Short-term changes in nematode communities from an abandoned intense sand extraction site on the Kwintebank (Belgian Continental Shelf) two years post-cessation

Jan Vanaverbeke *, Magda Vincx

Ghent University, Biology Department, Marine Biology Section, Krijgslaan 281/S8, B-9000 Gent, Belgium

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ABSTRACT

We investigated short-term changes (two years) in nematode communities (density, diversity, biomass and community composition) in an area on the Kwintebank (Belgian Continental Shelf) that was closed for sand extraction activities and compared these patterns to nematode community characteristics from another area on the Kwintebank were sand extraction was still ongoing. Six stations were sampled in 2003 and 2004 and nematode community composition and univariate measures of diversity were compared with values obtained during the extraction period and with a "pre-impact situation" sampled in 1978.

Although nematode density, diversity and biomass did not change two years after cessation of the exploitation, nematode community composition did and was more stable than in the extracted site. This is attributed to the absence of continuous disturbances associated with the extraction activities such as the creation and filling up of dredge furrows. As a consequence of the typical life history traits of nematodes, recovery seems to follow different pathways when compared to macrobenthic recovery from the same impact.

1. Introduction

Marine sand and gravel extraction has recently become a growing industry due to the increasing demand for these resources in combination with the closing of land-based extraction sites. Since these activities directly impact the seabed, many studies have been conducted investigating the effect of mineral extraction on the benthos inhabiting the seafloor. Most studies so far focused on the eventual changes in bottom topography, sediment composition and macrobenthos (see reviews by Newell et al., 1998; Boyd et al., 2004). The effects on the macrobenthos seem to be site-specific and dependent on local sedimentological and topographical characteristics of the extraction site in combination with the ability of the local macrobenthic communities to cope with the induced disturbance (Kenny and Rees, 1994; Desprez, 2000; van Dalfsen et al., 2000; Sardá et al., 2000; van Dalfsen and Essink, 2001; Guerra-Garcia et al., 2003; Newell et al., 2004; Robinson et al., 2005; Simonini et al., 2005). Many studies also investigated the possible recovery of extraction sites after cessation of the activities (Desprez, 2000; Sardá et al., 2000; van Dalfsen et al., 2000; van Dalfsen and Essink, 2001). Their results suggest that substantial progress towards full restoration of the macrobenthic communities can be expected within 2–4 years following cessation of the extraction activities. However, their studies concerned cases were dredging operations lasted only over a relatively short time scale (up to one year: Kenny and Rees, 1994; Sardá et al., 2000; van Dalfsen et al., 2000; van Dalfsen and Essink, 2001). In a long-term (1971–1995) extraction site (UK, Area 222) differences between macrobenthic assemblages from reference sites and sites exposed to high and low levels of extraction persisted after a period of six years (Boyd et al., 2005). Smith et al. (2006), investigating the epifaunal communities (macrobenthos sampled with a dredge or trawl) of the same area, reached the same conclusions. All this suggests that besides local characteristics and extraction intensity, duration of the activities and associated disturbances and environmental changes are important in determining restoration processes and timing.

In this paper, we report on the short-term (two years) changes in nematode communities in an abandoned extraction site on the Kwintebank on the Belgian Continental Shelf (BCS) and we compare these communities with nematode communities from a site on the Kwintebank where extraction is still ongoing. At the Kwintebank, extraction activities started in 1976. Total amounts of sand extracted from the BCS increased from 29,000 $m^3 y^{-1}$ in 1976 to 1,700,000 $m^3 y^{-1}$ in the mid 90s. Maximum exploitation was

* Corresponding author. Tel.: + 32 9 264 85 30; fax: +32 9 264 85 98.
E-mail address: Jan.Vanaverbeke@UGent.be (J. Vanaverbeke).

recorded in 2001 (1,900,000 m^3 y^{-1}). Extraction activities were concentrated in the central and northern part of the Kwintebank. 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 seven years. Since federal legislation prohibits further exploitation when a deepening of >5 m with respect to the most recent hydrographical charts occurs, this area had to be closed for extraction activities in February 2003. Nematode community composition at the sandbank changed considerably since the start of the extraction activities, which was attributed to long-term changes in sediment characteristics in combination with additional short-term disturbances by the creation and the filling of dredge furrows (Vanaverbeke et al., 2007). Since nematode communities are generally accepted to be a good monitoring tool for assessing changes in the benthic environment (Kennedy and Jacoby, 1999), we sampled these communities to assess a possible restoration of the community characteristics after cessation of the activities by comparing the post-extraction data with (1) data obtained at the start of the extraction period (Vincx, 1986); (2) data obtained from within the extraction period (Vanaverbeke et al., 2002) and (3) data obtained from the northern part of the Kwintebank where high intensity sand extraction was still ongoing. We investigated the hypotheses of no changes in nematode communities (density diversity and community composition) between sampling events within the different areas on the sandbank. In addition, we compared nematode biomass spectra (Vanaverbeke et al., 2003) from the abandoned sites and the extraction sites in order to further increase our understanding of the effects of sand extraction on nematode communities.

2. Material and methods

2.1. Collection and treatment of samples

Analyses in this paper are based on historical data from sampling campaigns conducted in June–September 1978 (Vincx, 1986), February 1997 (Vanaverbeke et al., 2002), December 2001 (Vanaverbeke et al., 2007), and new sampling campaigns in the central and northern area of the Kwintebank in October 2003 and February 2004. The central area was closed for extraction activities in February 2003, while extraction activies continued in the northern part. 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) and Vanaverbeke et al. (2002).

Collection and treatment of meiobenthic samples was identical during all sampling campaigns. The long-term sampling stations Kw1 and Kw2 in the northern area and Kw5 and Kw6 in the central depression were visited in 2003 and 2004. In both areas, an additional station was sampled as well: Kw14 in the northern area and Kw18 in the central depression (Fig. 1). Samples collected in
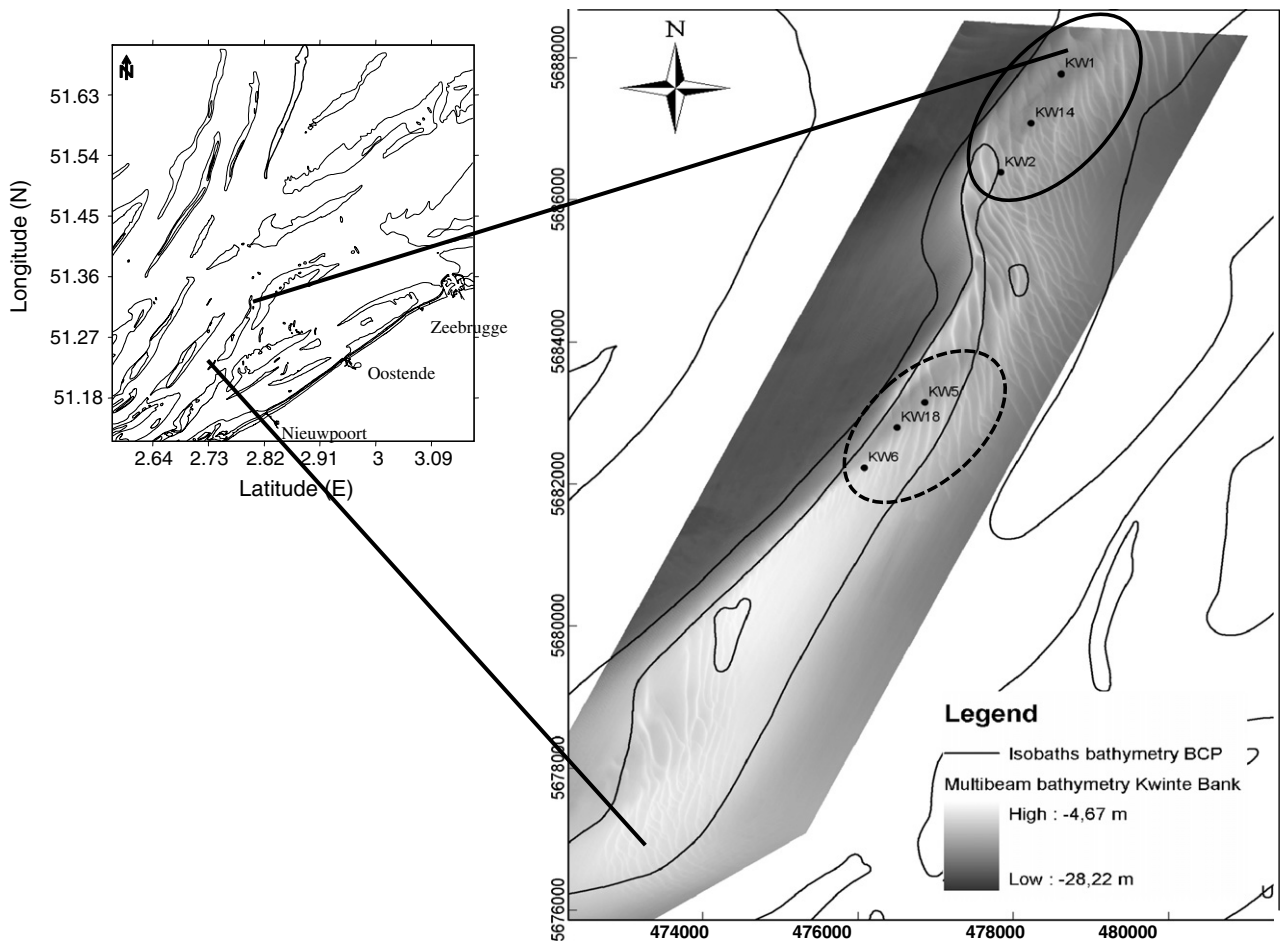
Fig. 1. Map of the Belgian Continental Shelf and detailed location of the sampling stations on the Kwintebank (Maps redrawn from UGent – RCMG and Federal Public Service Economy, SMEs, Self employed and energy – Fund for Sand Extraction). Full circle: area with ongoing sand extraction; Dotted circle: area closed for sand extraction.

2003 and 2004 in the central area are considered to reflect post-extraction situations. All stations were sampled with a Reineck box corer. The box corer was deployed three times at all stations, and from each box corer, subsamples for meiobenthic and sediment analysis were obtained using a perspex core ($10 \, \text{cm}^2$). Meiobenthic samples were fixed with a hot ($70 \, ^\circ\text{C}$) 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. 200 nematodes (or all individuals if less then 200 were present) 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. Nematode length and width from all nematodes from one replicate per station were measured for the sampling campaign in 2004. Measurements were done using the Quantimet 500+ image analyser. Nematode biomass was calculated from Andrassy's formula (Andrassy, 1956) and a dry-to-wet-weight ratio of 0.25 was assumed. Nematode biomass spectra (NBS) were constructed following Vanaverbeke et al. (2003). Kolmogorov–Smirnov two sample tests were used to compare NBS for 2004 with NBS from 1997 for the same area, recalculated from Vanaverbeke et al. (2003).

Grain size analyses were performed using the Coulter LS 100 Particle Size Analyser. For the latter method, sediment fractions up to 1000 μm are expressed as volume percentages, while the fraction between 1000 and 2000 μm and >2000 μm are mass percentages. For all sampling years, sediment fractions are defined according to the Wenthworth scale (Buchanan, 1984).

2.2. Data analysis

Grain size variables per area were compared by Principal Component Analysis using normalised Euclidean distance. Differences between stations and treatment (extraction versus no extraction) in the central depression were analysed using two-way crossed ANOSIM. Since sand extraction was ongoing in the northern area, differences between stations and subsequent years were analysed using the same procedure.

Nematode densities from different years were compared using one-way ANOVA. When assumptions for ANOVA were not met, data were root–root transformed. The non-parametric Kruskal–Wallis Analysis by Ranks was used when transformation did not result in suitable data for ANOVA. Data from October 2003 were excluded from this analysis, since Vanaverbeke et al. (2000) described higher densities in October as a consequence of seasonal dynamics. December and February are here considered as winter months.

Multivariate patterns in nematode communities from the periods 1997–2001 and 2003–2004 per area were investigated using non-metric multidimensional scaling (MDS) on non-transformed species densities (all species from all replicates) based on the Bray–Curtis similarity measure. This was followed by a two-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 (Clarke and Gorley, 2001). A cut-off of 50% was applied. This allows for investigating short-term changes in nematode community composition after cessation of the activities or further changes when extraction is ongoing.

Temporal trends for Stations Kw5 and Kw6 in the central depression, and Kw1 and Kw2 in the northern area for the period 1997–2004, were evaluated using MDS based on non-transformed species densities and the Bray–Curtis similarity measure. Spearman rank correlations between these similarity matrices underlying their temporal development were used as input for a 2nd stage MDS. This technique removes the site factor (site differences at one time) and concentrates on the consistency of temporal patterns across sites (Clarke et al., 2006).

In order to evaluate a possible recovery of the nematode communities in the central area, MDS was applied on all available data from the central depression (including 1978). All multivariate analyses were conducted using the Primer 5 package.

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 eveness (J), Shannon Wiener (H', $\log_e$ based), Simpson Index ($1-\lambda'$) and Hill numbers N_1, N_2 and N_∞. In addition, Average Taxonomic Distinctness (AvTD Δ^+) and Variation in Taxonomic Distinctness (VarTD Λ^+) based on presence/absence data were calculated following Warwick and Clarke (2001). These indices differ from the previously mentioned indices since they are not based on species richness but on taxonomic relatedness of species in the samples. For the calculation of the taxonomic indices equal step-lengths between each taxonomic level were assumed. In total seven taxonomic levels were used. All indices were calculated using Primer 5 (Clarke and Gorley, 2001) Differences between years were analysed using one-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.

3. Results

3.1. Sediment characteristics

No clear patterns in sedimentological characteristics in the central depression could be discerned (Fig. 2A). The first two axes of the PCA explained 67.8% of the variation of the dataset. Two-way crossed ANOSIM revealed no significant differences between stations ($R = 0.104$; $p = 0.08$), but a significant difference between the sedimentological characteristics before and after the cessation was observed ($R = 0.208$; $p = 0.047$). In the northern area (Fig. 2B), significant differences between the different years ($R = 0.256$; $p = 0.024$) and stations ($R = 0.31$; $p = 0.01$) were observed.

3.2. Nematode densities and community composition

Nematode densities ranged between 84 ± 14 ind. $10 \, \text{cm}^{-2}$ and $228.3 \pm 3.2\text{SE}$ ind. $10 \, \text{cm}^{-2}$ in the central depression and between 76 ± 14.8 ind. $10 \, \text{cm}^{-2}$ and 1208 ± 460 ind. $10 \, \text{cm}^{-2}$ in the northern area. There were no significant differences between densities observed in the different years for both areas (central depression: ANOVA: $F_{2,18} = 0.483$; $p > 0.05$ – northern area: Kruskal–Wallis Analysis by Ranks: H = 3.21; $p > 0.05$).

There were no differences (two-way crossed ANOSIM: $R = 0.927$; $p = 0.08$) in nematode community composition from the different stations in the central area (Fig. 3A). However, differences between years were obvious (global $R = 0.7019$; $p = 0.001$). Pairwise comparisons revealed that strongest differences occurred
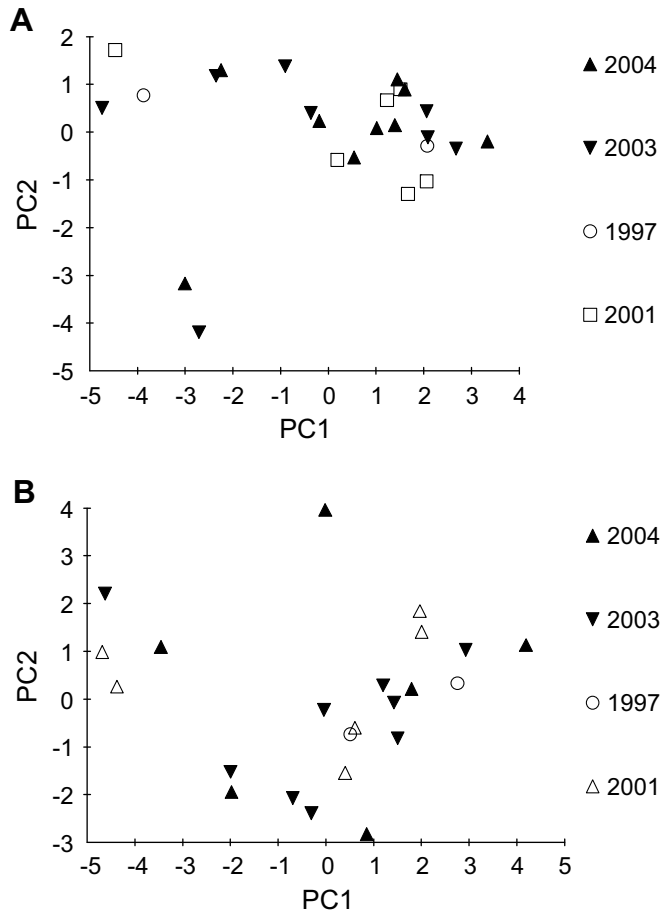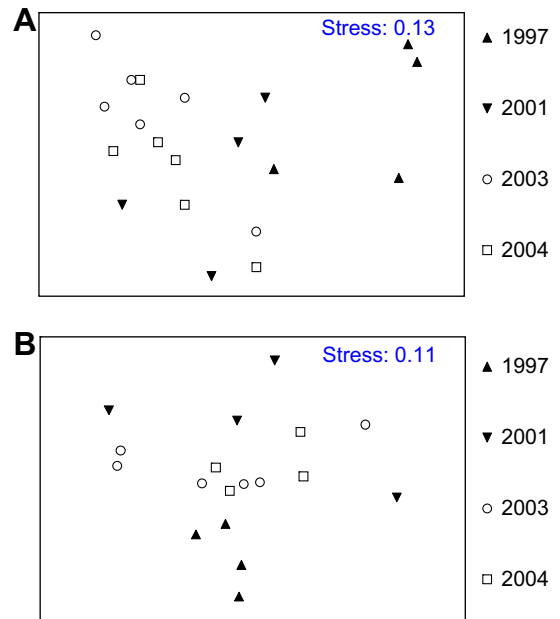
Fig. 2. PCA ordination plots of grain size variables. (A) Central depression, (B) northern area of the Kwintebank. Grain size variables included % clay, % silt, % very fine sand, % fine sand, % medium sand, % coarse sand; % between 1000 and 2000 μm, % >2000 μm, median grain size.

Fig. 3. Results of MDS analyses on non-transformed nematode species densities. (A) Central depression, (B) northern area of the Kwintebank.

In the northern area (Fig. 3B), significant differences in nematode community composition were observed between stations (two-way crossed ANOSIM: global $R = 0.78$; $p = 0.02$) and years (global $R = 0.67$; $p = 0.001$). Pairwise comparisons between the nematode communities sampled in subsequent years all showed strong differences (All pairwise $R > 0.625$). A SIMPER analysis (Table 2) revealed that within group similarity was due to different species in the different years. Only *Theristus bastiani* was found among the species contributing to 50% within group similarity in three years, while *O. perfectus* was important for within-group similarity in both 2003 and 2004.

The nematode communities from the individual stations of the central depression and the northern area revealed temporal differences since 1997 (Fig. 4) which was confirmed by the respective ANOSIM analyses (all $p < 0.02$). The 2nd stage MDS (Fig. 4) indicates that the temporal patterns in the stations of the central depression were similar and very different from the evolution of the communities at the stations at the northern area.

3.3. Nematode diversity

From the wide array of diversity indices calculated (Table 3), none were found to be significantly different between years in the central depression (one-way ANOVA or Kruskal–Wallis analy-

between communities sampled in 1997 and all other years (all pairwise $R = 1$) and between the communities encountered in 2001 and 2003 (pairwise $R = 0.875$). Smallest differences were found between the nematode communities from 2003 and 2004 ($R = 0.25$). SIMPER analysis revealed that a large part (>40%) of the within-group similarity is mainly due to different species during the extraction era (*Neochromadora munita* and *Metadesmolaimus pandus* in 1997; *Onyx perfectus* and *Viscosia franzii* in 2001), while after the cessation of the activities, the contribution of *O. perfectus* and *Mesacanthion hirsitum* made up the bulk of the within-group similarity (>40%) in both 2003 and 2004 (Table 1).

Table 1
Results of SIMPER analysis of the nematode data from the central depression, listing the main discriminating species and their abundance (Ab., ind 10 cm^{-2}) and contribution (Contr) to within group similarity (Av. Sim.)

1997 (Av. Sim.: 39.22)			2001 (Av. Sim.: 35.12)			2003 (Av. Sim.: 41.40)			2004 (Av. Sim.: 39.59)		
Species	Ab.	Contr (%)	Species	Ab.	Contr (%)	Species	Ab.	Contr (%)	Species	Ab.	Contr (%)
Neochromadora munita	42.36	29.84	Onyx perfectus	19.79	23.49	Onyx perfectus	62.69	35.84	Onyx perfectus	48.15	35.05
Metadesmolaimus pandus	18.95	11.43	Viscosia franzii	11.70	13.22	Mesacanthion hirsitum	14.98	6.36	Mesacanthion hirsitum	8.49	5.71
Enoploides spiculohamatus	6.93	7.49	Xyala striata	5.10	8.05	Enoploides spiculohamatus	10.80	5.25	Xyala striata	7.42	5.59
Viscosia franzii	5.56	6.09	Neochromadora munita	5.19	6.11	Chromaspirina pellita	8.51	4.54	Dichromadora cucculata	4.53	4.26

Table 2
Results of SIMPER analysis of the nematode data from the northern area of the Kwintebank, listing the main discriminating species and their abundance (Ab., ind 10 cm^{-2}) and contribution (Contr) to within group similarity (Av. Sim.)

1997 (Av. Sim.: 37.63)			2001 (Av. Sim.: 8.33)			2003 (Av. Sim.: 19.66)			2004 (Av. Sim.: 26.07)		
Species	Ab.	Contr (%)	Species	Ab.	Contr (%)	Species	Ab.	Contr (%)	Species	Ab.	Contr (%)
Neochromadora munita	49.10	27.88	*Sabatieria celtica*	50.49	25.72	*Onyx perfectus*	41.81	17.11	*Onyx perfectus*	18.06	16.84
Theristus maior	27.93	11.45	*Microlaimus arenicola*	99.95	10.05	*Microlaimus marinus*	105.21	13.03	*Theristus bastiani*	9.33	10.59
Theristus bastiani	55.22	7.37	*Actinonema celtica*	12.65	9.44	*Theristus bastiani*	31.02	12.53	*Dichromadora cucullata*	5.28	6.19
Onyx perfectus	16.30	6.45	*Leptonemella aphanothecae*	15.8	9.41	*Theristus longicollis*	6.14	4.20	*Richtersia inaequalis*	3.06	4.96
						Dichromadora cucullata	23.19	3.67	*Daptonema stylosum*	2.92	4.78
									Odontophora sp. 3	2.68	3.76
									Prochromadorella ditlevensi	1.65	3.37
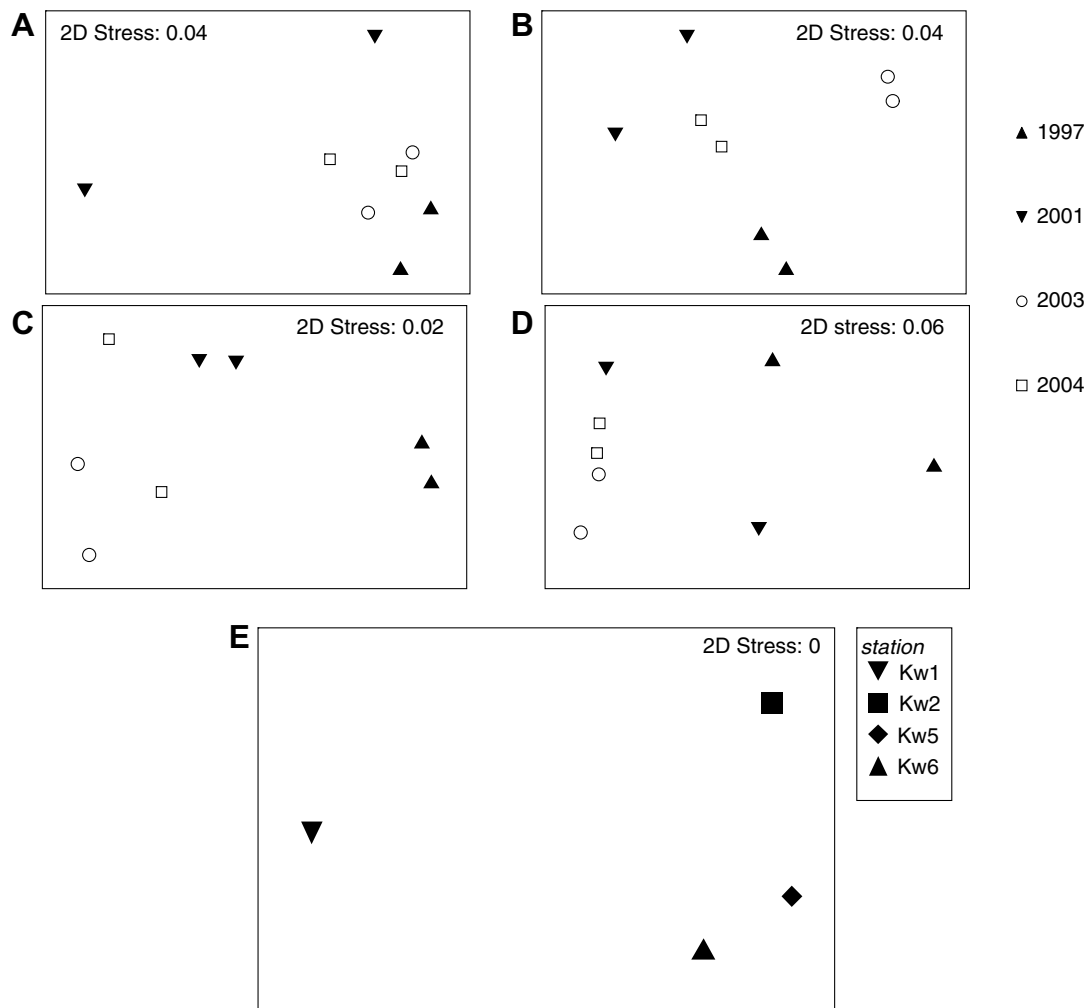
Fig. 4. Temporal development of nematode communities from Sts Kw1 (panel A), Kw2 (panel B), Kw5 (panel C) and Kw6 (panel D). Panel E: 2nd stage ordination based on the Spearman Rank Correlations between similarity matrices of original MDS analyses. Each symbol represents the patterns of community change at a site through time.

sis by ranks, all $p > 0.05$). Only in the northern part, significant differences between years were observed for J' ($F_{3,14} = 3.93$; $p < 0.05$) and Λ^+ ($F_{3,14} = 3.96$; $p < 0.05$) (Table 3). Tukey HSD for unequal N showed that significantly ($p < 0.05$) higher values were observed in 2004 in comparison with 1997. All other pairwise comparisons showed no significant differences. Concerning Λ^+, no significant differences were detected in the pairwise comparisons.

Table 3
Average univariate diversity values per year in the Northern and Central Area of the Kwintebank and results of the statistical tests for difference between years. Bold *p*-values indicate statistical differences at *p* < 0.05. For abbreviations of diversity indices: see Material and Methods Section

	1997	2001	2003	2004	F	p	H (Kruskal–Wallis)	p
Northern Area of the Kwintebank								
S	37	39.25	41.83	50.25			1.1	0.78
D	6.26	7.14	7.17	9.35	0.32	0.81		
J′	0.81	0.89	0.86	0.90	3.93	**0.03**		
H′(log$_e$)	2.91	3.12	3.167	3.41			3.42	0.33
1-Δ′	0.97	0.94	0.94	0.95	2.62	0.09		
N$_1$	18.75	25.40	24.06	33.54			3.47	0.33
N$_2$	11.46	16.78	14.59	20.38			2.69	0.44
N$_\infty$	5.16	6.58	6.09	6.46			1.76	0.63
Δ$^+$	39.08	39.79	38.76	39.27			5.18	0.16
Λ$^+$	64.86	67.77	53.87	60.97	3.96	**0.03**		
Central Area of the Kwintebank								
S	34.5	42	40.33	45.33			2.20	0.53
D	6.80	8.37	7.30	8.76	2.06	0.14		
J′	0.82	0.85	0.83	0.83	0.068	0.97		
H′(log$_e$)	2.92	3.14	3.06	3.17	0.60	0.62		
1-Δ′	0.90	0.92	0.91	0.91	0.12	0.95		
N$_1$	19.08	24.22	22.17	24.88	0.62	0.6		
N$_2$	11.31	14.77	13.45	13.74	0.2	0.89		
N$_\infty$	4.26	5.87	5.42	4.85	0.34	0.79		
Δ$^+$	39.24	39.07	39.54	38.35			4.15	0.25
Λ$^+$	63.02	67.36	61.70	60.07			2.28	
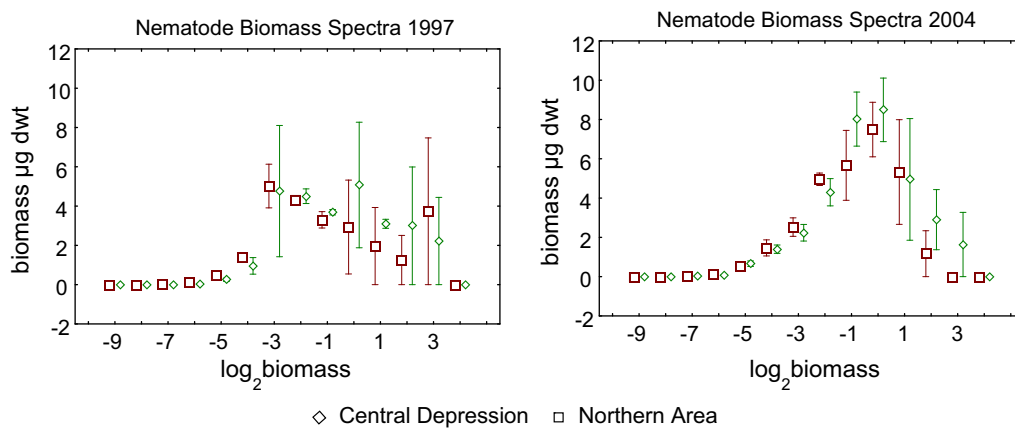
Fig. 5. Nematode biomass spectra of the central depression and northern area of the Kwintebank per year.

3.4. Nematode biomass spectra

Nematode biomass spectra in both the central depression and the northern area showed the same irregular pattern already described by Vanaverbeke et al. (2003). In 2004, a more traditional pattern is visible, with peak biomass values located in size class 0 (Fig. 5). In the lower size classes, highest biomass values are found in the northern part of the Kwintebank, while in the higher ranges the opposite trend emerges. However, differences between spectra were not statistically different (Kolmogorov–Smirnov two sample test, all *p* > 0.05).

4. Discussion

4.1. Environmental changes

Although a detailed discussion of the sedimentological and morphological changes on the Kwintebank is beyond the scope of this paper, some trends merit attention. Our results indicate a change in sedimentological variables in the central depression after cessation of the extraction activities. In a more detailed study, using a sampling grid of 100 m during four sampling campaigns

between September 2003 and February 2005, Béllec et al. (unpublished) reached the same conclusions. However, this does not indicate a morphological and sedimentological recovery of the central depression (Degrendele et al., in press) since a general filling up of the depression or a restoration of the height of the large sand waves in the depression was not observed in the two years after the closing of this area for extraction activities. On a smaller scale, the dredge furrows created by the suction hoppers have disappeared in the central depression (Degrendele et al., in press).

Since the closing of the central area for exploitation, extraction was very concentrated in the northern area of the sandbank where a new depression is being formed (Degrendele et al., in press). Our results indeed indicate a continuous change in the sedimentological environment which can be caused by long-term changes associated with sand extraction in combination with additional short-term disturbances by the creation and the filling of dredge furrows.

4.2. Changes in the nematode communities

Our results indicate changes in the nematode communities both in the central depression of the Kwintebank and in the northern area were extraction is still ongoing. However, the nature of

change in both areas is different. In the northern area, nematode community composition seems to be unstable and changing even on a short-term scale: pairwise ANOSIM showed large *R*-values when comparing the nematode communities sampled in October 2003 and February 2004.

The observed changes in the nematode communities in both areas can have several causes: (1) seasonal changes and/or (2) cessation or continuation of the extraction activities and/or (3) changes due to unmeasured non-seasonal, non-cessation factors. Although seasonal changes and changes due to unmeasured factors cannot be ruled out completely, we believe that this has a minor impact on the composition of the nematode communities. A first reason is given by Vanaverbeke et al. (2002) who found no differences in nematode communities from sandbanks on the BCS when sampled in different seasons. In addition, seasonal differences should be visible both in the northern part of the Kwintebank and in the central depression of the Kwintebank. This is clearly not the case: nematode communities in the central depression change from 1997 to 2001 and from 2001 to 2003, while differences between 2003 and 2004 were the smallest observed between subsequent years, which is confirmed by the SIMPER analyses for both areas.

The 2nd stage MDS confirms that the temporal development of the stations in the central depression is different from the stations in the northern area. This again suggests that seasonal changes and changes due to unmeasured factors had a minor impact on the observed differences between the central area and the northern area after cessation of the extraction activities. In the northern area, the temporal evolution of stations Kw1 and Kw2 is different as well, which reflects the local impact of sand extraction activities on the nematode communities (Vanaverbeke et al., 2007).

From this, we conclude that the continuous alteration of the nematode communities in the northern area is caused by the extraction activities whereas the establishment of a more stable community in the central depression is possible as a consequence of the absence of the exploitation.

Long-term changes (1978–2001) in the nematode communities from the Kwintebank were attributed to long-term changes in the sedimentological environment in combination with the extra dynamics imposed by the creation and filling up of dredge furrows (Vanaverbeke et al., 2007). Our results show that on a relatively short time scale, the absence of the creation and filling of dredge furrows can lead to the establishment of a more stable nematode community. Dredge furrows at the edge of the depression of the Kwintebank remained visible for six months (Degrendele et al., in press). There are no data available for the central parts of the depression, but we assume that regeneration of dredge furrows in the absence of sand extraction was completed before our sampling in October 2003. Hence, two major changes occurred in benthic environment of the central depression within the first year after closing: the daily creation of the furrows by the suction hoppers and the slow filling up of the furrows. This leads to a new and more stable nematode community which is able to cope with the daily ebb-flood related dynamics of the area.

Nematode diversity did not change, both in the depression and the northern area during our sampling period. These results are based on a low number of replicates and should be interpreted with care. However, our results are in accordance with Vanaverbeke et al. (2007) who did not observe a decrease in diversity during the long-term extraction period at the Kwintebank. Nematodes are indeed highly diverse, and there is a wide range of species, from those that are very sensitive to disturbances to very tolerant species (Kennedy and Jacoby, 1999). Therefore, nematode community composition can be different while diversity remains unaffected (Bolam et al., 2006). In our case, we suggest that sensi-

tive species are replaced by tolerant species without a significant loss/gain of species in the presence/absence of disturbance.

4.3. Recovery of nematode communities

Boyd et al. (2003) described 'recovery' as a two-step process. In a first step, recolonisation (the settlement of new recruits from the plankton or immigration of adults from outside the area) occurs, followed by restoration (the return of the community structure). An indication of the restoration can then be gained by comparing the attributes of the community (eg. species richness, abundance, biomass) with a reference community obtained from a reference site or pre-dredging communities (see Boyd et al., 2003 and references therein). These definitions are commonly applied in studies focusing on macrobenthos. Nematodes do not have planktonic life stages but in intertidal areas, adults do disperse through the water column after passive resuspension (Schratzberger et al., 2006). Passive resuspension should be no problem in a hydrodynamically stressed sandbank environment (Palmer and Brandt, 1981; Palmer and Gust, 1985; Thistle and Levin, 1998) and is most probably the main reason for the introduction of new nematode species in the central depression. However, introduction of new species should be considered a continuous process and ongoing while the exploitation still occurred. Therefore, the emergence of different communities after the cessation of sand extraction are most probably due to the fact that certain nematode species (already present in low numbers or introduced through pelagic dispersal) have better survival chances in the absence of the disturbances (eg. extra dynamics as a consequence of creating and filling up dredge furrows).

In order to assess the full recovery (return of community structure) we performed a MDS analysis (Fig. 6) in which the communities sampled in 1978 (Vincx, 1986) were included as well. Although the exploitation of the Kwintebank started already in 1976, extraction intensity was low in that period and therefore we are comparing the recently sampled communities with communities subjected to a very limited disturbance rather than comparing with a reference situation *sensu strictu*. However, it is very obvious that there is no return to the community structure of 1978, which is confirmed by ANOSIM (*R* = 0.595; *p* = 0.001). All pairwise comparisons, except 2003–2004 were significantly different in the pairwise comparison.

A second way of assessing the rate of recovery was indirectly through comparing the biomass spectra of the extracted sites with the abandoned sites. Vanaverbeke et al. (2003) showed peak biomass values in size classes −3 to 0 in the intensely extracted areas on the Kwintebank, while in unexploited sandbanks on the BCS and areas on the Kwintebank with low sand extraction intensity, highest biomass values were observed in size class −1 or 0. This indicates that nematode communities shift towards smaller individuals in areas with high physical disturbance. In the long-term, Vanaverbeke et al. (2007) reported a loss of large species in the
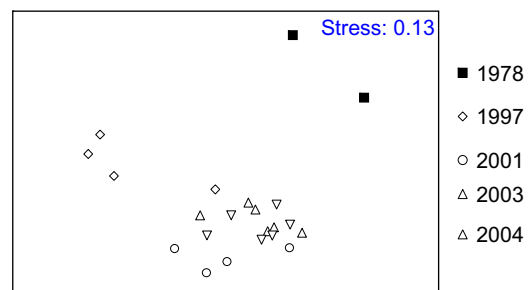
Fig. 6. Result of MDS plot on non-transformed nematode species densities from the central depression. All sampling years combined.

heavily exploited areas on the Kwintebank. Similar observations were made by Lampadariou et al. (2005) in the Aegean Sea where larger nematodes disappeared as a consequence of intense trawling. Although reference size distribution data of nematode populations on the Kwintebank are not available, we expected that nematode size spectra would reveal higher biomass in the larger size classes in the absence of extraction activities, which was clearly not the case. This can have two reasons: either the larger nematodes have not colonized the depression yet, or the environment is not suitable for these organisms and colonizing large nematodes will not survive. At the moment, there is no evidence underpinning a preference for one of the possible explanations.

Using the definition of Boyd et al. (2003), no recovery of the nematode communities occurred. However, there is no evidence that the original community would not have changed in the course of 26 years due to naturally occurring processes. Since even small differences in the median grain size and the fractions of medium sand and fine sand content are reflected in differences in the nematode communities (Vanaverbeke et al., 2002), it seems unlikely that nematode communities would remain unchanged during such a long period in this very dynamic environment. Bolam et al. (2006) summarised earlier discussions (see Bolam and Whomersley, 2003; Bolam and Whomersley, 2005; Schratzberger et al., 2006) on reference sites, defined as pre-impact situations or a non-impacted reference site. Although they studied the recolonisation of dredged material deposited in intertidal systems, their remarks are valid for the central depression as well: pre-impact situations are very different from the impacted situations (eg. the creation of a depression of more than 5 m depth) and this imposed difficulties when comparing impact and reference sites which will always show small differences in physical properties. Especially in the case of nematodes, which are very dependent on grain size characteristics (Vanaverbeke et al., 2002), finding a suitable reference site for sandbanks systems is very problematic. Therefore, we suggest to use the rate of change in nematode communities as a measure of recovery of the benthic system. In the central depression, nematode communities were not changing significantly anymore after 1.5–2 years of cessation of exploitation, while there was an ongoing change in areas were extraction still occurred.

4.4. Trends in nematode communities versus macrobenthic communities

Boyd et al. (2005) summarise the observed patterns in recovery of the macrobenthic communities in sites subjected to sand and gravel extraction. In a first phase, abundance and species numbers increase as a consequence of the colonisation of the area by larvae and adults of opportunistic species from surrounding areas. In a second phase, community biomass will be reduced since colonizers have to grow on to maturity comparable with the pre-dredging situation. In gravelly areas, abrasive effects of increased sediments can limit growth and survivorship of epifauna, which is an extra factor inhibiting the re-establishment of the original communities. However, there is no clear picture if the latter holds for sandy areas as well. When bedload transport eventually returns to pre-dredging levels, there is the possibility for the communities to fully return to the original state. In sandy muds, Hily (1983) adds a third phase, during which opportunistic species are replaced by a greater number of species as a consequence of interspecific competition.

Our results indicate that recovery of nematode communities follows a different path. We have no evidence of increased densities in the year following cessation of dredging. Moreover, densities in the abandoned area were not higher than densities in the exploited area. This can be explained by the life history traits of nematodes and their ability to cope with physical disturbance.

Nematodes reproduce constantly, hence there is a constant presence of juveniles facilitating the recolonisation of the impacted area (Vanaverbeke et al., 2002) even during the exploitation period. Macrobenthic reproduction on the other hand is limited to certain periods in the year. A disturbance event during the recruitment period therefore can destroy the population until the next recruitment. These mechanisms also explain the absence of a shift in species diversity in the nematode communities after cessation of extraction activities. The constant reproduction, in combination with the high diversity, ensures the presence of community with a constant level of diversity, consisting of species well adapted to the extra disturbance induced by the exploitation of the seabed. These species are then gradually replaced by species preferring a more stable environment who can outcompete the species present during the extraction period.

However, it is still unclear how the different phases of the recolonisation/restoration processes of the macrobenthic and meiobenthic communities match in time. More studies, incorporating both meiobenthic and macrobenthic data are needed to fully understand this process. This will most probably increase our understanding of recolonisation processes by fine-tuning the different phases in the very early (based on the nematode communities) and later (based on the macrobenthic communities) phases of these processes.

5. Conclusions

We showed that nematode communities in sites closed for sand extraction activities evolved differently from nematode communities inhabiting area that are still exploited. Diversity and density did not change, however nematode community composition was more stable due to the absence of the creation and filling of dredge furrows. In addition, we hypothesise that recovery of nematode communities follows different pathways than marcrobenthic recovery as a consequence of the typical nematode life history traits.

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