# CHAPTER VI

## Changes in structural and functional diversity of nematode communities during a spring phytoplankton bloom in the Southern North Sea

*Results presented in:*

Vanaverbeke J, Steyaert M, Soetaert K, Rousseau V, Van Gansbeke D, Parent J-Y, Vincx M (submitted) Changes in structural and functional diversity of nematode communities during a spring phytoplankton bloom in the Southern North Sea

## Acknowledgements

We would like to thank the master and crew from the RV *Belgica* , *Zeehond* en *Oostende XI* for their skilful help during the sampling. Annick Van Kenhove and Wies Ghijselinck are acknowledged for making of all the slides. Many people from the Marine Biology Section gave a a helping hand during the sampling period. This research was funded by Ghent University (BOF, 1998-2003) and OSTC (Belgium Sustainable Development-North Sea Project MN/DD[40-41-42] and TROPHOS Contract nr EV/02/25A. This is publication nr xxxx from NIOO-CEME.

## Abstract

The response of nematode communities to the sedimentation of a spring phytoplankton bloom in a sandy, well-oxygenated sediment in the Southern North Sea is investigated from early March to July 1999 with monthly intervals. Both structural (nematode density, diversity, vertical distribution and community composition) and functional (feeding type distributions, number of species within feeding groups) characteristics showed considerable changes shortly after the arrival of fresh organic material at the sediment surface. The general increase in density and diversity was related to changes within selective deposit feeding and epistrate feeding nematodes. Although temporal variability was significant for total nematode densities and deposit feeding nematodes, spatial variability (in the orders of 100 of meters) was high when single species were concerned. It is hypothesised that sedimentation and subsequent remineralisation of fresh organic matter during the spring phytoplankton bloom results in an increase of suitable food items (both living and dead). This, combined with the availability of oxygen and the high habitat heterogeneity at the sampling location (both in the order of meters and over the sediment depth profile), create conditions in which many nematode species can co-exist.

# Introduction

Shelf seas are areas with a high primary production in the euphotic zone and about 20-50% of this net phytoplankton production is deposited on the sediment (Jørgensen 1983) where it fuels benthic life (Graf 1992). The meiobenthos represents the smaller-sized (< 1mm) animals in the sediment and their response to the sedimentation of phytodetritus has been the subject of many studies. Results were equivocal: in certain cases, a clear response was lacking (*e.g.* Warwick & Buchanan 1971, Boucher 1980, Fleeger et al. 1989), while other studies showed prominent responses to phytoplankton deposition (*e.g.* Bovée & Soyer 1974, Rudnick et al. 1985, Ólafsson & Elmgren 1997, Ólafsson et al. 1999, Steyaert et al. subm). These differences seem to indicate that site-specific processes control the signal of the response to this pulsed food supply from the water column.

Few studies have examined the meiobenthic communities on the species level, although data on the major taxon level may conceal the more subtle changes occurring at the species level (Gooday et al., 1996). For instance, in a study of the nematodes, the dominant taxon within the meiobenthos, Steyaert et al. (subm) showed that closely related species inhabiting a fine-grained, anoxic North-Sea sediment, respond differently to the changes in the sediment caused by sedimentation of a spring phytoplankton bloom.

As the trophic composition of nematode assemblages reflects the quality and quantity of their food sources (Moens & Vincx 1997, Danovaro & Gambi 2002), changes in the distribution of feeding types are also expected.

Another factor that may change in response to pulsed food deposition is the way in which benthic animals are distributed vertically in the sediment. The remineralisation of fresh, high quality organic material results in changes in the biogeochemical environment of the sediment, at short time scales. Nematodes are particularly sensitive to the sediment biogeochemical conditions (Boyd et al. 2000, Hendelberg & Jensen

1993, Steyaert et al. 1999), and vertical profiles can change rapidly in time, while density and diversity are not yet affected (Steyaert et al. in press).

In previous papers we have documented the changes in biomass spectra and nematode shape, during and after sedimentation of phytodetritus and subsequent remineralisation in our sampling station (Vanaverbeke et al. 2003, Vanaverbeke et al. subm). Here we take a closer look at structural (densities, diversity and vertical profiles) and functional (feeding habit, number of species per feeding type) changes. We chose nematodes as a study object because they are the most dominant metazoan animals and because of the ease at which the morphology (Soetaert et al. 2002) and trophic position (Wieser, 1953) can be determined. Moreover, because of their high turnover rates and continuous reproduction (Heip et al. 1985), a clear signal is expected.
As the ability to track temporal changes not only depends on the time scale at which sampling was performed, but also on the degree of spatial variability, both temporal and spatial variability are compared.

## Material and methods

### Study site and sampling

Samples were obtained from the open sea site Station 330 (51°26.0'N; 02°48.5'E) (Fig. 1) on the Belgian Continental Shelf (Southern Bight of the North Sea). Sampling was performed weekly from March 1999 until July 1999.
Sampling took place from the *RV* Belgica, Zeehond or Oostende XI, using a modified Reineck boxcorer. At each sampling occasion, the boxcorer was deployed 3 times. Each boxcorer was sampled by means of 2 identical perspex cores (i.d. 3.6 cm) and one larger

core (i.d. 6 cm). All cores were sliced vertically: the upper 2 cm in 5 mm intervals, the deeper layers per cm. In July, only two good boxcores were retrieved.

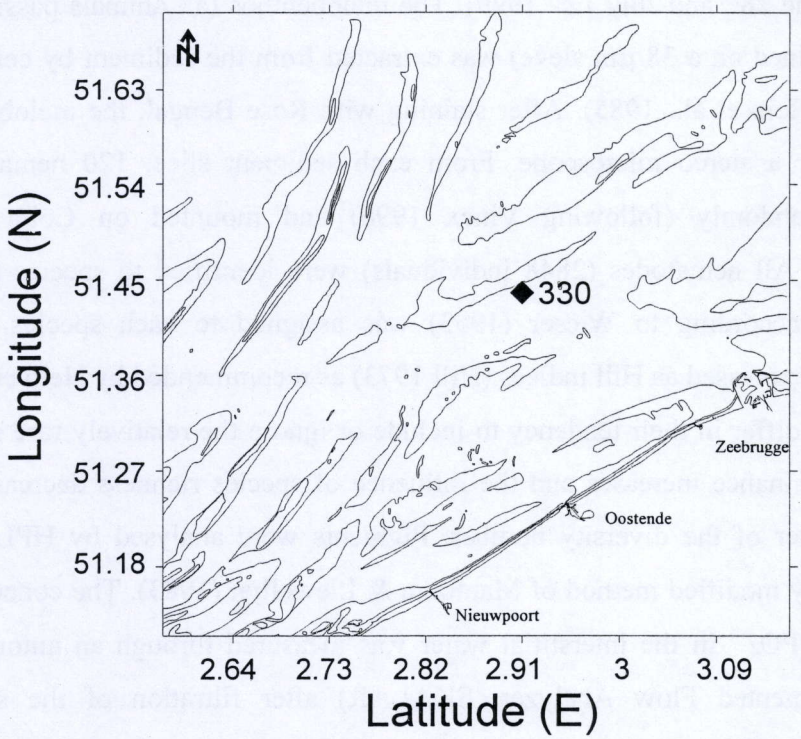


**Figure 1. Map of the Belgian continental shelf with indication of the sampling station**

Sediments from one core were stored in a hot (70°C), neutral formaldehyde tap-water solution for later faunal analysis.

From the remaining 10 $cm^2$ core, 1 ml of sediment was subsampled using a syringe from which the tip was removed. These samples were frozen for pigment analysis. Sediment slices for nutrient analysis were obtained from the larger cores and frozen until analysis.

On board, the redox potential of the sediment was measured using a mV meter.

Chlorophyll *a* (Chl *a*) values at the sea surface were obtained from Rousseau (2000). Bottom water Chl *a* values were obtained from the supernatant water of the Reineck boxcorer, which was carefully siphoned off, and 0.5 l was filtered on Whatman GF/C filters. Filters were stored in the freezer until processing.

## Laboratory treatment of samples

Samples for faunal analysis were processed on a monthly interval (March 9$^{th}$, April 27$^{th}$, May 12$^{th}$ , June 28$^{th}$ and July 12$^{th}$ 1999). The meiobenthos (all animals passing a 1 mm sieve and retained on a 38 µm sieve) was extracted from the sediment by centrifugation with Ludox (Heip et al.. 1985). After staining with Rose Bengal, the meiobenthos was counted under a stereo microscope. From each sediment slice, 120 nematodes were picked out randomly (following Vincx 1996) and mounted on Cobb slides for identification. All nematodes (2848 individuals) were identified to species level and a feeding type according to Wieser (1953) was assigned to each species. Nematode diversity was expressed as Hill indices (Hill 1973) as recommended by Heip et al. (1988). These 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. Pigments were analysed by HPLC (Gilson) using a slightly modified method of Mantoura & Llewellyn (1983). The concentration of $NH_4^+$, Si and $PO_4^{---}$ in the interstitial water was measured through an automatic chain ($SAN^{plus}$ Segmented Flow Analyzer, SKALAR) after filtration of the samples on Whatman GF/F filters. The remaining sediment was used for grain size analysis with a Coulter Counter LS Particle Size Analyser. Sediments were defined according to the Wentworth scale (Buchanan 1984).

## Statistical Analysis

Variation in total nematode densities, feeding type distribution and feeding type densities, number of species per feeding type and diversity indices per month were analysed using Analysis of Variance (ANOVA). Nematode densities were root-root transformed in order to meet the assumptions for ANOVA. Densities per feeding type required a log (x+1) transformation. When overall significant differences were detected, Tukeys Honest Significance Test for unequal N was used for pairwise comparisons. When the assumptions for ANOVA were not met, even not after transformation (Feeding Type

distribution), the non-parametric Kruskal-Wallis test was used. Overall significant differences were compared pairwise following Conover (1971).

In order to elucidate to what degree total nematode densities, feeding type densities and species densities are impacted by small-scale spatial heterogeneity (i.e. between replicate deployments of the Reineck boxcorer) or by temporal effects, we calculated the % variation among dates (Sokal & Rohlf 1997) in ANOVA on root-root (total and species densities) or log (x+1) (densities per feeding type) transformed densities.

Changes in nematode densities with time, sediment depth and time x depth were tested by constructing a univariate 'split-plot' ANOVA design on root-root transformed densities, following Steyaert et al. (2001). Replicates were nested within 'time'; however, not within depth.

Nematode community structure was analysed by means of a Detrended Correspondence Analysis (DCA) (Hill 1979). Species occurring less than 3 times in all sediment slices from all dates were eliminated from the dataset. Analyses were performed on mean abundances per sediment slice per date.

# Results

## Study site and environmental variables

Sediments at Station 330 were classified as medium sand (median grain size ranging from 329.3 µm in May to 360.7 µm in June) (Buchanan 1984), devoid of mud. Chl *a* values in the water column were maximal at April 29$^{th}$ and May $^{5th}$, reflecting the peak phytoplankton bloom (Rousseau 2000). Pigment concentrations in the water overlying the sediment closely followed the pattern at the surface (Fig. 2), indicating sedimentation of phytoplankton from the end of April.

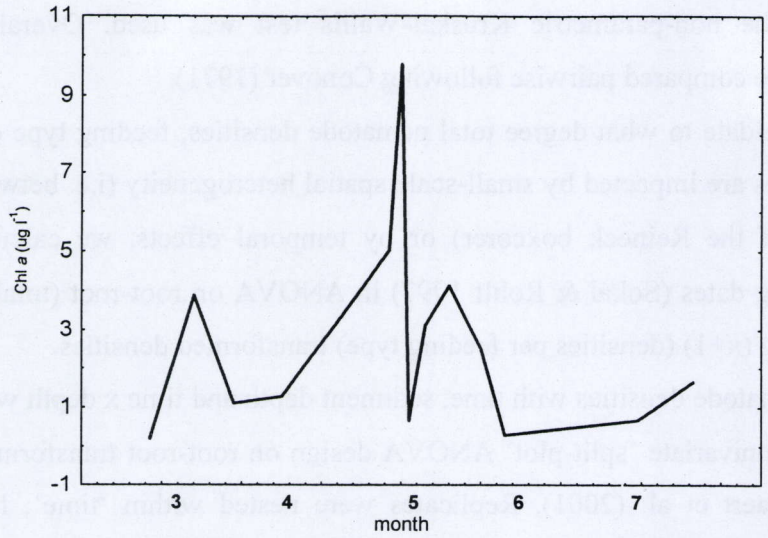


**Figure 2. Chlorophyll a concentrations in the bottom water at Station 330 (Belgian Continental Shelf –spring and summer 1999)**

Chl *a* values in the sediment (Fig. 3) were highest at the beginning of March (Chl *a* concentrations in all sediment layers > 100 ng/g on March 9$^{th}$), and decreased toward the end of March. From April until the end of the sampling period, mean concentrations per sediment layer ranged between 50 and 150 ng/g. Only on May 26$^{th}$ were higher concentrations recorded. Many chlorophyll versus depth profiles demonstrated clear subsurface peaks, around 3-5 cm deep.

Ammonium concentrations, averaged over the first 4 cm increased from March till May and then decreased (Fig. 4). Redox values remained positive (>100 mV) during the complete sampling periods and at all sediment depths (Fig. 5).

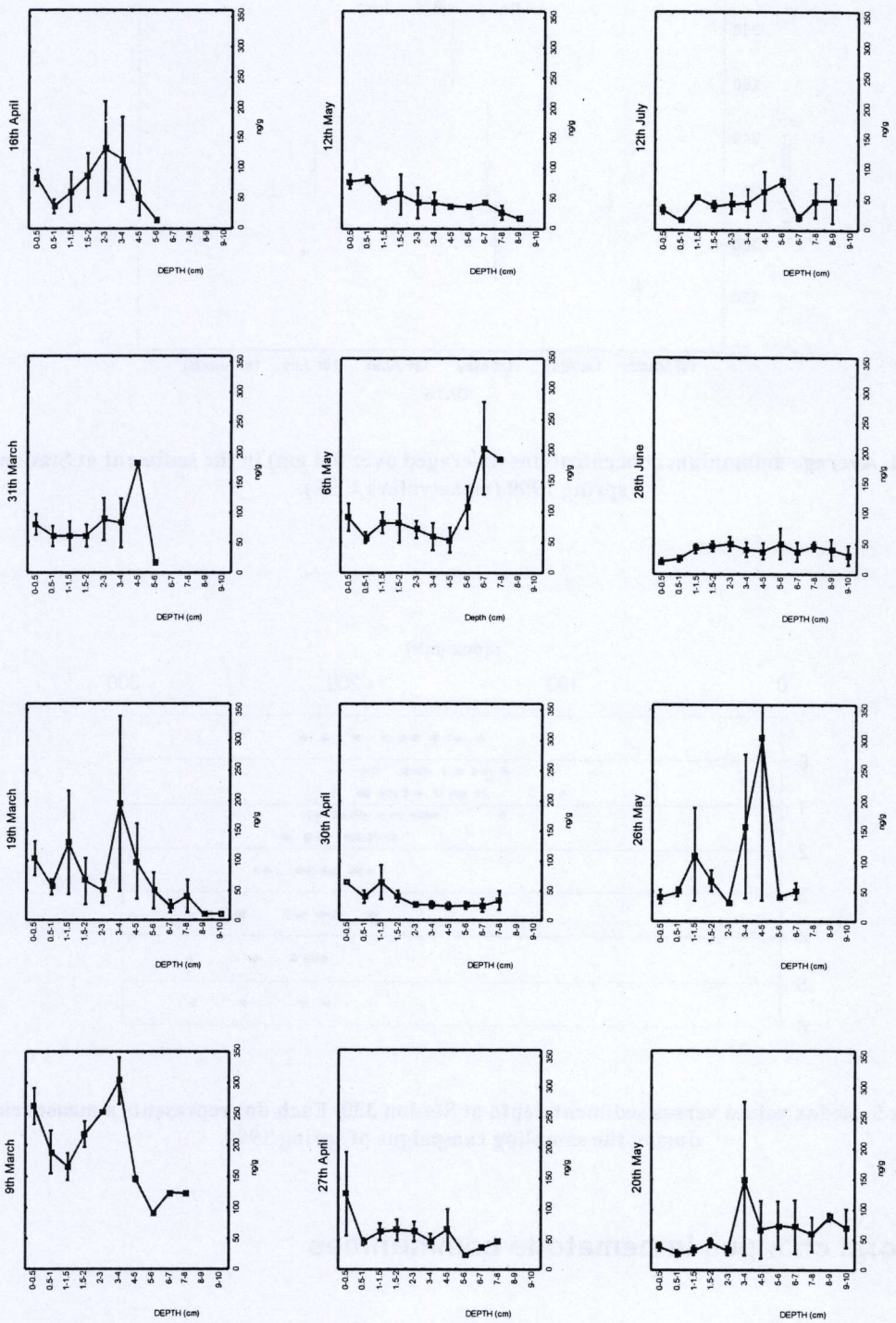


**Figure 3. Chlorophyll a depth profiles in the sediment at Station 330: spring and summer 1999 (mean values ± SE).**

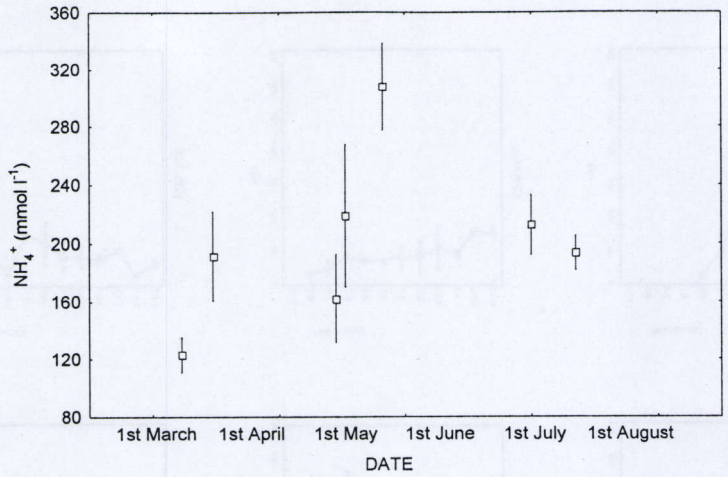


**Figure 4. Average ammonium concentrations (averaged over 0-4 cm) in the sediment at Station 330: spring 1999 (mean values ± SE).**

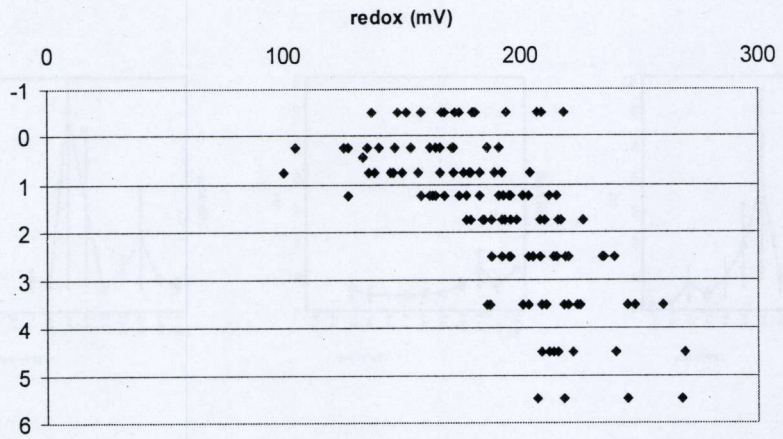


**Figure 5. Redox values versus sediment depth at Station 330. Each dot represents a measurement during the sampling campaigns of spring 1999.**

## Temporal changes in nematode communities

Nematode densities (Fig. 6) increase steadily from March till May, afterwards values decreased towards July. An ANOVA on root-root transformed values resulted in significant differences ($F_{4,9}$=16.43; p<0.001).

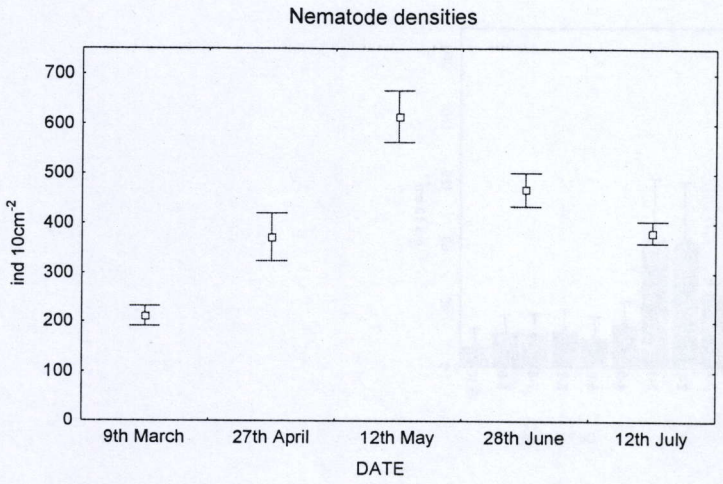


**Figure 6. Total nematode densities at Station 330: spring and summer 1999 (mean values ± SE)**

Pairwise comparisons revealed significantly lower densities in March compared to all other months, while the densities in April were significantly lower than in May (Table 1).

| | April | May | June | July |
|---|---|---|---|---|
| **March** | * | *** | ** | * |
| **April** | | * | NS | NS |
| **May** | | | NS | NS |
| **June** | | | | NS |
| **July** | | | | |

**Table 1. Significant differences between monthly nematode densities at Station 330 (spring 1999). Results of Tukeys HSD for unequal N (*:p<0.05; **p<0.01; ***p<0.001; NS: not significant).**

Nematodes tended to be concentrated in the upper 4 cm of the sediment in May (Fig. 7). In June, highest values were recorded at the upper 0.5 cm slice. The ANOVA 'split-plot' analysis demonstrated a significant effect for sediment depth ($F_{11,22}$= 9.49, df= 11, p<0.01) and the interaction term time x depth ($F_{44,110}$= 2.51,df= 44, p<0.001). Densities per sediment layer were not significantly affected by time ($F_{4,8}$= 1.25, df= 4, p=0.36).

Hill's diversity numbers (Fig. 8) of all orders were lowest in March. ANOVA's only reflected significant differences for $N_0$ ($F_{4,9}$=15.35; p<0.001) and $N_1$ ($F_{4,9}$=3.90; p<0.05). Pairwise comparisons (Tukeys HSD for unequal N) showed that the number of species ($N_0$) in March was significantly lower compared to all other months. Concerning $N_1$, values in March differed only significantly from April.

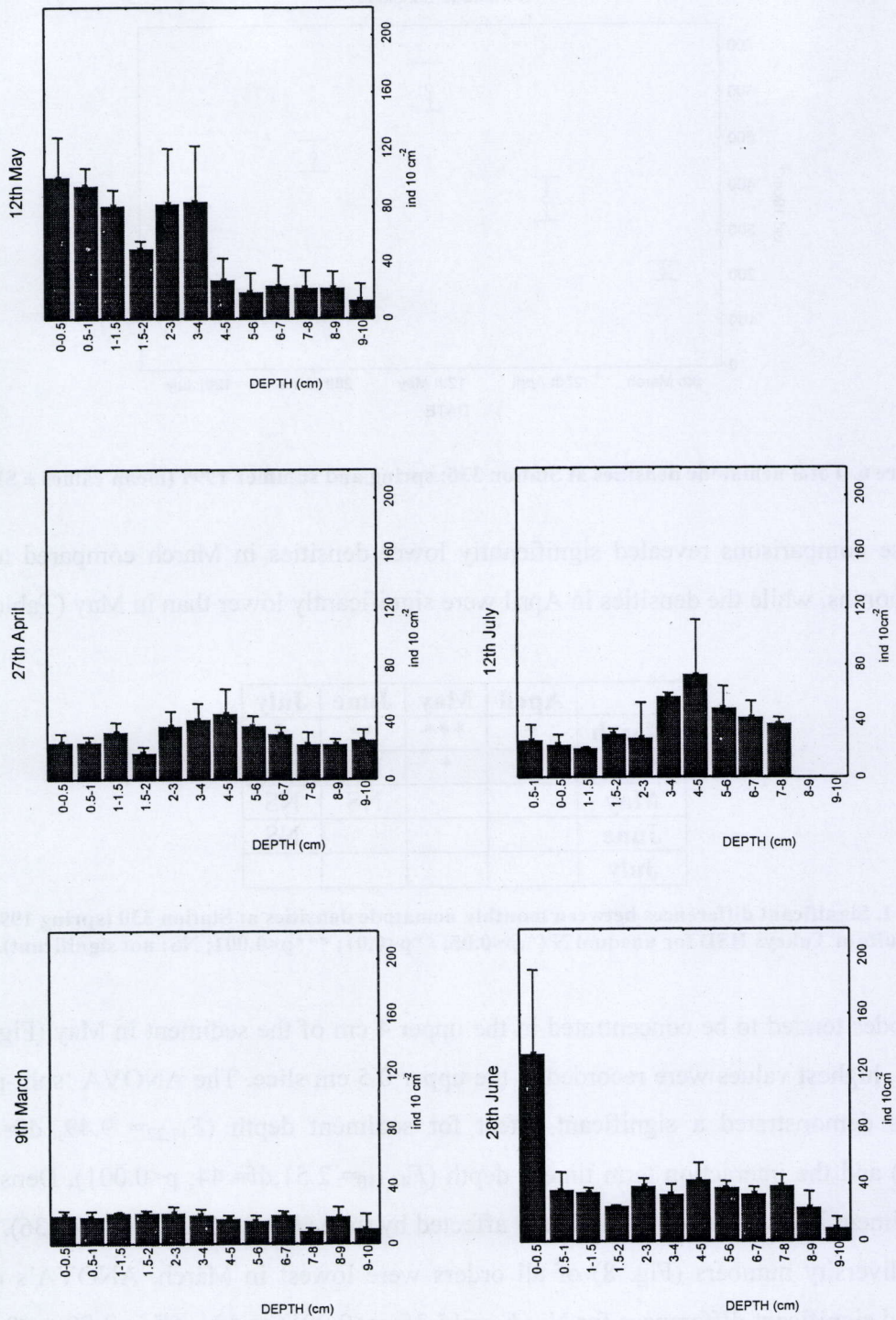


**Figure 7. Vertical distribution of nematodes at Station 330: spring and summer 1999 (mean values ± SE).**

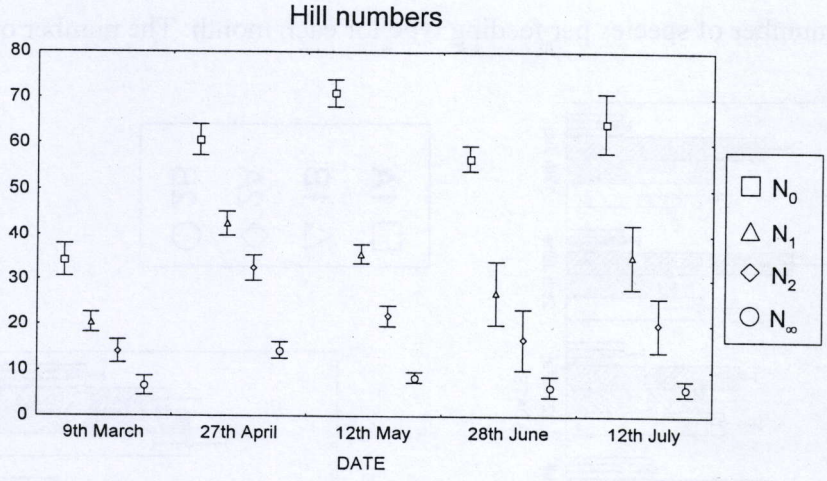


**Figure 8. Diversity indices (Hill numbers) of the nematode communities at Station 330: spring and summer 1999 (mean values ± SE)**

The densities from all feeding types changed during the sampling period (Fig. 9A). This was significant for 1A ($F_{4,9}$= 21.97, p<0.001) and 1B ($F_{4,9}$= 12.16, p<0.01) nematodes. Densities generally increased from March till May (Fig 9A, Table 2) but selective deposit feeders increased at a higher rate.

| | **April** | **May** | **June** | **July** |
|---|---|---|---|---|
| **March** | **1A, 1B** | *1A,1B* | *1A*,1B | **1A**, 1B |
| **April** | | 1A | NS | NS |
| **May** | | | NS | NS |
| **June** | | | | NS |
| **July** | | | | |

**Table 2. Significant differences between monthly densities per feeding type at Station 330 (spring 1999). Results of Tukeys HSD for unequal N. (no formatting: p<0.05, bold:p<0.01; italic:p<0.001; NS: not significant).**

Thus, the relative contribution of feeding types (Fig. 9B) showed a significant increase of the proportion of 1A nematodes (selective deposit feeders) during the sampling period (Kruskal-Wallis analysis by rank, p<0.01). Pairwise comparisons revealed that the proportion of the selective deposit feeders in March was significantly lower than in May, June and August (p<0.05), and April values were significantly lower than in May

($p<0.05$) No significant differences were found for the other feeding types. Fig. 9C depicts the number of species per feeding type for each month. The number of species

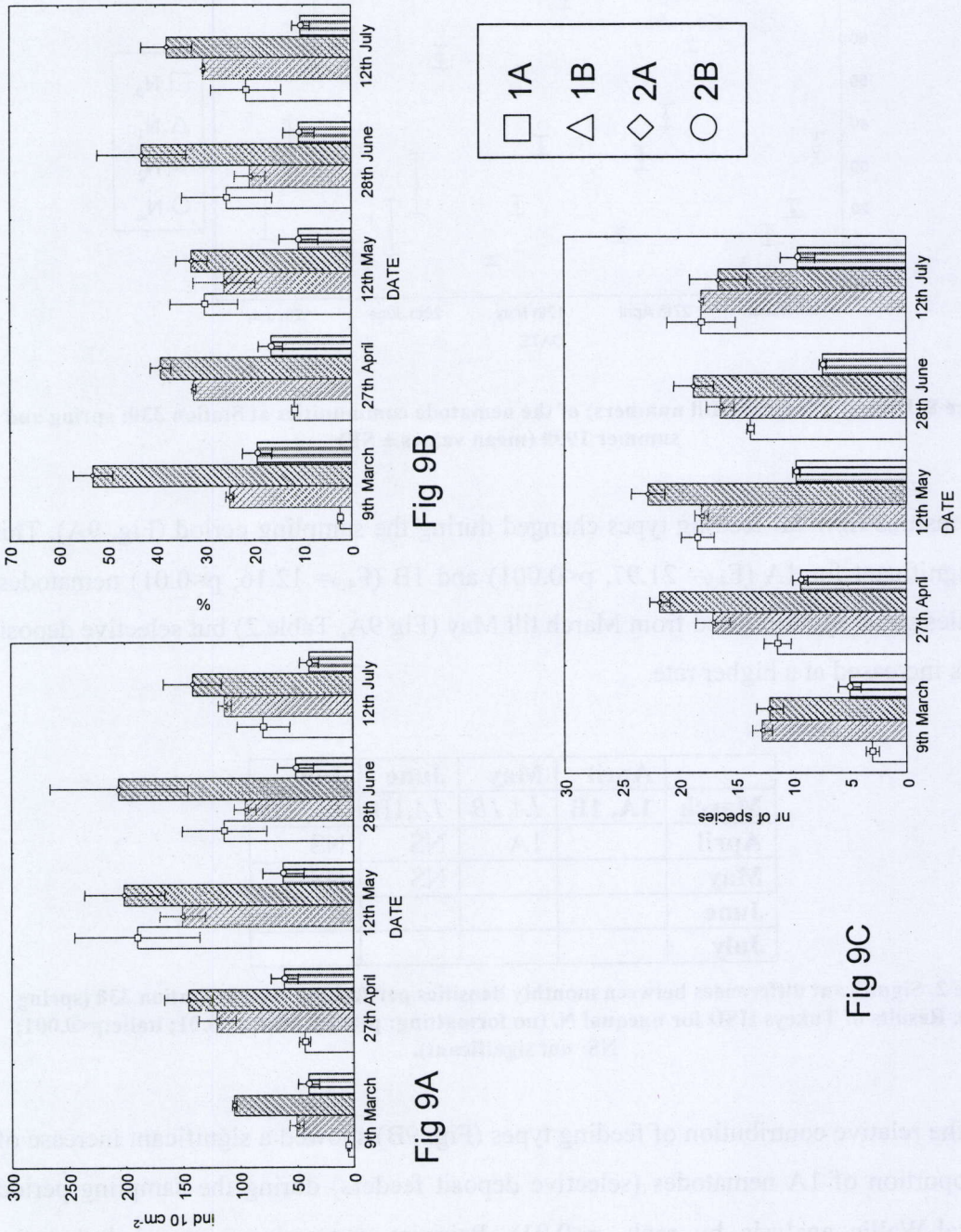


**Figure 9. A: Densities per feeding type at Station 330: spring and summer 1999. B: Relative contribution of feeding types per sampling date. C: Number of species per feeding type per sampling date. All values: mean values ± SE**

were significantly different for each feeding type between months (ANOVA, Table 3).

| Feeding Type | $F_{4,9}$ | p |
|---|---|---|
| **1A** | 24 | *** |
| **1B** | 4.3 | * |
| **2A** | 8.6 | ** |
| **2B** | 7.2 | ** |

**Table 3. Significant differences between the number of species per feeding type per month at Station 330 (spring 330). Summary of ANOVA results (*:p<0.05; **p<0.01; ***p<0.001).**

Especially in March, the number of species per feeding type was significantly lower compared to the other months (Tukeys HSD for unequal N, Table 4). Strongest differences were observed for the 1A and 2A feeding types.

| | **April** | **May** | **June** | **July** |
|---|---|---|---|---|
| **March** | **1A; 2A**; 2B | *1A*, 1B, **2A**, 2B | **1A** | *1A*, 2B |
| **April** | | 1A | | |
| **May** | | | | |
| **June** | | | | |
| **July** | | | | |
| | | | | |

**Table 4. Significant differences between the number of species per feeding type per month at Station 330 (spring 1999). Results of Tukeys HSD for unequal N. (no formatting: p<0.05, bold:p<0.01; italic:p<0.001)**

The variance structure of the 25 most abundant species was compared to the variance of the total nematode densities and the total densities of the feeding types (Table 5). The variation between sampling dates was significantly larger than the spatial variation for the total nematode densities and those nematodes feeding on bacteria and detritus (1A and 1B nematodes). Such large temporal versus spatial variation was not the case for all dominant species, since significant results were only obtained for 14 of the 25 dominant species.

| Species (n=14, a=5) | Mean | Standard Deviation | % among dates | p |
|---|---|---|---|---|
| *Microlaimus marinus* | 28.0 | 27.0 | 76 | * |
| *Chromadorita n. sp. 2* | 20.8 | 58.7 | 33 | |
| *Tricoma sp.1* | 20.0 | 21.7 | 84 | ** |
| *Metepsilonema comptum* | 19.2 | 32.1 | 73 | * |
| *Dichromadora cucullata* | 17.4 | 15.1 | 65 | * |
| *Onyx perfectus* | 14.1 | 15.1 | 21 | |
| *Richtersia inaequalis* | 13.1 | 15.2 | 60 | |
| *Enoploides spiculohamatus* | 11.8 | 10.3 | 36 | |
| *Theristus denticulatus* | 11.4 | 6.5 | 63 | * |
| *Camacolaimus longicauda* | 11.4 | 6.3 | 78 | ** |
| *Manunema annulatum* | 9.6 | 9.9 | 50 | |
| *Epsilonema pustulatum* | 9.3 | 15.1 | 67 | * |
| *Desmodora schulzi* | 9.3 | 9.2 | 94 | *** |
| *Prochromadorella ditlevseni* | 8.5 | 9.9 | 25 | |
| *Daptonema nanum* | 8.4 | 6.2 | 86 | *** |
| *Pomponema multipapillatum* | 7.6 | 8.3 | 79 | ** |
| *Rhynchonema sp1* | 7.4 | 5.2 | 57 | |
| *Sabatieria celtica* | 6.7 | 7.5 | 75 | ** |
| *Desmoscolex sp.1* | 6.7 | 5.4 | 84 | *** |
| *Trichotheristus mirabilis* | 6.5 | 6.8 | 45 | |
| *Paracyatholaimoides multispiralis* | 5.5 | 5.3 | 90 | *** |
| *Rhynchonema moorea* | 5.5 | 8.5 | 76 | ** |
| *Neochromadora munita* | 5.5 | 5.6 | 42 | |
| *Calomicrolaimus parahonestus* | 5.4 | 4.8 | 43 | |
| *Theristus heterospiculoides* | 5.3 | 3.9 | 53 | |
| 1A Feeding Type | 86.6 | 81.9 | 92 | *** |
| 1B Feeding Type | 105.1 | 40.1 | 86 | ** |
| 2A Feeding Type | 160.8 | 65.1 | 50 | |
| 2B Feeding Type | 51.3 | 21.8 | 15 | |
| TOTAL density (n=14, a=5) | 413.6 | 152.6 | 87 | *** |

**Table 5. Mean densities, standard deviation and percentage of variation due to temporal effects of the 25 most abundant species, feeding types and total nematode community at Station 330 (spring 1999). Significant ANOVA results: *:p<0.05; **p<0.01; ***p<0.001**

A Detrended Correspondance Analysis (Fig. 10) separated all sediment slices from March from the other months along the first axis (eigenvalue: 0.23). Along the second axis (eigenvalue: 0.13) a distinction between April samples and all other months can be noted.

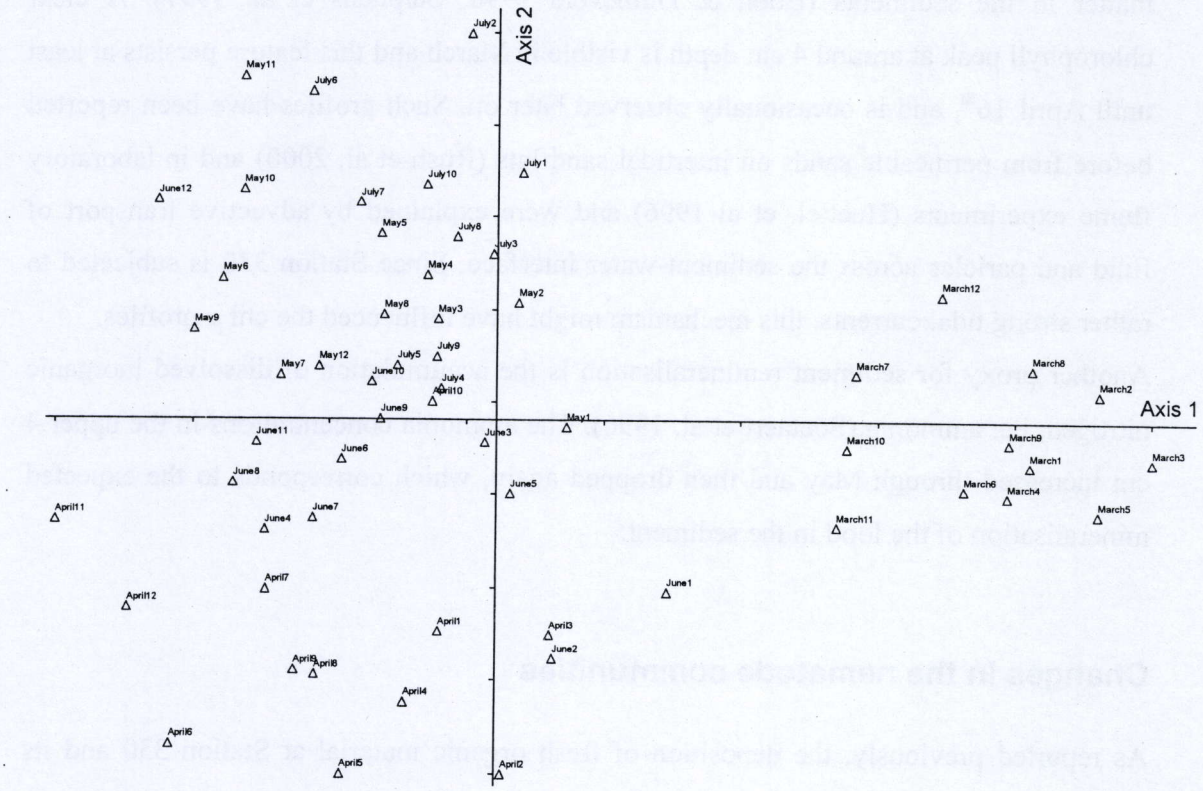


**Figure 10. Results of Detrended Correspondance Analysis (DCA): axis 1 vs axis 2. Numbers indicate sediment layers (March 1: March 0-0.5 cm,...March5:March 2-3cm,...,March 11: March 8-9 cm).**

# Discussion

## Environmental changes

The Chl *a* concentrations at the sea surface reflect the phytoplankton bloom as described previously for Station 330 (Rousseau 2000) and the North Sea in general (Boon et al. 1998). The bloom is initiated in early March and peaks at the end of April; later on, algal biomass declines rapidly. Since a similar pattern can be observed in the chlorophyll concentrations of the overlying bottom water, the bloom settles at least partially on the

sediment (Vanaverbeke et al. 2003). In certain studies, the Chl *a* inventories in the sediment have been used successfully as a proxy for the amount of labile fresh organic matter in the sediments (Boon & Duineveld 1998, Stephens et al. 1997). A clear chlorophyll peak at around 4 cm depth is visible in March and this feature persists at least until April 16$^{th}$, and is occasionally observed later on. Such profiles have been reported before from permeable sands on intertidal sandflats (Rush et al. 2000) and in laboratory flume experiments (Huettel. et al 1996) and were explained by advective transport of fluid and paricles across the sediment-water interface. Since Station 330 is subjected to rather strong tidal currents, this mechanism might have influenced the chl *a* profiles.
Another proxy for sediment remineralisation is the accumulation of dissolved inorganic nitrogen, i.e. ammonia (Soetaert et al. 1996). The ammonia concentrations in the upper 4 cm increased through May and then dropped again, which corresponds to the expected mineralisation of the food in the sediment.

## Changes in the nematode communities

As reported previously, the deposition of fresh organic material at Station 330 and its subsequent mineralisation had a considerable effect on the nematode biomass spectra (Vanaverbeke et al. 2003) and morphometric characteristics (Vanaverbeke et al. subm). Temporal changes in densities and vertical distribution were clearly present as well (this study). Total densities showed significant differences between the sampling dates, and relatively low small-scale variation (i.e 100 of meters between replicate drops of the Reineck boxcorer). This low degree of spatial variability was not the case for several dominant nematode species and for those nematodes feeding on algae and other animals (the epistratum and predatory feeders sensu Wieser, 1953). Here the temporal features, if present, were masked or overwhelmed by small-scale variation. The reason for this is unclear although it may relate to the patchiness of the deposition and subsequent burial of organic matter in sediments as already reported (Boon et al. 1998 and references therein). Tidal currents, which can be rather strong at our sampling site, can cause high variability in chl *a* content of the sediment (Jennes & Duineveld 1985). The variation in chl *a* (Fig.

3) and ammonia (Fig. 4) concentrations indeed reflect substantial variation of sources of organic matter and remineralisation activities between replicates.

Both structural (total densities, vertical profiles, diversity indices $N_0$ and $N_1$) and functional (feeding type distribution, species richness per feeding type) aspects of the nematode communities changed most drastically from March to April (ANOVA). Sedimentation of organic material from the water column in this period could be deduced from the chlorophyll concentrations of the bottom water and the increased ammonia loading of the sediments. Significant differences between April and May were also observed, but these were less prominent. These trends were corroborated by the multivariate analysis, which clearly showed similar changes in nematode community composition.

The increase in densities from March onwards is mainly due to the opportunistic behaviour of a limited number of species (mainly *Metepsilonema comptum*, *Epsilonema pustulatum*, *Manunema annulatum*, *Richtersia inaequalis* and several *Rhynchonema* species) with aberrant morphometric characteristics (Vanaverbeke et al. subm). Almost all of these species belong to Wiesers' selective deposit feeding (1A) nematodes, animals with small buccal cavities that feed on bacterial-sized organisms (Moens & Vincx 1997). The rise of these small, thick species partly explains the increasing importance of this feeding group within the total nematode community. However, later on, larger members of selective deposit feeders become more abundant: in July only 4.8 % of the total nematode community is comprised by the thick species (Vanaverbeke et al. subm), whereas 20% of all nematodes still belong to the 1A group. This indicates that selective deposit feeders benefit most from increased amounts of fresh organic material in the sediment by feeding on the remineralising bacteria (Graf 1992) that respond to this inputted material. Similar findings were reported from Baltic Sea sediments (Ólafsson & Elmgren 1997).

Diversity (indicated by Hill numbers $N_0$ and $N_1$) increased after sedimentation of the spring phytoplankton bloom. Since significant differences were restricted to these indices, diversity increased as a result of the appearance of "rare" species in the nematode communities. The species numbers increased in all feeding types, possibly in response to the "diversity" of organic particles in sediments (e.g. Whitlatch 1981, Danovaro &

Gambi 2002). At Station 330, the arrival of fresh organic material activates remineralising bacteria (Graf 1992), which are a food source for deposit feeding nematodes (Moens & Vincx 1997). Both increases in the amount and quality of the living (bacterial) and non-living (detrital) food sources of nematodes, and the "diversity" of the deposited and decomposing organic particles in the sediments probably affect the number of species that can co-exist within the deposit feeding nematode guilds (1A+1B nematodes). Experimental evidence has demonstrated specific responses of closely related nematode species to the quantity and quality of bacterial food items (Moens et al. 1999). Therefore, we hypothesise that the observed increase in species richness, especially within the deposit-feeding nematodes is a result of an increase of the quantity and diversity of its food resources following sedimentation of the spring phytoplankton bloom.

Diversity within the epistrate feeding nematodes (2A group) also almost doubled after the sedimentation of phytoplankton. These nematodes have buccal armature that is used to either scrape off particles from a substrate, or to damage and open food items before emptying them (Moens & Vincx 1997). They often feed on diatoms and other microalgae that are cracked or pierced using the large dorsal tooth, before the contents is sucked and digested (Nehring 1992, Moens & Vincx 1997). Recently, it has been shown that a considerable amount of chl *a* present in sediments after phytoplankton bloom sedimentation can be attributed to a large quantity of living pelagic diatoms (Hansen & Josefson 2001, 2003). The spring bloom at Station 330 is dominated by the same diatom genera (*Chaetoceros*, *Thalassiosira* and *Skeletonema*) as in the study of Hansen & Josefson (2003) (Rousseau 2003) and pelagic diatoms were observed in the samples (JV, pers obs). Hence living diatoms possibly constitute an addition to the diet of these epistrate feeders and this could be a factor explaining the increase of species diversity within this feeding guild.

The increase of diversity after increasing the organic loading of the sediment is not a consistent feature: in an organic-poor estuarine sediment, Schratzberger & Warwick (1998) observed a decrease in species richness possibly due to anoxia and the release of toxic products under high doses of organic enrichment. Similarly, Steyaert et al. (subm) could not find an effect of bloom deposition on nematode species diversity in an oxygen

stressed station at the Belgian continental shelf during the same period as this study. However, increasing diversity under mild food input and in oxic conditions is consistent with the general scheme presented by Levin et al. (2001), who put forward food supply, the availability of oxygen and sediment heterogeneity, disturbance and bottom current flow as key factors regulating species richness of local communities in the deep sea.

The vertical distribution of the nematode communities also changed during the sampling period, as indicated by the significant "time x depth" interaction term in the split-plot ANOVA. Nematodes tended to be concentrated in the upper sediment layers in May and in June, and this could be due to active migration (Graf 1992; Schulz, 1983) or net increase of the nematode communities within these layers. In Station 330, the concentration of nematodes in the upper sediment layers is mainly caused by the epistrate feeders (47.5% of all nematodes in the upper 0.5 cm in May, 55.6% in June), probably in response to the deposition of pelagic diatoms at the sediment-water interface. The vertical distribution of other feeding types did not show specific trends (not depicted) indicating that no vertical segregation of their preferred food items existed.

In conclusion:

Both small-scale spatial and temporal variability affect the nematode communities in a sandy station in the Southern Bight of the North Sea. For many nematode species, the small-scale spatial variability masked any temporal trend. However, the nematodes as a group and those feeding on detritus or bacteria responded significantly to the deposition of organic matter to the sediment. Nematodes that feed on fresh algal material did not respond significantly in terms of density, but were clearly seen to migrate upward when bloom deposition occurred. The sedimentation and subsequent mineralisation of the phytoplankton bloom caused an increase in suitable food items (living and dead), enabling many species to co-exist. The larger diversity was most prominent within the selective deposit feeders and the epistratum feeders.