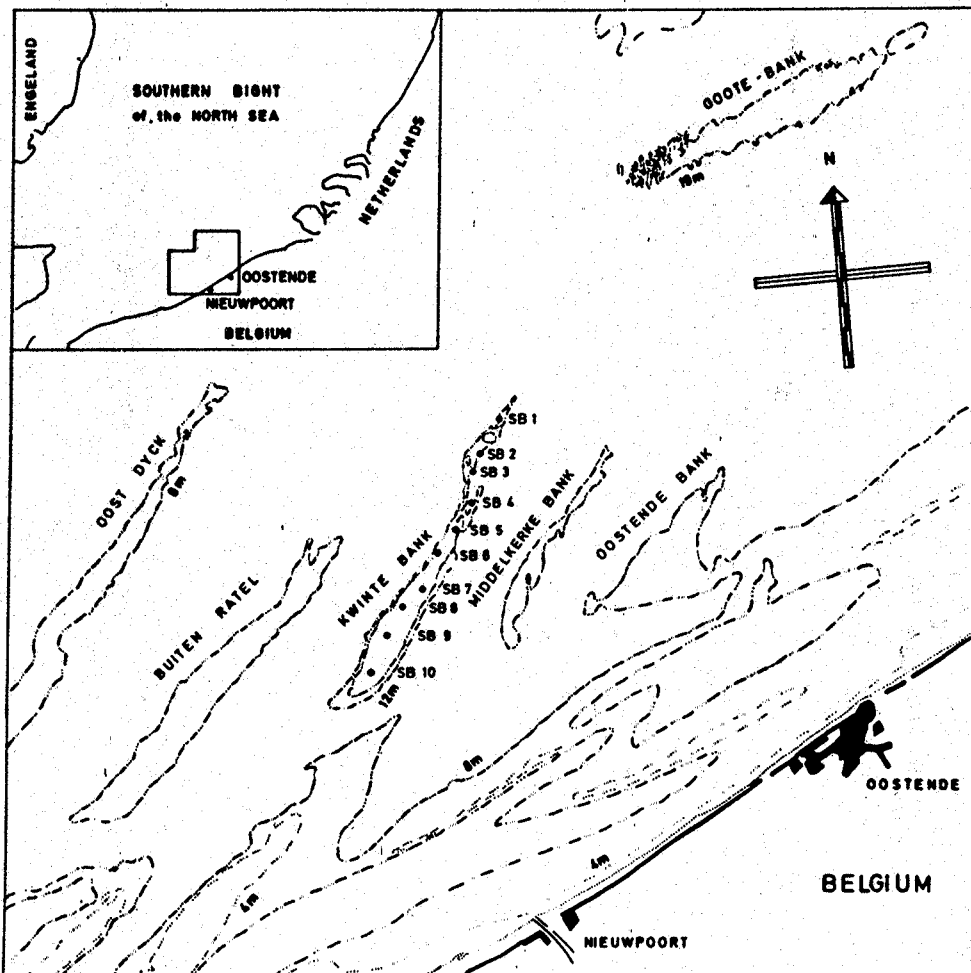


Fig. 1.

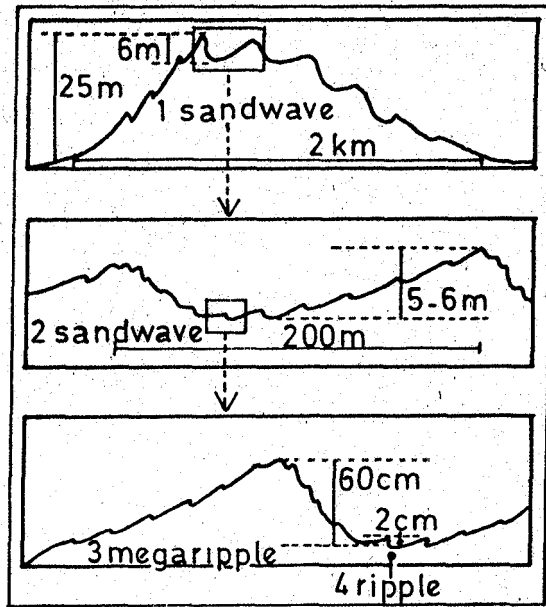
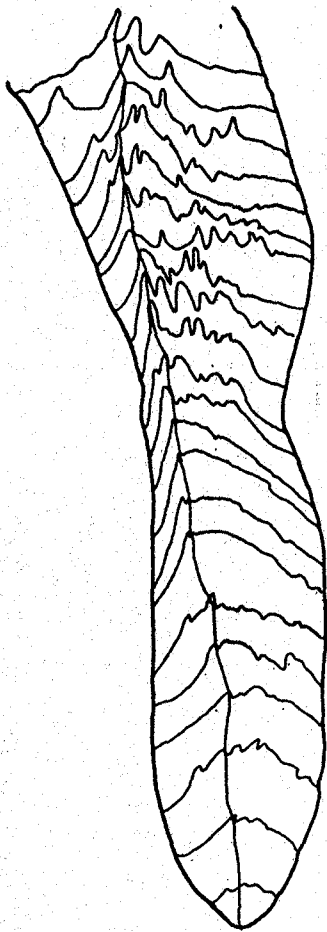


Fig. 2



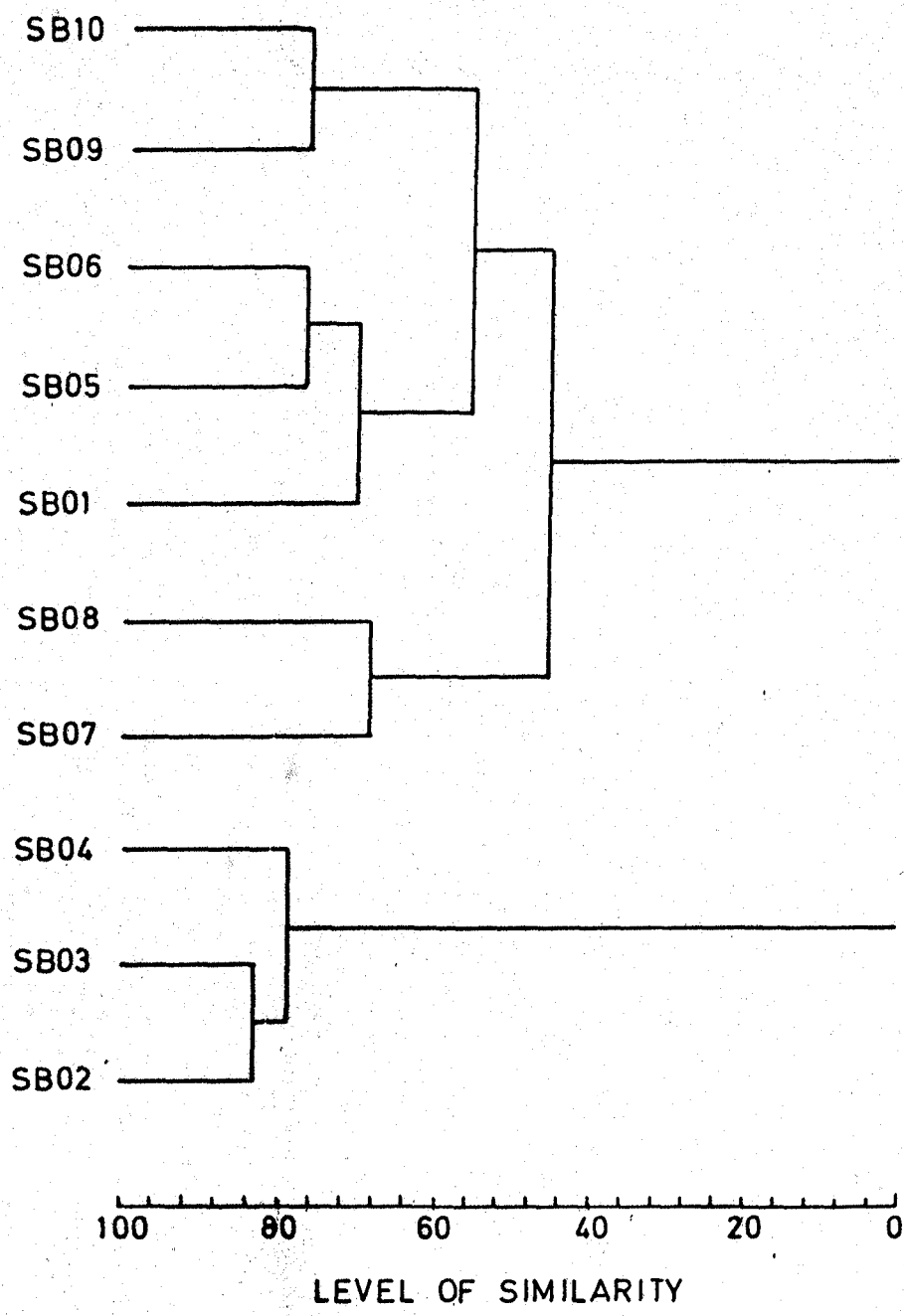


Fig. 3.

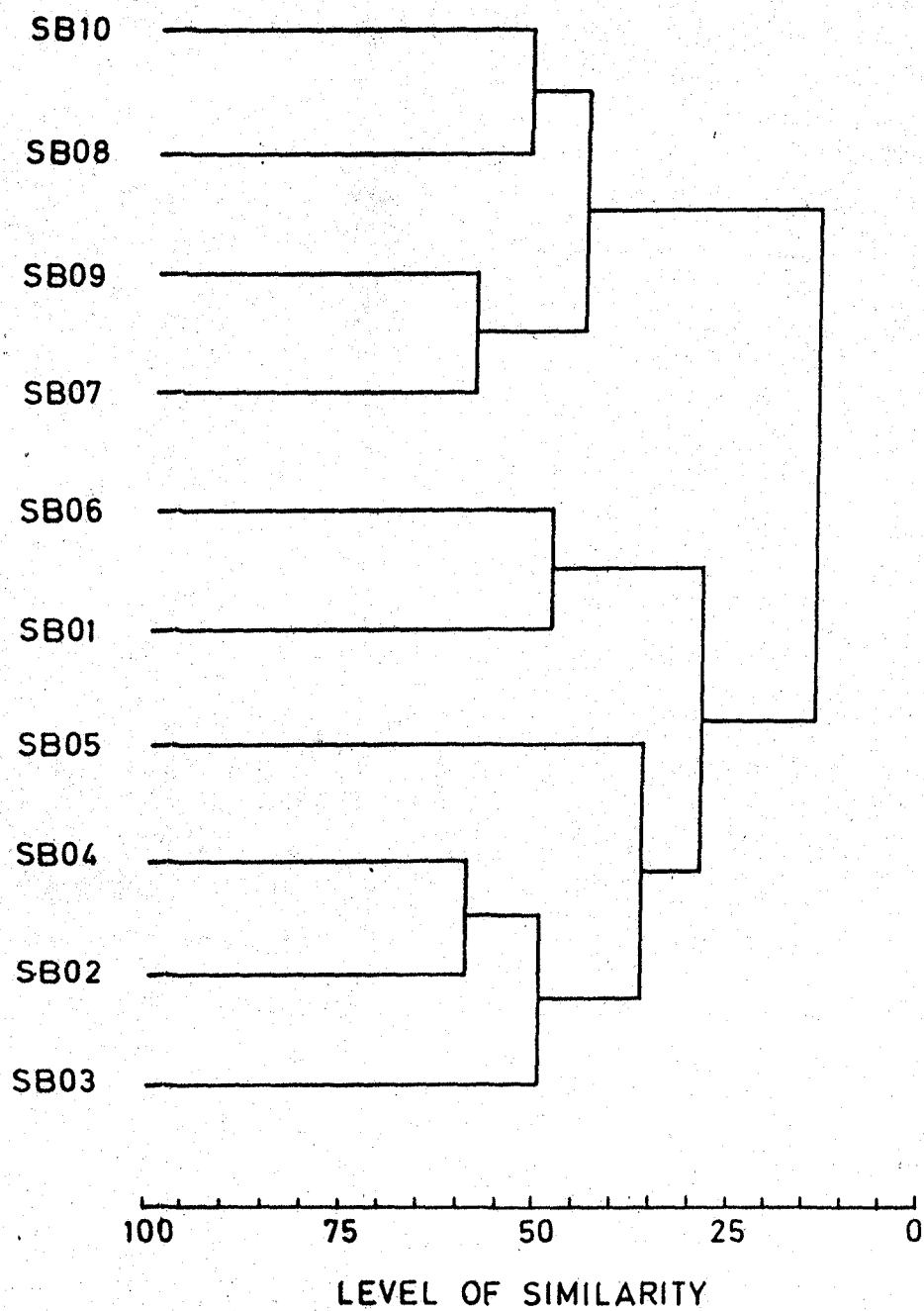


Fig. 4.

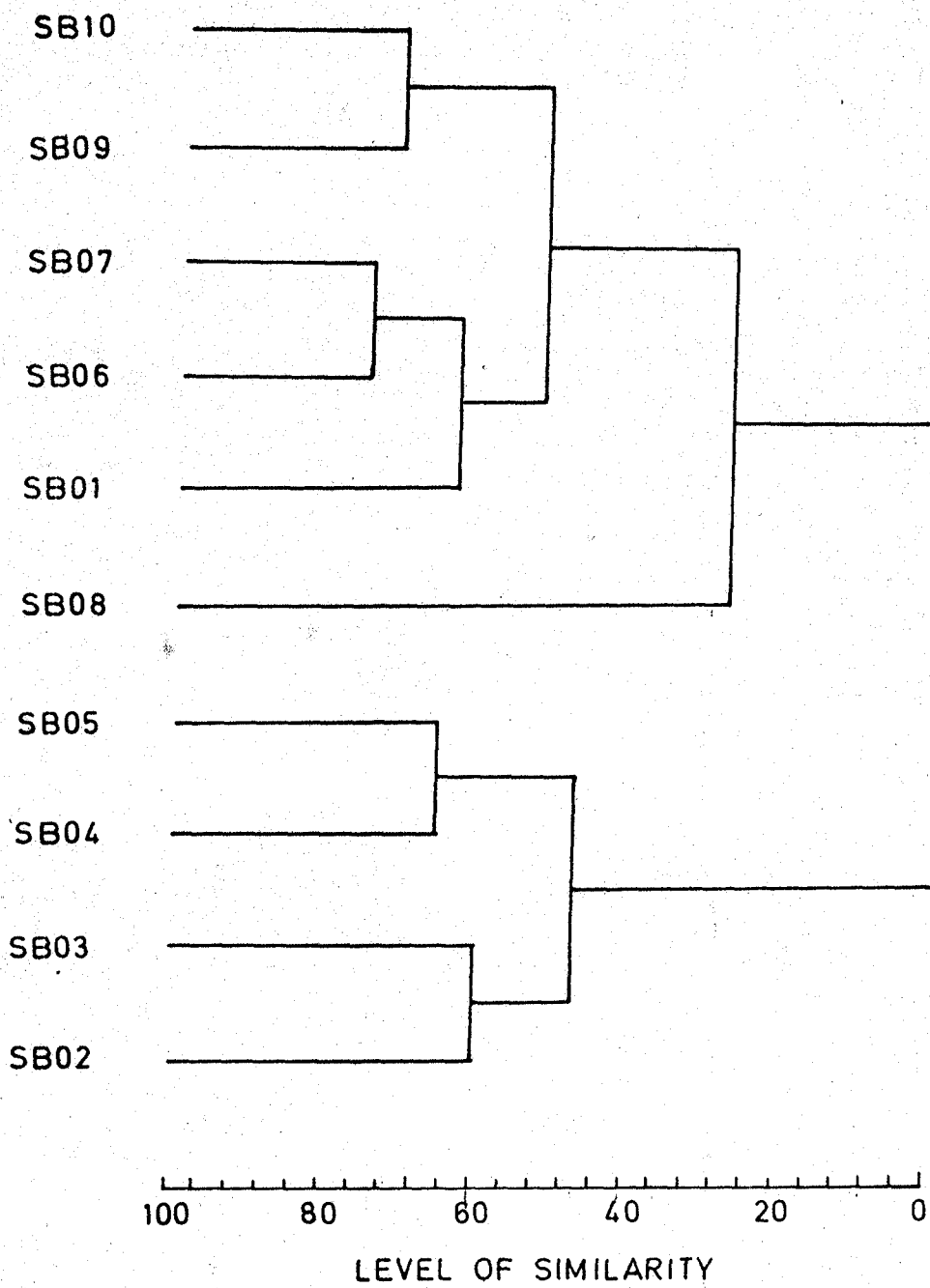


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Station	Coordinates		Depth (m)	Median particle diameter		Sorting		Mud (%) < 63 $\mu\text{m}$	Gravel (%) > 2000 $\mu\text{m}$	Organic matter %
	N. lat.	E. long.		( $\phi$ )	( $\mu\text{m}$ )	QD $\phi$	Sk $\phi$			
SB1	51°20'30"	2°41'40"	15.0	2.09	234	0.38	-0.19	1.61	6.84	1.46
SB2	51°19'45"	2°41'00"	16.0	1.41	375	0.38	+0.25	0	10.62	2.79
SB3	51°19'20"	2°40'45"	15.0	0.61	654	0.28	+0.07	0.30	3.42	1.37
SB4	51°18'40"	2°40'45"	16.0	1.32	402	0.30	+0.02	0.05	1.13	0.70
SB5	51°18'00"	2°40'10"	13.5	0.95	517	0.24	-0.11	0	0.24	1.14
SB6	51°17'30"	2°39'30"	15.0	1.83	281	0.36	+0.25	0.14	2.21	0.66
SB7	51°16'42"	2°38'57"	10.0	2.41	188	0.41	+0.37	0.12	0	1.81
SB8	51°16'20"	2°38'15"	14.0	2.28	205	0.40	+0.36	0	0	0.12
SB9	51°15'35"	2°37'35"	14.0	2.24	211	0.39	+0.32	0.15	0	0.78
SB10	51°14'48"	2°37'08"	14.0	2.12	230	0.38	+0.33	0.26	0	0.54

Table 4

	SBI		SB2		SB3		SB4		SB5		SB6		SB7		SB8		SB9		SB10		Mean	
	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A
MACROFAUNA																						
Polych.	230±99	69.3	542±55	72.1	682±329	80.7	1047±151	68.3	602±64	82.8	181±87	64.8	22±5	42.8	14±3	27.7	67±24	50.8	105±49	50.6	349±70	71.1
Archian.	18±14	5.5	160±58	21.3	104±34	12.3	87±28	5.7	68±14	9.4	31±11	11.1	+	1.9	0	0	27±19	20.4	61±46	29.5	56±12	11.4
Oligoch.	26±13	7.7	16±8	2.1	15±3	1.8	80±42	5.2	20±6	2.8	15±3	5.3	0	0	+	0.6	+	0.5	+	0.3	17±6	3.5
Nemertini	21±10	6.3	20±10	2.6	24±6	2.9	62±25	4.0	26±4	3.6	42±19	15.0	8±0.3	15.9	4±2	7.4	23±5	17.8	27±15	12.9	26±4	5.3
Mollusca	34±31	10.3	13±4	1.8	19±1	2.2	165±67	10.8	2±1	0.3	6±3	2.2	+	1.9	0	0	2±1	1.2	+	0.5	24±11	4.9
Crustacea	3±1	0.8	0	0	+	0.1	5±2	0.3	8±2	1.2	5±1	1.6	10±6	37.4	32±7	64.3	12±4	9.4	13±6	6.1	10±2	2.0
Echinod.	+	0.1	+	0.1	0	0	86±69	5.6	0	0	+	0.1	0	0	0	0	0	0	0	0	9±7	1.8
Total	332±132		751±119		845±358		1533±60		727±94		280±69		52±8		50±9		131±41		207±104		491±91	
MEIOFAUNA (N.10 <sup>2</sup> )																						
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	280±6	77.9	155±3	83.3	214±7	39.2	150±16	29.8	366±77	65.1
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	64±10	17.8	25±6	13.4	294±6	54.0	327±67	64.9	161±26	28.6
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	11±3	3.1	4±2	2.4	30±6	5.5	14±2	2.8	17±3	3.0
Ostracoda	+	0.1	14±2	1.9	19±8	7.2	32±8	3.2	20±2	3.4	0	0	0	0	0	0	0	0	0	0	9±3	1.6
Halacarida	+	0.1	6±1	0.8	19±1	7.2	18±4	1.8	11±4	1.9	+	0.2	0	0	0	0	0	0	6±3	1.2	6±2	1.1
Hydrozoa	0	0	4±4	0.5	2±2	0.8	+	0.1	2±1	0.3	+	0.2	4±4	1.1	2±2	1.1	6±6	1.3	7±2	1.4	3±1	0.5
Total	1234±272		771±126		266±29		983±35		581±22		192±43		358±17		186±9		544±12		503±86		562±77	

Table 2



	Macrofauna			Polychaeta			Nematoda			Copepoda		
	H'	J'	S	H'	J'	S	H'	J'	S	H'	J'	S
	SB1	2.02	0.95	29	0.95	0.26	15	3.60	0.84	34	1.96	0.58
SB2	2.28	1.44	29	1.44	0.35	19	4.55	0.88	49	2.74	0.74	17
SB3	2.10	1.33	34	1.33	0.31	22	3.29	0.82	25	2.58	0.66	19
SB4	2.61	1.37	42	1.37	0.32	21	3.96	0.75	47	3.15	0.86	22
SB5	1.55	0.65	25	0.65	0.19	12	3.36	0.83	25	3.08	0.63	37
SB6	3.16	2.21	27	2.21	0.74	10	3.68	0.84	33	1.98	0.65	11
SB7	3.28	2.69	24	2.69	0.93	12	3.51	0.92	30	2.06	0.64	15
SB8	2.53	1.83	16	1.83	0.95	8	3.39	0.88	20	1.24	0.63	5
SB9	3.05	2.02	24	2.02	0.65	11	4.58	0.87	54	1.92	0.49	17
SB10	2.43	1.22	20	1.22	0.38	11	3.91	0.92	31	2.62	0.72	14

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Table 7

	SB2	SB3	SB4	SB5	$\bar{X}_1$	SB1	SB6	SB7	SB8	SB9	SB10	$\bar{X}_2$
<b>CYCLOPINIDAE</b>												
<i>Metacyclopsina brevisetosa</i> Herbst, 1974 .....	7.7	-	11.6	19.9	12.8	-	-	-	-	-	+	+
<b>ECTINOSOMATIDAE</b>												
<i>Ectinosoma reductum</i> Bozic, 1954 .....	-	42.2	-	+	10.1	-	-	-	-	-	-	-
<i>Halectinosoma herdmanni</i> (T. & A. Scott, 1894) .....	-	+	-	-	+	-	11.0	5.3	4.0	-	-	1.2
<i>Halectinosoma erythropus</i> (Brady & Robertson, 1875) .....	2.8	4.1	2.5	-	1.7	-	-	-	-	-	-	-
<i>Halectinosoma sarsi</i> (Boeck, 1872) .....	-	-	-	-	-	+	+	1.4	-	-	+	+
<i>Halectinosoma tenerum</i> Sars, 1920 .....	2.0	-	-	-	+	-	-	-	-	-	-	-
<i>Halectinosoma distinctum</i> (Sars, 1920) .....	-	1.3	-	+	+	-	-	-	-	-	-	-
<i>Halectinosoma oblongum</i> (Kunz, 1949) .....	+	-	-	+	+	-	-	-	-	-	-	-
<i>Pseudobradya minor</i> (T. & A. Scott, 1894) .....	-	-	-	+	+	-	-	-	-	-	-	-
<i>Arenosetella germanica</i> Kunz, 1937 .....	-	-	-	+	+	-	-	-	-	-	-	-
<i>Arenosetella</i> sp. A .....	-	-	6.4	+	+	-	-	-	-	-	-	-
<i>Arenosetella</i> sp. B .....	-	-	-	+	+	-	-	-	-	+	1.1	+
<i>Arenosetella</i> sp. C .....	-	-	-	+	+	-	-	-	-	-	-	-
<i>Ectinosomatida</i> sp. A .....	-	16.0	-	+	3.8	-	-	-	-	-	-	-
<b>TACHIDIIDAE</b>												
<i>Euterpina acutifrons</i> (Dana, 1848) .....	-	-	+	+	+	-	1.7	1.4	-	+	-	+
<i>Thompsonula hyaenae</i> (I.C. Thompson, 1889) .....	-	-	-	-	-	-	-	1.4	-	+	-	+
<b>DIOSACCIDAE</b>												
<i>Amphiascus varians</i> (Norman & T. Scott, 1905) .....	-	2.5	-	-	+	-	-	-	-	-	-	-
<i>Amphiascus paracaudaespinosus</i> Roe, 1958 .....	+	-	-	-	+	-	-	-	-	-	-	-
<i>Bulbamphiascus</i> sp. A .....	-	-	-	-	-	4.2	-	-	-	-	-	+
<i>Robertgurneya ilievicensis</i> (Monard, 1935) .....	3.5	18.6	3.9	+	4.7	-	-	-	-	-	-	-
<i>Psammotopa phyllosetosa</i> (Noodt, 1952) .....	5.7	-	3.1	2.8	2.5	-	-	2.8	-	1.2	-	+
<b>AMEIRIDAE</b>												
<i>Ameira brevipes</i> Kunz, 1954 .....	-	+	1.4	13.6	6.9	-	-	-	-	-	-	-
<i>Ameiropsis brevicornis</i> Sars, 1907 .....	-	+	-	-	+	-	-	-	-	-	-	-
<i>Leptomesochra confluens</i> Sars, 1911 .....	-	-	-	4.2	2.1	-	-	-	-	-	-	-
<i>Sarsameira exilis</i> (T. & A. Scott, 1894) .....	-	-	-	-	-	3.1	-	-	-	-	-	+
<i>Sarsameira</i> sp. A .....	7.7	-	-	-	1.8	+	-	-	-	+	14.5	5.4
<i>Sicameira leptoderma</i> Klie, 1950 .....	-	-	2.2	+	+	-	-	-	-	-	-	-
<i>Interleptomesochra tenuicornis</i> (Sars, 1911) .....	-	1.3	-	-	+	-	-	-	-	-	-	-
<i>Interleptomesochra attenuata</i> (A. Scott, 1896) .....	-	+	-	-	+	-	-	-	-	-	-	-
<i>Interleptomesochra eulitoralalis</i> (Noodt, 1952) .....	1.0	+	-	29.7	15.0	-	-	-	-	-	+	+
<i>Parevansula mediterranea</i> Guille & Soyer, 1966 .....	-	-	-	+	+	-	-	-	-	-	-	-
<i>Ameiridae</i> sp. A .....	-	-	-	+	+	-	-	-	-	-	-	-
<i>Ameiridae</i> sp. B .....	-	-	-	+	+	-	-	-	-	-	-	-
<i>Ameiridae</i> sp. C .....	-	+	-	+	+	-	-	-	-	-	-	-
<b>PARAMESOCHRIDAE</b>												
<i>Paramesochra similis</i> Kunz, 1936 .....	-	-	-	+	+	-	-	-	-	-	-	-
<i>Paramesochra helgolandica</i> Kunz, 1936 .....	2.8	3.2	-	-	1.3	-	-	-	-	-	-	-
<i>Leptopsyllus</i> sp. A .....	-	-	1.6	-	+	-	-	-	-	-	-	-
<i>Diarthrodella secunda</i> Kunz, 1954 .....	3.8	4.4	14.9	3.6	5.0	-	-	1.4	-	+	-	+
<i>Apodopsyllus</i> sp. A .....	-	-	3.9	+	+	55.3	+	1.4	-	-	-	-
<i>Kliopsyllus holsaticus</i> s.str. (Klie, 1929) .....	1.0	-	9.7	-	1.2	+	+	6.9	-	2.5	8.6	4.6
<i>Kliopsyllus coelebs</i> (Monard, 1935) .....	-	-	2.1	+	+	-	-	-	-	-	-	-
<i>Kliopsyllus constrictus</i> s.str. (Nicholls, 1935) ..	-	-	-	-	-	-	-	1.9	5.4	5.4	10.0	5.5
<i>Kliopsyllus</i> sp. A .....	16.0	3.5	6.1	1.6	5.3	-	1.7	-	-	6.5	8.3	5.3
<i>Kliopsyllus</i> sp. B .....	4.4	-	-	-	+	1.4	1.7	-	-	5.6	+	2.3
<i>Intermedopsyllus intermedius</i> (T. & A. Scott, 1895) ..	2.8	+	3.7	-	+	-	-	-	-	-	-	-
<i>Scottopsyllus robertsoni</i> (T. & A. Scott, 1895) ..	-	-	-	-	-	-	-	1.4	-	-	-	+
<i>Scottopsyllus</i> sp. A .....	-	-	-	-	-	+	-	-	-	-	-	+
<b>TETRAGONICIPITIDAE</b>												
<i>Pteropsyllus consimilis</i> (T. Scott, 1894) .....	-	+	-	+	+	-	-	-	-	-	-	-
<b>CYLINDROPSYLLIDAE</b>												
<i>Cylindropsyllus laevis</i> Brady, 1880 .....	-	-	+	-	+	-	-	-	-	-	-	-
<i>Evansula pygmaea</i> (T. Scott, 1903) .....	-	-	-	+	+	+	3.4	1.2	-	5.4	6.7	4.6
<i>Stenocaris</i> sp. A .....	-	-	-	-	-	16.7	-	-	-	-	-	2.3
<i>Stenocaris</i> sp. B .....	-	-	-	-	-	9.1	-	-	-	-	-	1.3
<i>Leptastacus macronyx</i> (T. Scott, 1892) .....	-	+	+	+	+	-	-	-	-	-	-	-
<i>Leptastacus laticaudatus intermedius</i> Kunz, 1938 ..	36.6	+	21.4	8.7	13.6	6.0	39.2	36.0	9.8	65.8	41.3	43.1
<i>Leptastacus rostratus taurica</i> Marinov, 1974 .....	-	-	-	+	+	-	-	-	-	-	-	-
<i>Leptastacus minutus</i> Chappuis, 1954 .....	-	-	-	5.7	2.8	-	-	1.2	-	-	-	+
<i>Paraleptastacus espinulatus</i> Nicholls, 1935 .....	-	-	-	+	+	1.4	37.1	33.3	68.6	3.1	+	8.3
<i>Paraleptastacus holsaticus</i> Kunz, 1937 .....	-	-	-	+	+	-	-	-	-	-	-	+
<i>Psammastacus remanei</i> Noodt, 1964 .....	-	-	-	+	+	-	-	-	-	1.1	2.4	1.3
<i>Arenocaris bifida</i> Nicholls, 1935 .....	-	-	-	+	+	-	-	-	-	+	5.0	3.0
<i>Leptopontia curvicauda</i> T. Scott, 1902 .....	+	-	1.6	+	+	-	-	-	-	-	-	-
<i>Arenopontia subterranea</i> Kunz, 1937 .....	-	-	-	+	+	-	-	-	-	1.0	-	+
<i>Arenopontia</i> sp. A .....	-	-	-	2.6	1.3	-	-	-	-	-	-	+
<i>Syrticola flandrica</i> Willems & Claeys, (in press) ..	-	-	-	1.4	+	-	-	-	-	-	-	-
<b>CLETODIDAE</b>												
<i>Rhizothrix minuta</i> (T. Scott, 1903) .....	-	-	+	-	+	-	-	-	-	-	-	-