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# Nematode assemblages from subtidal sandbanks in the Southern Bight of the North Sea: effect of small sedimentological differences

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## Abstract

Nematode assemblages from four subtidal sandbanks belonging to different sandbank systems on the Belgian Continental Shelf were investigated both in spring and fall. The assemblages were characterised by different species composition patterns on the different sandbanks. This is in contrast to results of earlier studies which showed that neither meiobenthic nor macrobenthic taxa differed among these sandbanks. Although the sediments on these sandbanks could all be classified as medium sands, the use of Multiple Discriminant Analysis (MDA) suggested that median grain size and the proportions of median sand and very fine sand were the variables explaining the difference in nematode community composition. These findings emphasise the strong relationship between the relative abundance of nematode species and sediment composition. The influence of sand extraction on these sandbanks resulted in coarsening of the sediment, which had a direct effect on the nematode species composition. Diversity was not affected, indicating that nematodes inhabiting highly dynamic environments are well adapted to physical disturbance. The diversity at sandbanks is not necessarily very different from the surrounding areas, since in more offshore parts of the Belgian Continental Shelf, clean and rather coarse sands prevail and the differences in sediment composition are not sufficient to induce large differences in diversity.

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## 1. Introduction

The Belgian Continental Shelf (BCS), located in the Southern Bight of the North Sea, is characterised by the presence of extensive sandbank systems. These sandbanks differ considerably from the regular seabed, since strong hydrodynamic currents induce

changes in their topography. These changes are irregular (e.g. migration direction of superimposed bed forms changes over relatively short time intervals) (Trenteseaux, 1993; Houthuys et al., 1994; Lanckneus et al., 1994) and can be influenced by high wind speeds (Houthuys et al., 1994). These unique geological circumstances create an environment that is unique, especially for sediment-inhabiting animals. Moreover, these sandbanks act as internationally important areas for seabirds (Maes et al., 2000), indicating them as valuable potential marine protected

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areas. Alternatively, some of the sandbanks are concession areas for sand extraction (Maes et al., 2000), and the gullies between the sandbanks are important for fisheries, creating a conflict situation between human and natural interests.

Given the importance of the sandbanks for the functioning of the North Sea ecosystem on the Belgian Continental Shelf (e.g. nursery area for fish (Dewicke, 2001), feeding and wintering area for seabirds (Maes et al., 2000)), baseline data describing benthic life and explaining distribution patterns are needed in order to propose a sustainable management policy for these areas. Meiobenthic communities, and especially nematodes, are accepted to be very suitable for providing this kind of data. Nematodes show high abundances, a ubiquitous distribution, short generation times and are restricted to the sediment throughout their lives (Heip et al., 1985; Kennedy and Jacoby, 1999; Schratzberger et al., 2000).

Vanaverbeke et al. (2000) published data concerning the composition of meiobenthos on taxon level of all sandbanks systems (Flemish Banks, Hinder Banks and Zeeland Banks). However, on nematode species level, only three studies have been published (Willems et al., 1982; Vincx, 1990; Vincx et al., 1990). All of these focused on the same sandbank, Kwintebank, located in the Flemish Banks area. The nematode communities from this sandbank were clearly different from the communities sampled in the regular seabed, and diversity at the sandbank was significantly higher than at the adjacent area, but similar to the more offshore part of the BCS (Vincx, 1990).

This paper aims to fill the gap in knowledge of benthic life in highly dynamic environments in shallow coastal waters by (1) describing nematode communities from isolated sandbanks/sandbank systems ( $H_0$ : Nematode communities originating from different sandbanks are not different in terms of diversity and assemblage structure), (2) relating nematode communities to sediment granulometry ( $H_0$ : Differences in nematode communities are not related to differences in sediment composition), and (3) describing differences between nematode communities from the individual sandbanks and surrounding flat sea beds ( $H_0$ : nematode communities from the sandbanks and the surrounding seabed do not differ in terms of diversity and assemblage structure).

## 2. Material and methods

### 2.1. Study area

Sandbanks on the BCS are grouped into three major sandbank systems: the Flemish Banks, the Zeeland Banks and the Hinder Banks (Fig. 1). Detailed information on depth and orientation of these sandbanks can be found in Vanaverbeke et al. (2000). The crests of the Flemish Banks are situated some 4 m below MLLWS, while the crests of the other sandbanks are deeper (Zeeland Banks: below the 10 m depth line; Hinder Banks: well below the 10 m depth line) (Maes et al., 2000). Of each system, at least one sandbank was sampled for meiobenthos using a modified Reineck boxcorer. The Kwintebank, located within the Flemish Banks, was visited in February 1997, while the Noordhinder and Bligh Bank (both Hinder Banks) and the Gootebank (a Zeeland Bank) were sampled in February and October 1998. Stormy weather prevented an autumn sampling on the Kwintebank in 1997. At all sandbanks, seven stations were sampled: five of them were located at regular distances along the crest of the sandbanks; two additional stations were situated on the sides of the banks, thereby avoiding spatial pseudoreplication. On the Kwintebank, 10 stations were located on the crest of the sandbank, and two additional stations were sampled in the deeper channels neighbouring the sandbank. Station locations corresponded to those mentioned in Willems et al. (1982).

### 2.2. Sample collection and processing

The Reineck boxcorer was deployed three times per station and from each boxcorer, one subsample for meiobenthos and another one for sediment analysis were obtained using a perspex core (10 cm<sup>2</sup>). Meiobenthos was fixed with a hot (70°C) neutral formaldehyde tap-water solution (final concentration: 4%). Metazoan meiobenthic organisms were extracted from the sediment by centrifugation with Ludox (Heip et al., 1985). Macrofauna was excluded using a 1 mm sieve. All animals retained on a 38- $\mu$ m sieve were stained with Rose Bengal counted and classified to the taxon level. Results on meiobenthic taxon distribution patterns were published in Vanaverbeke et al. (2000). From two

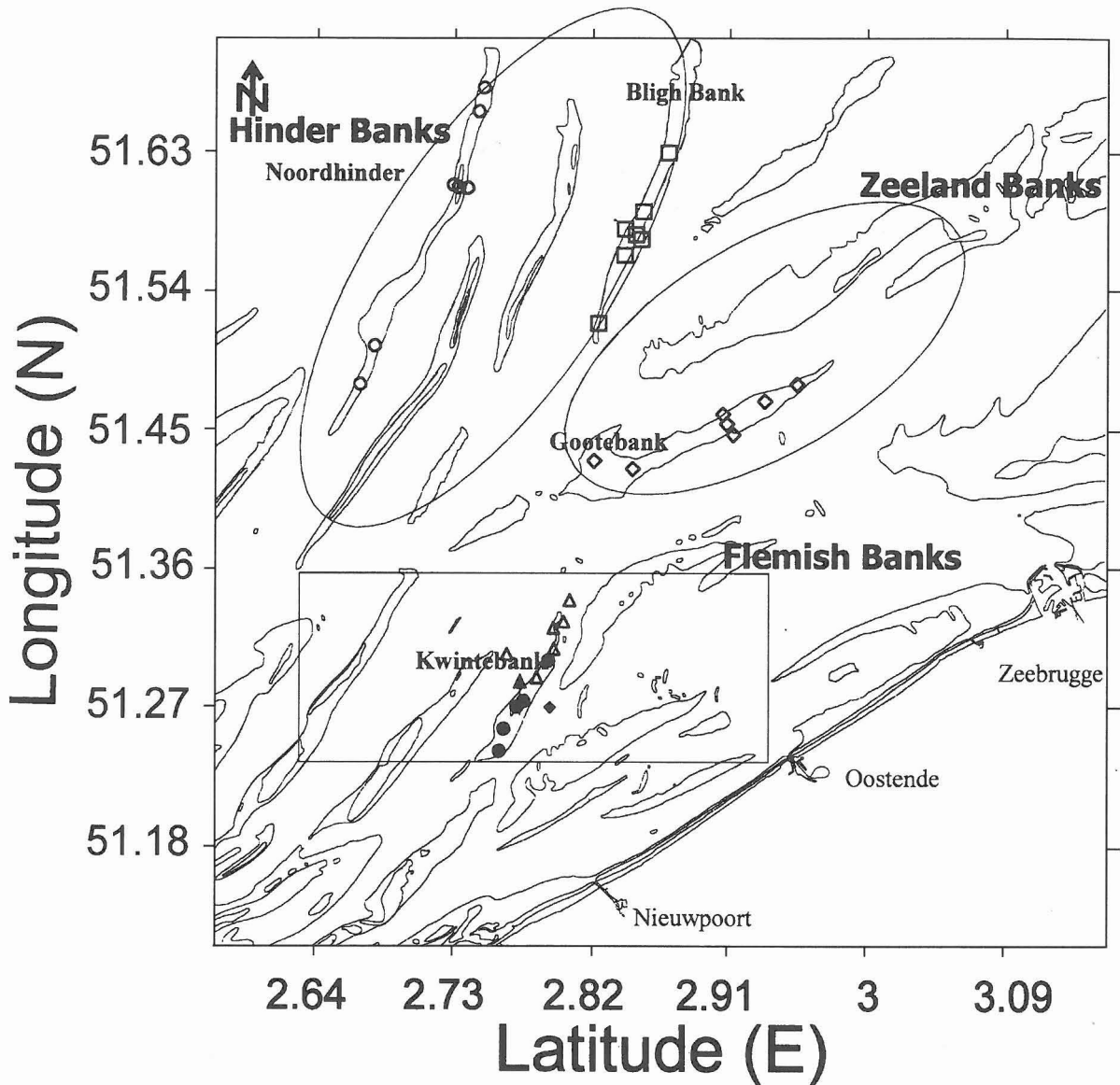


Fig. 1. Map of the Belgian Continental Shelf with indication of the sampling stations.

replicates, 200 nematodes were picked at random (following Vincx, 1996), transferred to glycerine and mounted on slides for identification to species level. When less than 200 individuals were present, all nematodes were identified.

Grain size analysis was performed using a Coulter LS100 Particle Size Analyser. Sediment fractions up to 1000  $\mu\text{m}$  were expressed as volume percentages,

while the fractions between 1000–2000  $\mu\text{m}$  and >2000  $\mu\text{m}$  were reported as mass percentages. Sediment fractions were defined according to the Wentworth scale (Buchanan, 1984).

The nematode community composition was analysed by TWINSpan (Hill, 1979a) on mean nematode species densities per station. Data reduction consisted of eliminating all species with an abundance



and DCA allows checking the validity of the groups discerned.

Non-parametric Multi-Response Permutation Procedures (MRPP) were used for testing multivariate differences among pre-defined groups (Mielke et al., 1976; Whaley, 1983; Zimmerman et al., 1985).

Diversity per TWIN group was calculated and expressed as Hill numbers of the order of 0, 1, 2 and  $+\infty$  (Hill, 1973), as recommended by Heip et al. (1988). The indices differ in their tendency to include or ignore the relatively rare species: the impact of dominance increases and the influence of species richness decreases with an increasing order of the diversity number. Differences in diversity between TWIN groups were tested using the non-parametric Kruskal-Wallis test since transformation of the data was not sufficient to meet the assumptions for ANOVA. When significant differences were observed, multiple comparisons between the TWIN groups were made, following Conover (1971). Differences in diversity between seasons per sandbank for each TWIN group were tested by a Mann-Whitney U test.

To assess the role of different sediment components in structuring the nematode communities, a Multiple Discriminant Analysis (MDA) was performed. This approach has rarely been used in marine data but has been proved to be powerful in unravelling patterns that are difficult to analyse using ANOVA or non-parametric alternatives (Shin and Fong, 1999). MDA allows determining which variables discriminate between two or more naturally occurring groups. These groups were the station assemblages based on the multivariate analysis of the nematode communities. Before entering the abiotic variables in the data matrix, correlated variables were removed in order to

prevent ill conditioning of the matrix. Finally, median grain size and proportions of clay, very fine sand, medium sand,  $>1000\ \mu\text{m}$  and  $>2000\ \mu\text{m}$  were retained. All variables were tested for ANOVA assumptions prior to the analysis. A forward selection procedure was performed in order to identify the most important variables. Only statistics for variables significantly incorporated in the model are reported. Squared Mahalanobis Distances were calculated to detect significant differences between groups (StatSoft, 1995), while factor structure coefficients identify those variables that are most associated with the discriminant functions. Analyses were performed using the STATISTICA software package (StatSoft, 1995).

### 3. Results

#### 3.1. Nematode community composition and diversity

Both TWINSPAN and DCA indicated the existence of 6 different nematode communities (Fig. 2). TWIN 1 comprised all stations from the Noordhinder, while the Bligh Bank stations were grouped in TWIN 2. The Gootebank stations were put together in a third group (TWIN 3). Kwintebank stations were divided into three groups: TWIN 4 comprised stations located in the northern part of the sandbank (plus channel station Kw12), while the southern stations were grouped in TWIN 5. TWIN 6 was a single station group containing the other channel station Kw13. MRPP showed these groups to be significantly different at  $p < 0.001$ . Table 1 lists the 10 dominant species per TWIN group and their relative abundance. Table 1

Twin 4		Twin 5		Twin 6	
<i>Neochromodora munita</i>	13,82	<i>Neochromodora munita</i>	16,52	<i>Sabatieria celtica</i>	16,56
<i>Theristus bastiani</i>	12,53	<i>Metadesmolaimus pandus</i>	12,81	<i>Sabatieria punctata</i>	13,38
<i>Theristus maior</i>	4,33	<i>Bathylaimus capacosus</i>	8,81	<i>Synonchiella riemanni</i>	12,74
<i>Enoploides spiculohamatus</i>	3,54	<i>Viscosia franzii</i>	8,81	<i>Microlaimus acinaces</i>	4,78
<i>Onyx perfectus</i>	3,15	<i>Theristus maior</i>	3,60	<i>Microlaimus marinus</i>	4,78
<i>Chromadorita</i> sp. 2	2,92	<i>Cyatholaimide</i> sp.	3,30	<i>Daptonema</i> sp.	4,14
<i>Cyatholaimide</i> sp.	2,92	<i>Bolbolaimus teutonicus</i>	2,80	<i>Metalinhomoeus</i> sp. 2	3,50
<i>Odontophora exharena</i>	2,64	<i>Pomponema loticum</i>	2,70	<i>Metalinhomoeus</i> sp. 1	2,87
<i>Calomicrolaimus parahonestus</i>	2,47	<i>Enoploides spiculohamatus</i>	2,60	<i>Odontophora exharena</i>	2,87
<i>Metadesmolaimus pandus</i>	2,25	<i>Microlaimus ostracion</i>	1,80	<i>Terschellingia longicaudata</i>	2,87

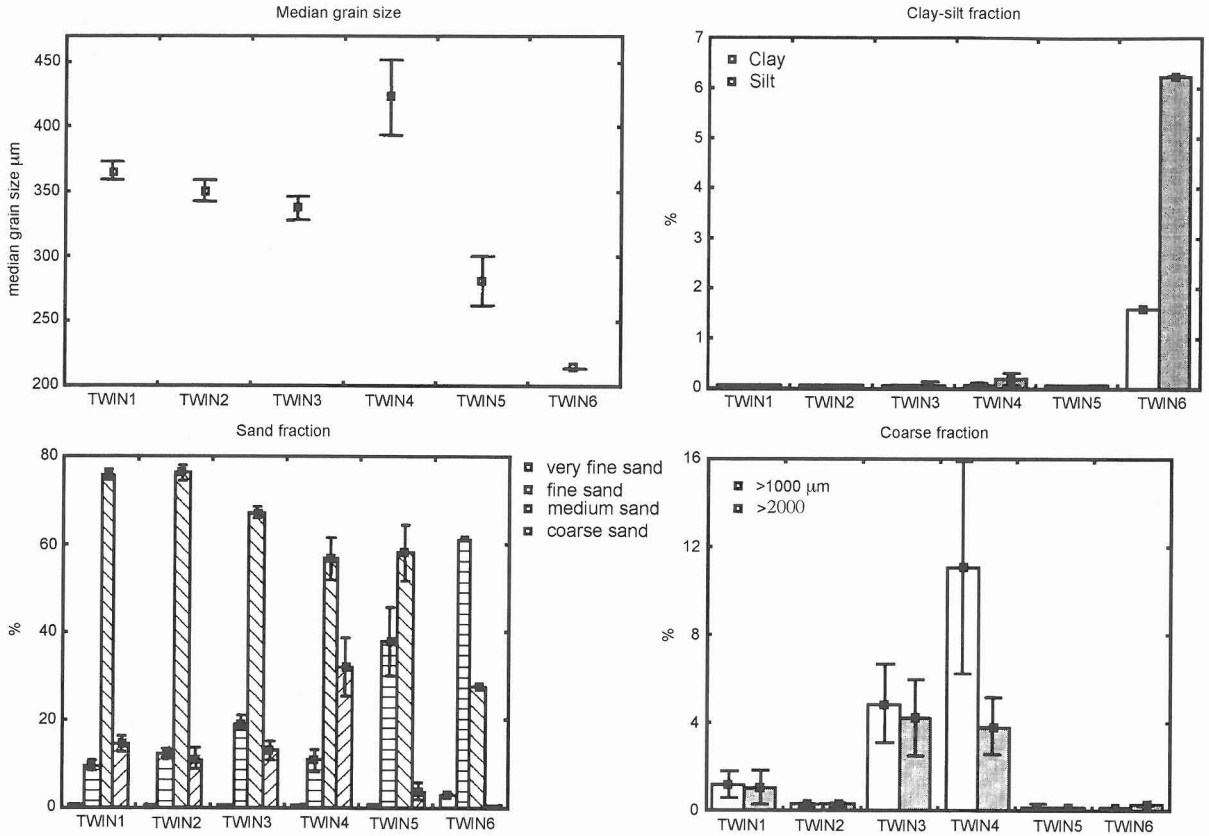


Fig. 3. Mean sediment characteristics (after Buchanan, 1984) per Twin group.

clearly shows the difference in the nematode communities: *Leptonemella aphanothecae* was dominant in both the Hinder Bank TWIN groups (TWIN 1 and 2) and *Neochromadora munita* was dominant in TWIN 4 and TWIN 5 (both Kwintebank), but differences in the species lists among all the groups are obvious.

Hills' diversity indices (with the exception of  $N_{\infty}$ ) were significantly different between the 6 groups (Kruskal-Wallis test:  $N_0$ :  $p < 0.01$ ;  $N_1$ :  $p < 0.001$ ;  $N_2$ :  $p < 0.01$ ). Multiple comparisons revealed that these differences were mainly due to a significantly lower diversity in the nematode communities of the Kwintebank groups compared to communities inhabiting

Table 2  
 Summary of the stepwise multiple discriminant analysis of the sedimentological variables of the Twin groups

Discriminant function	1	2	3	4
Eigenvalue	1,81	0,92	0,38	0,0012
Cumulative separation	0,58	0,87	0,99	100
Variable	Factor structure coefficients (correlations between variables in the model and the discriminant functions)			
% medium sand	-0,68	-0,48	0,41	-0,39
median grain size	-0,34	0,85	-0,18	0,36
% very fine sand	0,42	0,31	0,29	-0,8
%>2000 µm	0,16	0,32	0,49	0,8

Table 3

Squared Mahalanobis distances between the Twin groups with indication of the significance (\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ )

	Twin 1	Twin 2	Twin 3	Twin 4
Twin 1				
Twin 2	0.21 ns			
Twin 3	6.21 ***	5.92 ***		
Twin 4	10.34 ***	11.71 ***	8.01 ***	
Twin 5	19.53 ***	16.89 ***	9.42 ***	19.59 ***

the other sandbank sediments. No significant differences (at  $p < 0.05$ ) were recorded when diversity indices from February and October per sandbank were compared.

### 3.2. Relation with sediment granulometry

Mean sediment characteristics per station group are shown in Fig. 3. Although significant differences between all the variables (except % silt) were found (using ANOVA or Kruskal-Wallis), an explanation of the differences in community composition between the sandbanks/sandbank systems is not straightforward. Therefore, forward stepwise MDA was applied, elucidating the relative importance of the different sedimentological variables in discriminating between

the nematode communities. TWIN 6 (Kwintebank station 13) was excluded from the analysis since this was a single-station group, and caused ill conditioning of the data matrix. However, Fig. 3 clearly shows that sediments at this channel station are much finer than other sediments at the sandbank proper. This coincides with the presence of a relative large amount of clay-silt in the sediment, a feature almost absent in the other sediments. The first two discriminant functions explained 87% of the variation (Table 2), and since the eigenvalues of discriminant functions 3 and 4 were low, only the first two roots will be reported upon. Four variables were retained in the model (Wilks' Lambda: 0.13,  $p < 0.001$ ) and % medium sand and % very fine sand seemed to be the most important variables in discriminant function 1, while the second root was influenced by median grain size and % medium sand (Table 3, Fig. 4). Squared Mahalanobis distances and their significance level are listed in Table 3. Both Fig. 4 and Table 3 show that Kwintebank sediments are quite different from sediments found at the other sandbanks (Kwintebank southern stations along root 1; Kwintebank northern stations along root 2). Differences between sediments from the Gootebank and the Hinder Banks (Bligh Bank and Noordhinder) were significant as well, whereas no

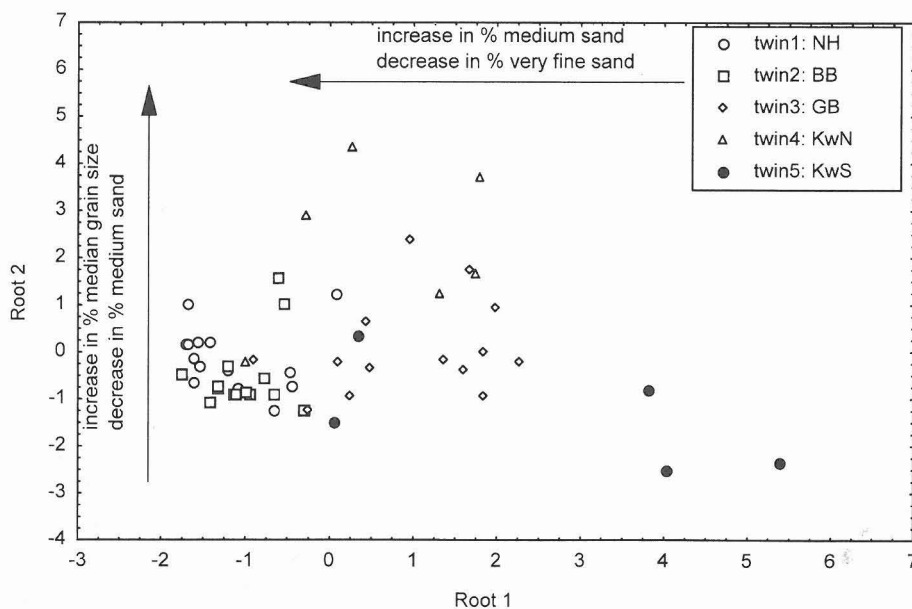


Fig. 4. Plot of location groups from stepwise MDA based on sediment granulometry.

significant differences were found between the Hinder Bank sediments (Noordhinder and Bligh Bank).

#### 4. Discussion

##### 4.1. Nematode community structure in relation to sediment granulometry

Both multivariate methods (TWINSPAN and DCA) discerned six different nematode assemblages on the sandbanks of the BCS. These groups were significant as revealed by MRPP, resulting in the rejection of the first null hypothesis (no difference in nematode communities from different sandbanks/sandbank systems).

However, a study of all the meiobenthic communities of the sandbanks on the BCS indicated that geographical position (e.g. sandbank/sandbank system) was not important in structuring the communities: stations originating from the same sandbank were distributed over different groups in multivariate analyses (Vanaverbeke et al., 2000). This was due to the specific sediment preferences of rare taxa, while the same study indicates that the chance of finding nematodes is independent of sediment composition. Studies on macrobenthic communities also failed to reflect the difference in sandbank systems (Coenjaerts, 1997; Philips, 1998). Once again, these results stress the importance of using nematode species data in order to distinguish differences in benthic life: the presence of nematodes as a taxon is independent of the sediment composition (Vanaverbeke et al., 2000), while the species composition of the nematode communities is mainly structured by the sedimentological features (Vanreusel, 1990; Vincx et al., 1990). The dominant species in TWIN groups 1 to 5 are all typical of clean, well-oxygenated sands devoid of mud (Vincx, 1989; Vanreusel, 1991), while the community composition of the fine-grained channel station TWIN group 6, dominated by two *Sabatieria* species, indicates a poor oxygenation of these sediments (Steyaert et al., 1999; Boyd et al., 2000). This points to a major difference in the ecology of sandbank sediments compared to the regular seabed in certain areas.

Personal observations confirmed these results: sediment cores obtained from the channel station

showed black sediments at a few cm depth, indicating reduced and oxygen-depleted sediments, while this was never the case on the sandbank crests.

Although generally the different communities reflect the geographical position of the sandbanks, this position alone offers a poor explanation of the existence of well-delineated groups. The existence of different nematode communities in the Southern Bight of the North Sea is often linked to differences in sediments (eg. Vincx, 1990; Vincx et al., 1990 and references therein), but in their studies a wide variety of sediments, from clay-silt to coarse sand, were compared. The present study investigated nematode communities from sediments belonging to a single sediment class: medium sand (median grain size: 250–500  $\mu\text{m}$  (Buchanan, 1984)).

Therefore, MDA was applied to elucidate the relative importance of the different sedimentological features. A graphical presentation of root 1 vs. root 2, explaining 87% of the variation in the sedimentological data (Fig. 4) revealed that groupings based on sedimentological data matched the biological groupings based on nematode species abundance data. Squared Mahalanobis distances confirmed these findings, emphasising the great differences between the Kwintebank groups and the other sandbanks, the close resemblance between the Hinder Bank groups and the intermediate position of the Gootebank. The identical groupings of both the biological and sedimentological data are due to the structuring effect of the sediment granulometry on the nematode community composition.

The separation of the Kwintebank stations into a northern and a southern group based on the nematode assemblages was confirmed by granulometric differences associated with the second discriminant function (median grain size and % medium sand). Indeed, median grain size reached highest values in this TWIN group (Fig. 3). These coarser sediments are probably a result of intensive sand extraction activities occurring in this area, where up to 20 cm of sediment is removed each year (Bonne pers. comm., 2002).

Sand extraction is known to induce coarsening of the sediment (Anonymous, 1993). Although such activities have a severe impact on macrobenthic communities (Kenny and Rees, 1996; Desprez, 2000), the influence on nematode diversity seems to be less drastic. Diversity in this area was not significantly different from the southern part of the



sandbank, indicating that these nematode species surviving in this area are well adapted to frequent physical disturbance of their environment. Their continuous reproduction strategy renders the community less vulnerable than for instance the macrobenthos, where a disturbance event during the recruitment period can destroy the population until the next recruitment. Another advantage of the continuous reproduction strategy is the constant presence of individuals, facilitating recolonisation of disturbed areas, while recolonisation of a sediment extraction area by macrobenthos can take more than 2 years (Kenny and Rees, 1996). Moreover, Schratzberger and Warwick (1999) demonstrated that nematodes living in a coarse sandy environment are less influenced by physical disturbance than are nematode species inhabiting muddy sediments. Since sandbank sediments can be considered a dynamic environment, nematode communities surviving here must be adapted to a regularly changing environment.

Differences between the other sandbanks are mainly associated with the first root, showing that sediments at the Gootebank have intermediate medium sand content, compared to the Kwintebank and both Hinder Banks. Differences between these Hinder Banks are not significant. The nematode communities of the latter

sandbanks also show the highest level of resemblance (Table 1): among the 10 dominant species, 4 are common (*Leptonemella aphanothecae*, *Microloaimus marinus*, *Desmodora schulzi* and *Stephanolaimus elegans*) or closely related (species within *Chromaspirina*). Although all these communities live within the same sediment category (medium sand) the second null hypothesis (differences in nematode community composition is not related to sediment granulometry) should be rejected, again emphasising the extreme way in which the presence/absence or relative abundance of nematode species is influenced by minor differences in sediment composition.

#### 4.2. Nematode diversity and differences with surrounding channels

Nematode diversity followed the general pattern already described in Vanaverbeke et al. (2001): diversity of nematode communities on the BCS increases with distance from the coast. This was attributed to sedimentological differences, higher offshore diversity being associated with clean, coarser sand rather than with finer-grained coastal sediments where anoxia resulting from eutrophication can have a drastic impact on the nematode communities, especially

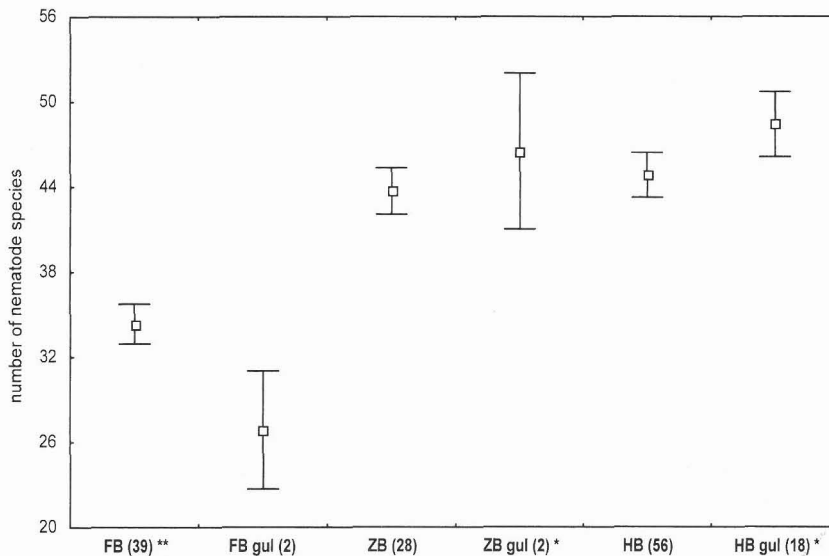


Fig. 5. Mean nematode species number ( $\pm$  SE) for different areas on the BCS (FB: Flemish Banks; FB gul: Flemish Banks gullies; ZB: Zeeland Banks; ZB gul: Zeeland Bank gullies; HB: Hinder Banks; HB gul: Hinder Bank gullies). \* Data from Vanaverbeke et al. (2001). \*\* Data recalculated from Vanaverbeke et al. (2001) and the present study. The number of species registered is indicated between brackets.

on the east coast (Steyaert et al., 1999). Lowest diversity in this study was indeed associated with the finest sediments (Twin groups 5 and 6) at the Kwintebank. Comparing nematode species numbers from sandbanks and the surrounding area was done using the new data presented in this study and the compilation of data on the BCS listed in Vanaverbeke et al. (2001) (Fig. 5). Statistical comparison of these data is not recommended, since differences in data collection might influence the reliability of the results of such testing, but Fig. 5 clearly demonstrates that differences between the sandbanks and the surrounding areas are very obvious in the Flemish Bank area. This is probably because differences in sediment composition between the sandbanks are largest in that area. Since a strong hydrodynamic regime occurs around sandbanks, sediments are coarser and saturated with oxygen, while in the channels, fine sediment particles can settle to the seabed, and oxygen is not refreshed as often as in the more dynamic sandbank sediments. The lower diversity in fine-grained sediments, associated with low oxygen content or oxygen depletion, has been documented already (Steyaert et al., 1999). When sediments in the channels consist of clean sands (e.g. those sediments in the Hinder Bank area and the Zeeland Bank area), nematode diversity increases and can be even slightly higher than on the sandbanks, possibly a result of the stronger hydrodynamic circumstances prevailing on the sandbanks. In these areas, the third hypothesis (no difference in nematode diversity between sandbanks and surrounding seabed) should not be rejected, while in the Flemish Bank area the compiled data indicate the existence of marked differences.

## 5. Conclusions

This study shows that nematode assemblages from isolated sandbanks differ. Such differences were not found in investigations of spatial patterns on the same sandbanks using data on meiobenthic and macrobenthic taxon distribution. This emphasises the high spatial resolution obtained when nematode species data are used to describe possible differences in sediment ecology. Although all sediments belonged to a single sediment category (medium sand), it is shown that the median grain size and both the medium sand

and very fine sand contents are important variables explaining biological differences. These findings emphasise the extreme way in which nematode species composition can reflect minor differences in sediment composition.

Nematode diversity on the sandbanks is not necessarily very different from diversity in the surrounding areas but dependent on local variations in sediment granulometry.

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