



# Changes in nematode communities at the long-term sand extraction site of the Kwintebank (Southern Bight of the North Sea)

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## Abstract

We investigated the long-term effects of sand extraction activities on the nematode communities from the Kwintebank. Although changes in nematode community composition cannot be completely uncoupled from natural processes, we suggest that the morphological changes in the sandbank and physical disturbance associated with the dredging activities indeed affected nematode community composition. Nematode diversity did not change since the start of the extraction activities but nematode community composition changed significantly. The SIMPER routine identified predatory nematodes to be important for the within group similarity at the start of the exploitation, while similarity in 1997 and 2001 was determined by the contribution of deposit feeding nematodes. In addition, long nematodes, vulnerable to physical disturbance became less important. These changes are attributed to long term changes in sediment characteristics in combination with additional short-term disturbances by the creation and filling of dredge furrows which are related to the extraction activities.

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## 1. Introduction

Due to an increasing demand for suitable sands needed for construction works and other purposes (e.g. beach regeneration), in combination with increasing costs involved with sand extraction on the main land, sand extraction at sea offers a valuable alternative to sustain the growing demand for aggregates.

The effect of sand and aggregate extraction on the marine environment was studied mainly through assessing eventual changes in bottom topography, sediment composition and benthic macrofauna (see reviews by Newell et al., 1998; Boyd et al., 2004). Most of these studies documented a decrease in diversity, density and biomass of the macrobenthic species within the extraction areas (Kenny and Rees, 1994; Deprez, 2000; van Dalfsen et al., 2000; Sardá et al., 2000; van Dalfsen and Essink, 2001; Guerra-Garcia et al., 2003; Newell et al., 2004; Simonini et al.,

2005). However, dredging in a sandy gravel deposit in the southern North Sea did not induce such dramatic changes (Robinson et al., 2005) suggesting that impacts of extraction activities are site specific and dependent on both local sedimentological/topographical characteristics of the site and the ability of the local macrofauna to cope with the induced disturbance. However, many of these studies were designed to investigate the initial effect of extraction activities, while habitat changes due to long-term sand extraction cause macrofaunal assemblages to change as well (Deprez, 2000).

On the Kwintebank, a sandbank located on the Belgian Continental Shelf (BCS) in the Southern Bight of the North Sea, sand extraction has taken place since 1976. At least 75% of all sand extracted from the BCS originates from the Kwintebank, due to the presence of suitable sands and its close location to the harbour of Oostende (Degren-dele et al., in press). Total amounts of sand extracted from the BCS increased from 29,000 m<sup>3</sup> y<sup>-1</sup> in 1976 to 1,700,000 m<sup>3</sup> y<sup>-1</sup> in the mid 90s. Maximum exploitation was recorded in 2001 (1,900,000 m<sup>3</sup> y<sup>-1</sup>).

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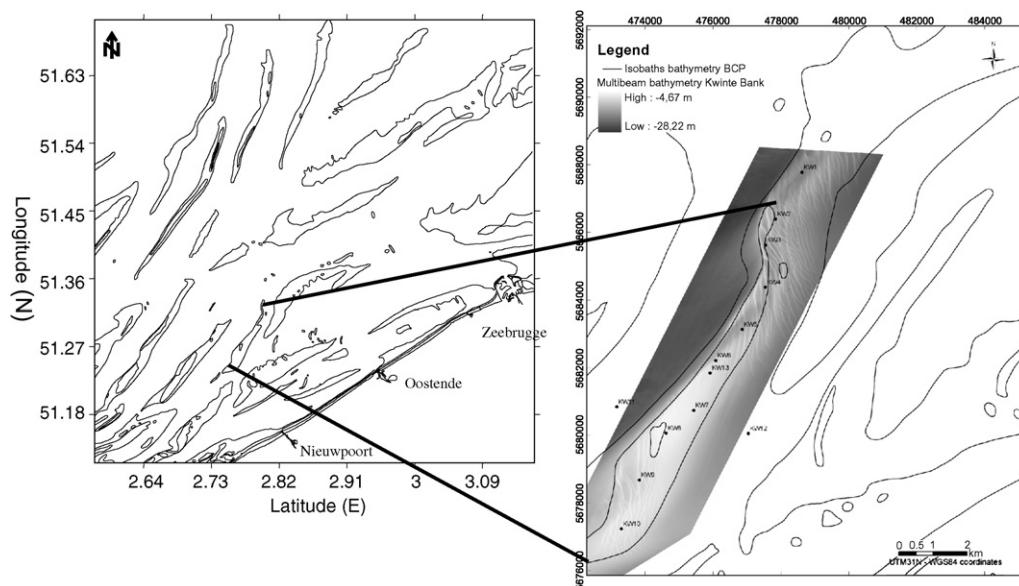


Fig. 1. Map of the Belgian continental shelf and detailed location of the sampling stations on the Kwintebank (Maps redrawn from UGent – RCMG and Federal public service economy, SMEs, Self employed and energy – Fund for sand extraction).

Extraction activities on the Kwintebank were concentrated both in the northern and central part of the Kwintebank (Degrendele et al., in press). Investigating the bathymetric and morphological evolution of the sandbank by single beam profiles, Degrendele et al. (in press) observed the formation of a depression in the central Kwintebank since 1992, which reached a depth of 5 m after 7 years. Later on, in the period 1999–2003, an additional deepening of about 0.5 m occurred.

In this paper, we aim to investigate the effects of long-term extraction activities on the Kwintebank on the nematode communities. Nematodes are accepted to be an ideal biological tool for detecting changes in the benthic environment (Kennedy and Jacoby, 1999).

However, no detailed studies on the response of nematodes in particular and meiobenthos in general to sand extraction are available. Only Bonne (2003), Vanaverbeke et al. (2002) and Vanaverbeke et al. (2003) provided evidence that meiobenthic life was negatively impacted. These studies were limited to a single sampling campaign in 1997 and showed that both harpacticoid communities and nematode communities have changed since the early extraction period in 1978. For both taxa, a decrease in vulnerable large organisms was observed as well. However, repeated sampling campaigns are needed to fully understand the effects of sand extraction on the benthos in order to avoid possible bias due to sampling an exceptional situation.

In this study, we analyse changes in nematode community characteristics (diversity and community composition) from the Kwintebank by analysing the available data on the period 1978–2001, spanning a period where extraction activities were ranging from low to very high. To our knowledge, this is the only study presenting very long-term data (23 years) with respect to the effect of sand extraction

on marine benthic life. We investigate the hypotheses of no changes in diversity and community composition between periods with different extraction intensities.

## 2. Material and methods

### 2.1. Collection and treatment of samples

The analyses presented in this report are based on historical data from sampling campaigns conducted in June–September 1978 (Vincx, 1986), February 1997 (Vanaverbeke et al., 2002) and December 2001. The samples collected in 1978 are considered as samples from the period before the intense sand extraction activities, while the samples obtained in 1997 and 2001 reflect the situation during intense extraction activities. Detailed information about the location of the Kwintebank is given in Vanaverbeke et al. (2000, 2002).

Collection and treatment of meiobenthic samples was identical during all sampling campaigns: 10 stations along the crest of the Kwintebank were sampled using a Reineck box corer (Fig. 1). From each box corer, sub-samples for meiofaunal and sediment analysis were obtained using a perspex core (10 cm<sup>2</sup>). Meiobenthic samples were 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 by means of a 1 mm sieve and all animals retained on a 38 µm sieve were stained with Rose Bengal, counted and classified to the taxon level. A fixed amount of nematodes were picked at random, transferred to glycerin and mounted on slides for species identification using the pictorial keys of Platt and Warwick (1983, 1988), Warwick et al.

(1998) and the NeMys online identification key (Steyaert et al., 2005). Nematodes from two replicates were identified for the 1997 and 2001 sampling campaigns; in 1978 nematodes from only one replicate were identified to species level. All nematode species were assigned to a feeding type according to Wieser (1953).

Sediment samples obtained in 1978 were analysed using a dry-sieving procedure (Wentworth, 1922) and were obtained from Bonne (2003). In 1997, sediments were analysed using both the dry-sieving method (data in Bonne, 2003) and a Coulter LS100 Particle Size Analyser (data in Vanaverbeke et al., 2000, 2002). Grain size analysis for the sampling event in 2001 was only performed using the Coulter LS 100 Particle Size Analyser. For the latter method, sediment fractions up to 1000  $\mu\text{m}$  are expressed as volume percentages, while the fraction between 1000 and 2000  $\mu\text{m}$  and >2000  $\mu\text{m}$  are mass percentages. For all sampling years, sediment fractions are defined according to the Wentworth scale (Buchanan, 1984).

## 2.2. Data analysis

Stations were grouped a priori according to their sand extraction history in 1997 (Bonne, 2003). Stations Kw1, Kw2, Kw5 and Kw6 were grouped together (“Very High” group) as 5000–8300  $\text{m}^3$  of sediment per month were removed. A second group consisted of stations Kw3, Kw7, Kw8, Kw9 and Kw10 (“High” group). Sand extraction in those stations ranged between 150 and 1380  $\text{m}^3$  per month. The “Very Low” group contained only station Kw4, since maximum extraction reached only 28  $\text{m}^3$  per month.

Data were analysed with non-parametric multivariate methods using Primer 5 (Clarke and Gorley, 2001).

Differences in methodology do not allow for a comparison of the grain size data between sampling dates. Therefore, the comparison between 1978 and 1997 is based on Bonne (2003) using the results of the dry-sieving method. Principal Component Analysis using normalised Euclidean distance was applied to show spatial and temporal differences in the grain size variables of the sampling campaigns from 1997 to 2001. Two-way crossed ANOSIM was performed to test for differences between years (allowing possible differences between stations) and vice versa (Clarke and Gorley, 2001).

General multivariate differences in nematode community composition between the different years were analysed using non-metric Multidimensional Scaling (MDS) on square root-transformed nematode data (all species from all replicates) based on the Bray–Curtis similarity measure. One-way Analysis of Similarity (ANOSIM) was used to test for significant differences in community composition between years. In a second step differences between years per “intensity group” were analysed using MDS followed by a 2-way crossed ANOSIM, allowing to test for differences between years while allowing for differences between

stations and vice versa. Species accounting for the similarity between samples within the different years were identified using the SIMPER routine within the Primer package. A cut-off of 50% was applied.

Nematode diversity was analysed by calculating a wide array of diversity indices available in Primer 5, including total species (S), Margalef species richness (d), Pielou’s evenness (J), Shannon Wiener ( $H'$ , log e based), Simpson Index ( $1-\lambda'$ ) and Hill numbers  $N_1$ ,  $N_2$  and  $N_\infty$ . Differences between years were analysed using 1-way ANOVA after testing for the assumptions for ANOVA. Values were subjected to a double square root transformation when needed to meet the assumptions. When the assumptions were not met, the non-parametric Kruskal Wallis analysis by ranks was applied. When significant differences were observed in the ANOVA approach, Tukey’s HSD for unequal N was used to test for pairwise differences between years. All ANOVA and Kruskal Wallis analysis were performed using the Statistica 6 software package.

In addition, Average Taxonomic Distinctness ( $\Delta^+$ ) and Variation in Taxonomic Distinctness ( $\text{VarTD } \Delta^+$ ) based on presence/absence data were calculated following Warwick and Clarke (2001). Basically,  $\Delta^+$  is a measure of the degree to which species in an assemblage are related taxonomically to each other while the degree to which species from the regional species pool are over- or under-represented is reflected in the variation in taxonomic distinctness ( $\Delta^+$ ). The latter can be seen as the ‘evenness’ of the distribution of taxa across the nematode taxonomic tree.

For the calculation of the taxonomic indices equal step-lengths between each taxonomic level were assumed. In total 7 taxonomic levels were used. Calculation of  $\Delta^+$  from simulated sub-samples of different numbers of species  $m$  from the master list (based on all nematode species ever found on the Kwintebank) were used to produce probability funnels against which distinctness values for all zones were checked. This formally addresses the question whether these zones have a lower than expected taxonomic spread, assuming a null hypothesis that each sample is a random selection from the regional species pool (Warwick and Clarke, 2001). The same procedure was applied to  $\Delta^+$ . Actual values falling below the lower probability part of the funnel indicate disturbed communities.

## 3. Results

### 3.1. Sediment characteristics

When comparing the sediment characteristics from all stations in 1978 with 1997 (Fig. 2), a general increase in median grain size can be observed. In 1978, median grain size increased from Kw1 to Kw3 and decreased again further south. From Kw7 onwards, median grain size was about 200  $\mu\text{m}$ . The median grain size in Kw3 and Kw5 was finer in 1997 but all other stations revealed a coarsening

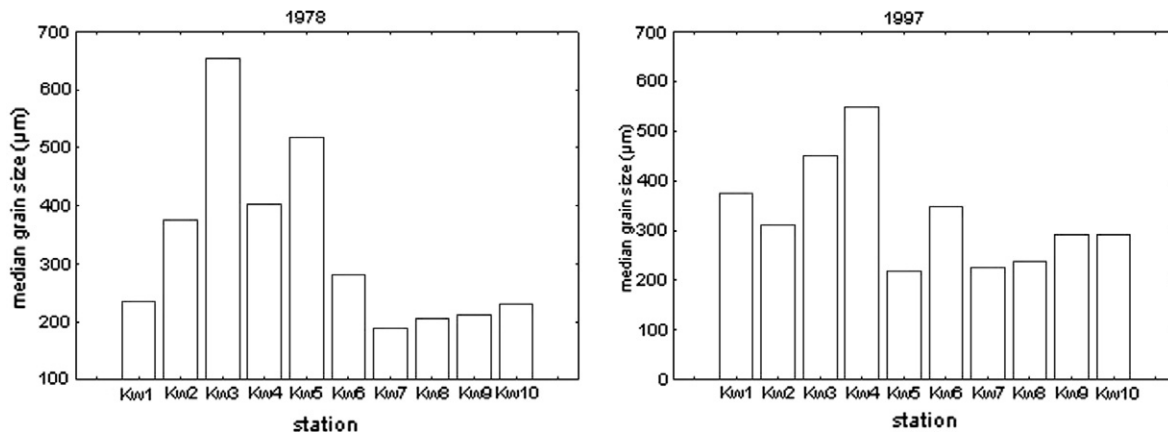


Fig. 2. Median grain size ( $\mu\text{m}$ ) at the Kwintebank stations from 1978 and 1997 (data from Bonne, 2003).

of the sediment. In general this was due to an increase of the relative amount of the medium sand fraction (mean value of 33% in 1978 to 50% in 1997) coinciding with a decrease in the proportion of fine sands (from 44% in 1978 to 35% in 1997). At Kw3, the medium sand fraction partly replaced the coarse sand fraction, while at Kw5 the proportion of coarse sand was replaced with a fine sand fraction. Even at the least impacted station Kw4 coarsening was observed (median grain size of 402  $\mu\text{m}$  in 1978, 548  $\mu\text{m}$  in 1997) due to the partial replacement of fine sand with a very coarse sand (1–2 mm) fraction.

Grain size variables of 1997 and 2001 (Coulter Counter data) were compared using PCA (Fig. 3). The two first principal components explained 72.6% of the variance. Two-way crossed ANOSIM revealed significant differences between stations ( $R = 0.479$ ,  $p = 0.001$ ) and years ( $R = 0.444$ ,  $p = 0.006$ ), indicating a further change in sedimentological characteristics with time.

### 3.2. Nematode community composition

Changes in nematode communities with time over the complete sandbank were obvious (Fig. 4a). One-way ANOSIM ( $R = 0.74$ ,  $p = 0.001$ ) showed significant differences in community composition between the different sampling years. Pairwise tests showed that largest differences occurred between 1978 and 2001 (Table 1).

Differences per intensity group were analysed using MDS (Fig. 4b–d) followed by 2-way crossed ANOSIM. Nematode community composition clearly changed over the years in all groups irrespective of the extraction intensity. Two-way crossed ANOSIM for both the “Very High” and the “High” intensity stations revealed significant differences in nematode communities between the sampling years ( $R = 0.969$ ;  $p = 0.001$  and  $R = 0.9$ ;  $p = 0.001$ , respectively) and stations (Very High:  $R = 0.615$ ;  $p = 0.01$  and High:  $R = 0.725$ ;  $p = 0.01$ ). Differences between the communities as observed in 1978 showed the largest differences with both the other sampling years (Table 2).

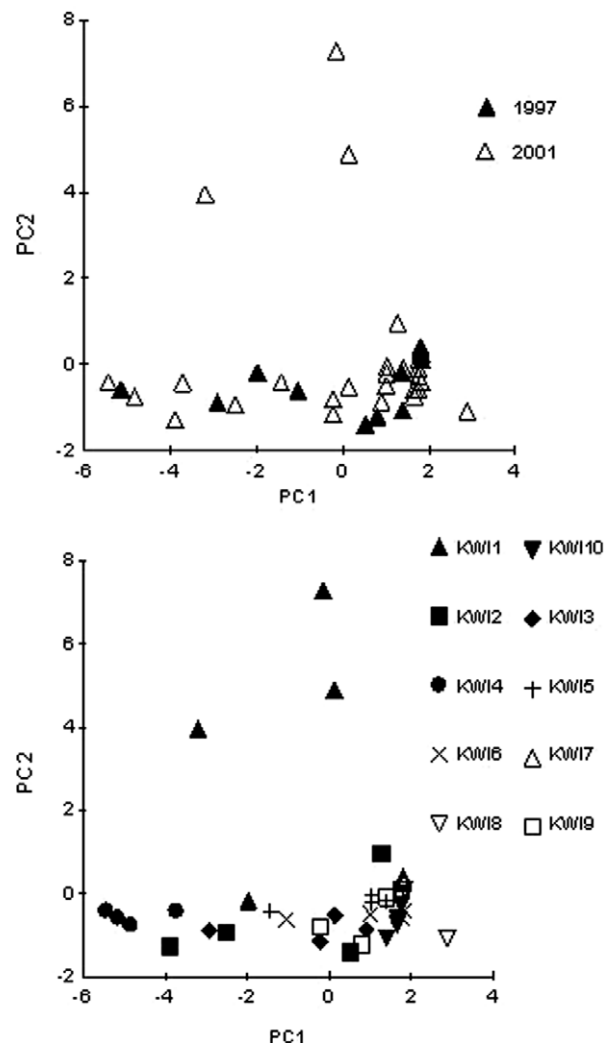


Fig. 3. PCA ordination plot of grain size variables of the Kwintebank Stations. Left panel: comparison 1997–2001. Right panel: comparison per station.

Multivariate changes in nematode communities in the “Very Low” intensity group were observed as well. Due



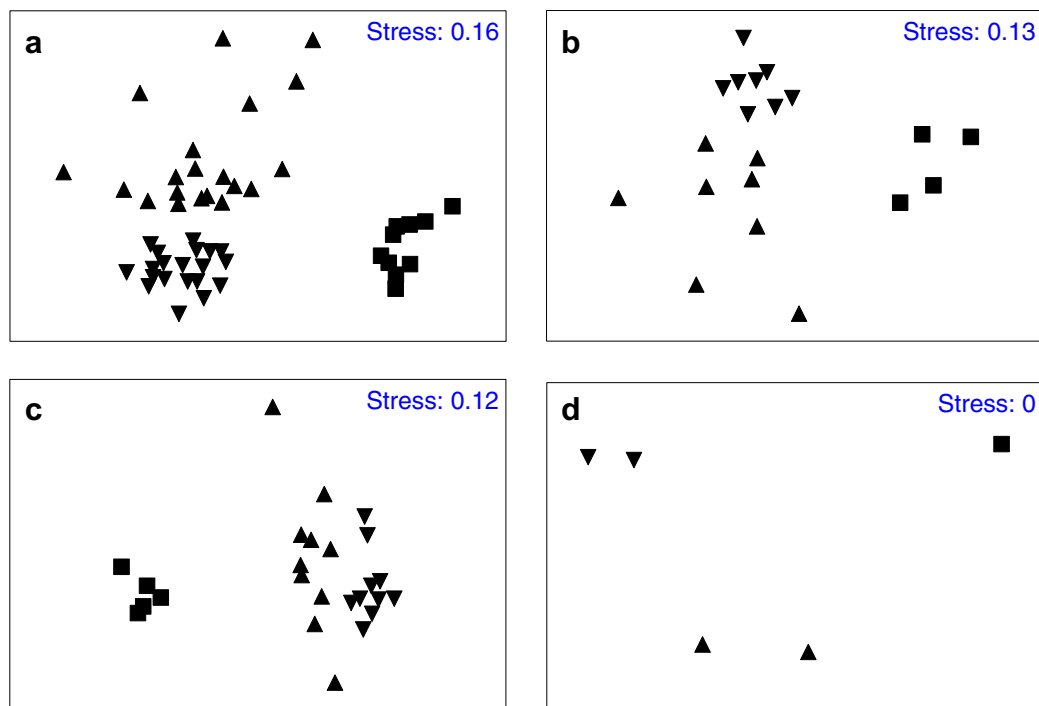


Fig. 4. Result of MDS analyses. (a) All stations; (b) ‘Very High’ group; (c) ‘High’ group and (d) ‘Very Low’ group. Squares: 1978, Reversed triangles: 1997, Triangles: 2001.

Table 1

Results of pairwise-ANOSIM tests on root-transformed species densities from all stations

Years compared	<i>R</i>	<i>p</i>
1978–2001	1	0.001
1978–1997	0.829	0.001
1997–2001	0.524	0.001

Table 2

Results of pairwise 2-way crossed ANOSIM tests on root-transformed species densities per intensity group

Years compared	“Very High”		“High”	
	<i>R</i>	<i>P</i>	<i>R</i>	<i>p</i>
1978–1997	1	0.012	1	0.004
1978–2001	1	0.012	1	0.004
1997–2001	0.94	0.012	0.8	0.004

to the lack of replication during the 1978 sampling event, 1-way ANOSIM was applied, revealing significant differences between the sampling year ( $R = 1$ ;  $p = 0.007$ ).

SIMPER analyses for the “Very High” and “High” groups revealed clear shifts in feeding type composition over time (Tables 3 and 4). In 1978, a substantial amount (>35%) of the similarity between the stations was due to predatory nematodes (2B). In 1997, the importance of the epistrate feeders (2A nematodes) and non-selective deposit feeders (1B) increased at the “Very High” and “High” stations. Non-selective deposit feeders were dominant at both intensity groups in 2001. This comparison could not be

made for the “Very Low” station, since only 1 replicate is available from 1978. We therefore list relative abundances in 1978 and SIMPER results restricted to 1997 and 2001 in Table 5.

Although using an indirect method, a shift from 2A + 2B dominated community towards a community where deposit feeding nematodes are dominant becomes clear, although the high contribution of *Theristus bastiani* to the within group similarity of 1997 is striking.

### 3.3. Nematode diversity

Diversity indices based on species abundance (not depicted) for the “Very High” stations were not significantly different between the years (1-way ANOVA or Kruskal–Wallis tests). In contrast, significant differences between years were observed for the “High” group for all indices with the exception of total species (*S*), species richness and Margalev’s species richness. Tukey HSD for unequal *N* showed for all significantly different indices (except for the Simpson index) that diversity was significantly lower in 1978 compared to 1997. No significant differences between 1978–2001 and 1997–2001 were observed.

Both  $\Delta^+$  and  $\Lambda^+$  values (Fig. 5) for 1978 were higher than the expected mean value. Values for the Very High Extraction sites were above the 95% confidence intervals. In 1997 and 2001, both indices decreased but values were still within the probability funnels. For both the “Very High” and “High” group, no significant differences were observed between the years (1-way ANOVA or Kruskal–Wallis Analysis by Ranks).

Table 3  
Results of SIMPER analysis of nematode data from the 'Very High' group, listing the main characterising species and feeding types per sampling year

1978			1997			2001		
Species	FT	Contr. (%)	Species	FT	Contr. (%)	Species	FT	Contr. (%)
<i>Onyx perfectus</i>	2B	9.45	<i>Neochromadora munita</i>	2A	15.54	<i>Viscosia franzii</i>	2B	7.75
<i>Desmodora hirsuta</i>	2A	6.83	<i>Enoploides spiculohamatus</i>	2B	7.5	<i>Calomicrolaimus honestus</i>	2A	7.64
<i>Enoploides spiculohamatus</i>	2B	6.56	<i>Calomicrolaimus monstrosus</i>	2A	4.93	<i>Onyx perfectus</i>	2B	6.73
<i>Viscosia</i> sp.	2B	6.21	<i>Viscosia franzii</i>	2B	4.77	<i>Theristus bastiani</i>	1B	6.57
<i>Trefusia</i> sp. 1	1A	4.93	<i>Metadesmolaimus pandus</i>	1B	4.57	<i>Sabattieria celtica</i>	1B	5.27
<i>Trefusia</i> sp. 2	1A	4.93	<i>Theristus bastiani</i>	1B	4.37	<i>Xyala striata</i>	1B	4.81
<i>Polygastrophora</i> sp.	2B	4.93	<i>Ascolaimus elongatus</i>	1B	4.34	<i>Leptonemella aphonotheca</i>	1A	4.24
<i>Enoplolaimus</i> 1 sp.	2B	4.93	<i>Onyx perfectus</i>	2B	3.98	<i>Neochromadora munita</i>	2A	3.22
<i>Enoplolaimus</i> 2 sp.	2B	4.93	<i>Bathylaimus capacosus</i>	1B	3.58	<i>Theristus major</i>	1B	3.2
						<i>Enoploides spiculohamatus</i>	2B	3.12
Feeding type contribution								
	1A	9.86		1A	0		1A	4.24
	1B	0		1B	16.86		1B	19.85
	2A	6.83		2A	20.47		2A	10.86
	2B	37.01		2B	16.25		2B	17.6

Table 4  
Results of SIMPER analysis of nematode data from the 'High' group, listing the main characterising species and feeding types per sampling year

1978			1997			2001		
Species	FT	Contr. (%)	Species	FT	Contr. (%)	Species	FT	Contr. (%)
<i>Viscosia</i> sp.	2B	5.53	<i>Neochromadora munita</i>	2A	13.16	<i>Xyala striata</i>	1B	9.36
<i>Enoploides spiculohamatus</i>	2B	4.9	<i>Viscosia franzii</i>	2B	10.54	<i>Onyx perfectus</i>	2B	8.52
<i>Rhabdodemanina</i> sp. 1	2B	4.41	<i>Bathylaimus capacosus</i>	1B	7.85	<i>Viscosia franzii</i>	2B	7.35
<i>Enoplolaimus</i> sp.	2B	4.41	<i>Theristus major</i>	1B	6.26	<i>Theristus major</i>	1B	7.18
<i>Enoplolaimus</i> aff. <i>zosteriae</i>	2B	4.36	<i>Metadesmolaimus pandus</i>	1B	4.59	<i>Enoploides spiculohamatus</i>	2B	4.85
<i>Rhynchonema quemer</i>	1B	4.31	<i>Xyala striata</i>	1B	4.01	<i>Odontophora</i> sp. 1	1B	4.4
<i>Polygastrophora</i> sp.	2B	4.29	<i>Onyx perfectus</i>	2B	3.98	<i>Calomicrolaimus honestus</i>	2A	4.12
<i>Mesacanthion hirsutum</i>	2B	4.14				<i>Gonionchus longicaudatus</i>	1B	3.66
<i>Trefusia</i> sp. 1	1A	4.04				<i>Tubolaimoides</i> aff. <i>tenuicaudatus</i>	1A	3.45
<i>Trefusia</i> sp. 2	1A	4.04						
<i>Halalaimus</i> sp.	1A	4.04						
<i>Eurystomina</i> sp.	2B	4.04						
Feeding type contribution								
	1A	12.12		1A	0		1A	12.81
	1B	4.31		1B	22.71		1B	24.6
	2A	0		2A	13.16		2A	4.12
	2B	36.08		2B	14.52		2B	20.72

Table 5  
Results of SIMPER analysis of nematode data from the 'Low' group, listing the main characterising species and feeding types per sampling year

1978			1997			2001		
Species	FT	RA (%)	Species	FT	Contr. (%)	Species	FT	Contr. (%)
<i>Desmodora hirsuta</i>	2A	18.7	<i>Theristus bastiani</i>		51.39	<i>Rhynchonema quemer</i>	1B	18.81
<i>Onyx perfectus</i>	2B	15.17				<i>Metepsilonema emersum</i>	1A	16.36
<i>Microlaimus</i> sp.	2A	12.32				<i>Dracognomus tinae</i>	1B	12.27
<i>Rhynchonema quemer</i>	1B	5.69				<i>Actinonema celtica</i>	2A	7.57
Feeding type contribution								
	1A	0		1A	0		1A	16.36
	1B	5.69		1B	51.39		1B	31.08
	2A	31.02		2A	0		2A	7.57
	2B	15.17		2B	0		2B	0

Results for 1978 are based on relative abundance (RA).

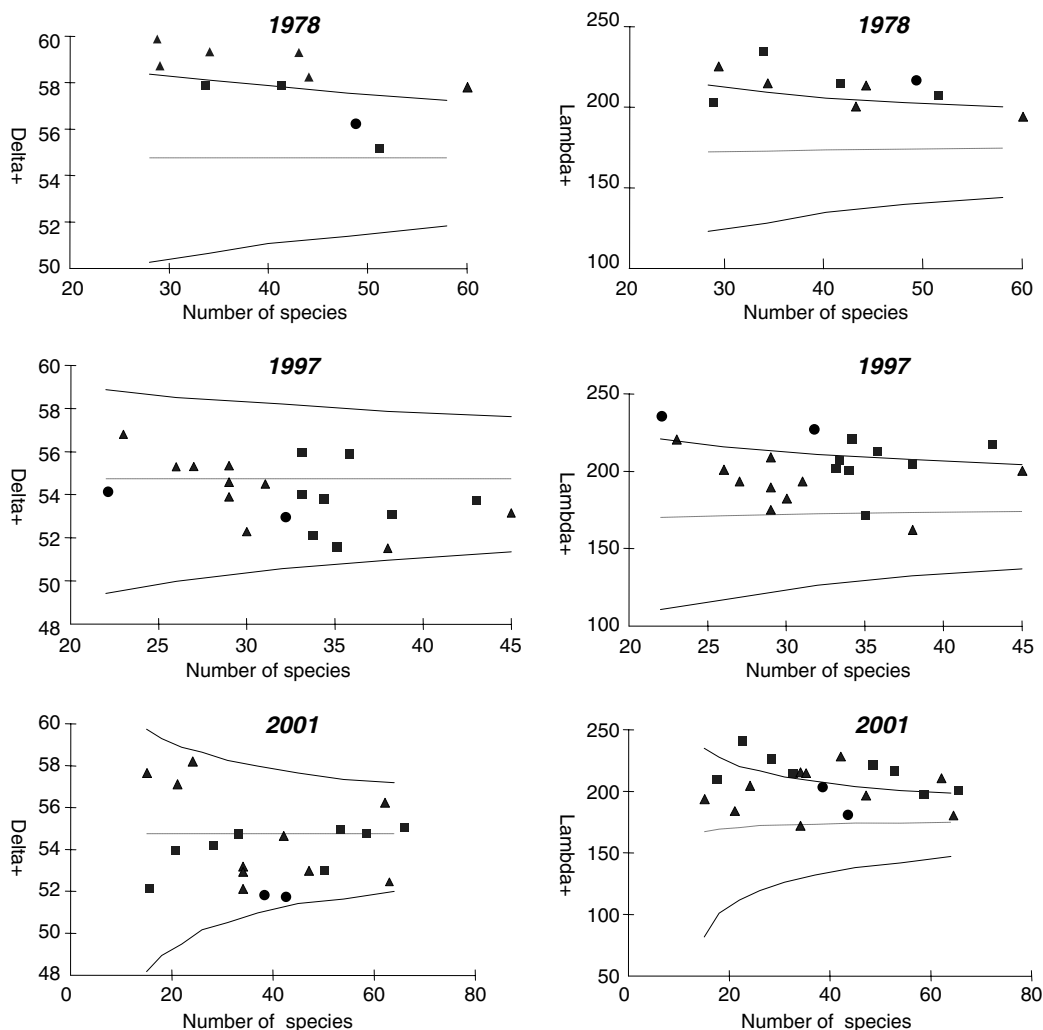


Fig. 5. The 95% probability funnels (thick line) for  $\Delta^+$  (left) and  $\Lambda^+$  (right) for 15,000 simulations. Dotted line indicates theoretical mean values. Superimposed squares (Very High extraction sites); triangles (High extraction sites) and circles (Very Low extraction sites) indicate actual values per station.

## 4. Discussion

### 4.1. Limitation of the dataset

Assessing the impact of sand extraction on the nematode communities from the Kwintebank is not an easy task. The earliest data available originate from a sampling campaign conducted in 1978. Extraction activities had already started in 1976, in 1977 220,000 m<sup>3</sup> was extracted on the BCS and this increased to 1,700,000 m<sup>3</sup> in the mid of the 90s and 1,900,000 m<sup>3</sup> in 2001 (Degrendele et al., in press). At least 75% of the extraction activities were concentrated on the Kwintebank until 2003. Since the earliest biological samples were retrieved in 1978 there is no real baseline study available. Therefore we compare periods of intense extraction (1997 and 2001) with periods of a very limited exploitation (1978) rather than assessing the effect of sand extraction *sensu strictu*.

During this long period, scientific methods have changed considerably. However, for this study, sampling and

treatment of the benthos was identical throughout the study period. Methodology for characterising the sediments did change and therefore a direct comparison of data from 1978 with 2001 was not possible. Changes in the sediment composition of all stations seemed obvious, but needs further refinement taking into account spatial and seasonal variation. Since meiobenthos in general and nematodes in particular live in very close contact with the sediment, even minor changes in the grain size variables can result in changes in the nematode community composition (Vanaverbeke et al., 2002). Therefore, changes in the sediment composition will be inherently reflected in changes in the nematode communities.

### 4.2. Changes in sediment characteristics

Since 1978, considerable changes in sediment characteristics seem to have occurred at the Kwintebank, but a causal relationship with sand extraction and sand extraction methodology has never been proven for the whole area

of the sandbank. So far most effort was spent on assessing changes in the morphology of the Kwintebank (Degrendele et al., in press). Results indicate that in areas with high extraction intensity, changes in the morphology are obvious and changes in sedimentological characteristics are most probably related to the exploitation of the sandbank, while changes outside these areas could result from deviations in sedimentation and erosion patterns (Bonne, 2003). In addition to the above mentioned general long-term changes related to the exploitation activities, the meiobenthos will also be influenced by short-term disturbances. The extraction technique creates dredging furrows with a depth of 10–50 cm. In sandbank areas, those furrows remain visible for a maximum of 6 months (Degrendele et al., in press). Likely, the creation and subsequent filling up of these furrows enhances the sediment dynamics.

#### 4.2.1. Changes in nematode communities

Changes in nematode community composition between the different years and for each level of extraction intensity were obvious although no clear and consequent differences in diversity were noted. This holds for both the indices based on species abundances and taxonomic relationship. A lack of response for the indices based on taxonomic relationship has been described before (Salas et al., 2006). Heip et al. (1985) and Kennedy and Jacoby (1999) stated that nematode communities are an excellent tool for assessing disturbances to the sediment. One of the reasons for this is the high diversity observed within the nematode communities, with a wide range from species that are very sensitive to disturbance to very tolerant species. Therefore, diversity does not have to change as a consequence of perturbations, but community composition can. Since the impacts of sand extraction on nematode communities are possibly related to changes in grain size variables (Vanaverbeke et al., 2002), a drastic reduction of species diversity is not to be expected. Although the calculated diversity indices based on taxonomic relatedness ( $\Delta^+$  and  $\Lambda^+$ ) are independent to changes in species abundances, they do not reflect the changes in nematode community composition in our study. Both species and genus identity changed over time, but their distribution within the taxonomical tree reflected more or less the same pattern during the successive sampling campaigns. Hence, diversity indices based on taxonomic relatedness offer no valuable alternative to the species richness-based indices, which are affected by sample size when it comes to assessing possible impacts of sand extraction on the nematode communities.

The observed shifts in community structure could be related to natural evolution of the communities, to the exploitation of the sandbank or to the timing of sampling campaigns. Timing of sampling campaigns within a year is probably not important for explaining the observed patterns: Vanaverbeke et al. (2002) showed no difference in community composition or diversity when comparing seasonally different sampling campaigns on sandbanks on the

BCS, including the Kwintebank. Moreover, both December and January can be considered winter months. On the other hand, inter-annual differences might have influenced the nematode community composition since changes were observed for the “Low” intensity group as well. However, the extreme differences between the years (very high R values in pairwise-ANOSIM) are most probably not the result of inter-annual variation alone. In addition, Vanaverbeke et al. (2007) found no significant differences in nematode communities on the Kwintebank between years (2003–2004) in the absence of sand extraction, while this was still the case in areas where sand extraction was ongoing.

The changes in the “Low” intensity group cannot be considered a direct effect of the exploitation activities since these are very low in this area. However, this sampling station is located in between the northern and central depression and therefore these changes in sandbank topography might have influenced these nematode communities indirectly. Such indirect effects were described for macrobenthic communities at the east coast of the UK, although these effects were less clear (Cooper et al., 2007). The fast deepening of the central depression on the Kwintebank might have caused changed hydrodynamics and erosion/sedimentation patterns which resulted in clear changes in the nematode communities from the low intensity group. However, we have no explanation of the high contribution of *Theristus bastiani* to the within group similarity from the 1997 sampling campaign.

As the deviations in the topography of the sandbank in the central and northern depression are related to the exploitation of the sandbank (Degrendele et al., in press), it can be logically deduced that the observed changes in grain size are a consequence of this changed sandbank morphology. On the short-term, the creation and filling up of the dredging furrows creates an extra human disturbance on the nematode populations. We believe that the observed shifts in nematode community composition are a consequence of a combination of changes in the sedimentological environment of the nematode communities and the frequent dynamics induced by the creation and filling of the dredge furrows. Indeed, the medium and very fine sand content and median grain size are known to be the most important sedimentological characteristics structuring nematode communities on sandbanks (Vanaverbeke et al., 2002). Hence, changes in the grain size of the sediment as described above will trigger shifts in nematode community composition. The observed shift coincides with the disappearance of predatory nematodes (2B group) in favour of epistrate feeders (2A) and on the long-term deposit feeding nematodes (1A + 1B nematodes). It should be noted that in 1978, selective deposit feeders (1A) contributed about 10% to the within year similarity for both ‘Very High’ and ‘High’ station groups. However, this relatively large contribution was due to species belonging to the genus *Trefusia*, which is a rather long nematode genus (length between 2 and 3 mm, Warwick et al., 1998). Species from this genus are not among the species contributing to the 50% within group



similarity in 1997 and 2001. Equally, predatory nematodes are generally large nematodes and become less important in the communities as observed in 1997 and 2001.

Being large in size seems to be a disadvantage when living in an environment where frequent physical disturbances occur as nematodes were generally smaller in the ‘Very High’ stations compared to the remaining stations (Vanaverbeke et al., 2003). During the 1997 sampling campaign in general, nematodes on the Kwintebank were smaller compared to other sandbanks where no exploitation was ongoing. Several explanations can be given. Firstly, smaller nematodes have higher growth rates (Peters, 1983) and therefore reach adulthood faster, but they also have higher reproduction rates (Kooijman, 1986). These nematodes have less difficulty to maintain their populations in a frequently disturbed environment in comparison to larger nematodes. A second reason is given by Galluci et al. (2005) who showed that predatory nematodes have less success in catching prey (other nematodes) when incubated in sediments deviating from their natural environment. Changing sedimentological conditions might lead to a reduction in predatory nematodes as a consequence of starvation. Moreover, predatory nematodes have a significant top-down impact on nematode prey communities (Moens et al., 2000). The decrease in dominance of 2B nematodes therefore could trigger better survival rates and increased dominance of the other sandbank inhabiting nematodes. This change in ratio between predators and prey might have important consequences for the functioning of the benthic ecosystem (Galluci et al., 2005).

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