
CHAPTER V

Changes in morphometric characteristics of nematode communities during a spring phytoplankton bloom deposition.

Results presented in:

Vanaverbeke J, Soetaert K, Vincx M (submitted) Changes in morphometric characteristics of nematode communities during a spring bloom deposition

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Abstract

Nematode body size was investigated in terms of body length, width and length/width (L/W) ratios, before, during and shortly after a spring phytoplankton bloom deposition in the Southern North Sea. Sediments consisted of medium sand (median grain size: 333 μm), were devoid of mud and always fully oxygenated. During the peak of the spring phytoplankton bloom in May 1999, several small-sized species (adult length < 700 μm) emerged. Most prominent was the appearance of a “stout” nematode assemblage characterised by low L/W ratios. Most of these small nematode species were virtually absent before the peak blooming and they decreased in abundance shortly after deposition of phytoplankton to the seafloor. This indicates the opportunistic behaviour of these nematodes, which is consistent with their small length, enabling them to rapidly reach adulthood. The net rate of increase of the stout nematodes during the bloom was estimated at 6.4% day⁻¹. This is much larger than the estimated net rate of 1.5% day⁻¹ for the total nematode community.

The species composition of the stout nematode assemblage differed from similar stout assemblages described before for continental slope and deep-sea areas. In the Southern North Sea, Epsilonematidae were dominant while members of the Desmoscolecidae were prominent in offshore deeper areas. Possibly these differences relate to the relatively strong hydrodynamic forces prevailing at the North Sea site.

The small species in the North Sea were only present in reasonable densities shortly after the spring bloom, while they seem to be a consistent member of deep-sea nematode communities. We hypothesise that this is caused by the quality of organic matter reaching the sea floor, together with differences in sedimentology and temperature, influencing the duration of the presence of suitable food items for these nematodes.

Introduction

Research on the response of benthic communities to food enrichment mostly focuses on changes in species composition and/or biomass patterns. A combined approach, where species data are linked with the corresponding body size parameters has rarely been published. This is surprising, since body size influences many aspects of animal life such as: life history, physiology, energy requirements, biotic and abiotic interactions (Calder 1984, Peters 1983, Schwinghamer 1983). As the optimal size of an organism is linked to food input (Sebens 1987, Rex & Etter 1998), changes in the size structure of a community are expected during a food deposition event.

Nematodes are amongst the most abundant metazoan organisms in marine sediments and, as their length and width are easily measured using non-destructive methods (Soetaert et al. 2002) they are especially suited for analysing body size distributions. Moreover, the ratio of the nematodes' length to the maximal width (L/W) offers a quantitative measure of their shape. Whereas most nematodes have a typical snake-like body, some species are conspicuously plumper. Ratsimbazafy et al. (1994) were the first to report on the existence of these two different nematode morphotypes in fine sandy sediments (median grain size: 130-160 μm) of the North Sea. Soetaert et al. (2002) analysed nematode morphology from various continental slope areas around the world and confirmed the existence of both morphotypes. As this group included members of distantly related taxa, they concluded that these groups arose as an adaptation to evolutionary conflicting constraints. Based on indirect evidence, they hypothesised that the short, plump type could persist due to its more rapid development compared to longer nematodes, whereas the presence of 'armor' and its thickness were effective against predation pressure. The concomitant lowered mobility and a reduced capacity to withstand anoxic conditions however precluded these plump organisms to live in the well-oxygenated surficial layers of the sediment (Soetaert et al. 2002).

Our study investigates the morphometry of nematode communities as triggered by a spring bloom phytoplankton deposition in a well-oxygenised North-Sea sampling station. We describe the changes in length, width and L/W ratios as a result of the changing food availability in the sediment. We examine whether the two morphotypes can be discerned and how both respond to food pulse and in the absence of oxygen gradients.

Material and methods

Study site, sampling and treatment of samples

Samples were obtained from the open sea site Station 330 (51°26.0'N; 02°48.5'E) (Fig 1) at the Belgian Continental Shelf (Southern Bight of the North Sea). Sampling was performed weekly from March 1999 until July 1999 (Vanaverbeke et al. in prep). Nematode species were identified on a monthly interval (March 9th, April 27th, May 12th, June 28th and July 12th 1999) (Vanaverbeke et al. in prep.). Morphometric analysis of the communities was performed on the samples from March, May and July, i.e. before, during and after the spring phytoplankton bloom.

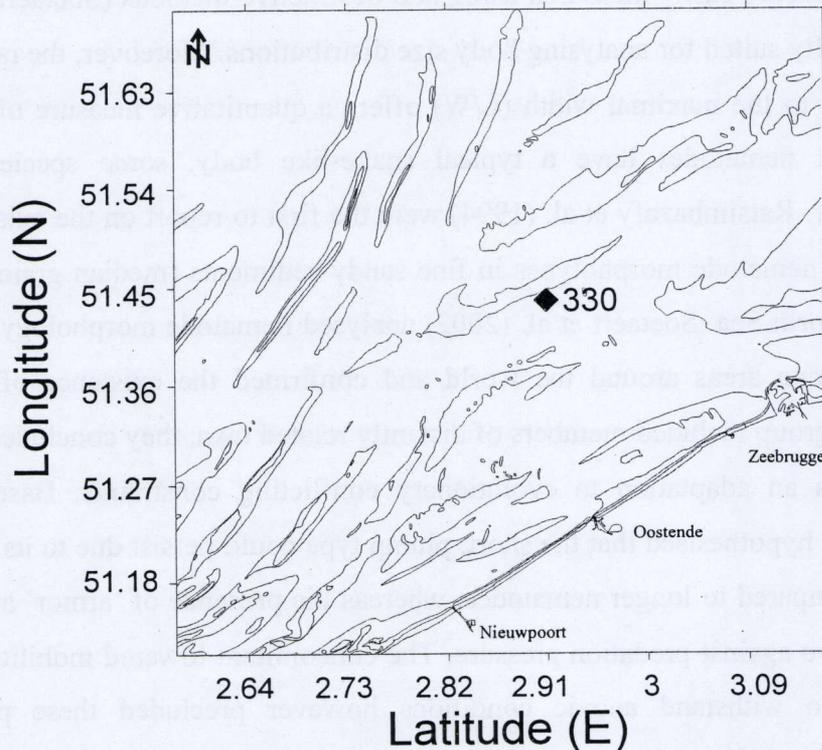


Figure 1. Map of the Belgian continental shelf with indication of the sampling station

Sampling took place aboard of the RV Belgica using a modified Reineck boxcorer. The boxcorer was deployed three times at each sampling occasion. From each boxcorer, one perspex core (10 cm²) was used for faunal analysis up to 10 cm sediment depth. Additional cores were used for the analysis of sediment characteristics, pigment concentrations and

nutrient profiles (Vanaverbeke & Steyaert, unpublished). In July, only two cores for faunal analysis were available. Sediments were sliced vertically: the upper 2 cm in 5mm intervals, the deeper layers per cm. A hot (70°C), neutral formaldehyde tap-water solution was used for fixation. At the laboratory, all metazoans passing a 1-mm sieve and retained by a 38 µm sieve were extracted from the sediment by centrifugation with Ludox (Heip et al. 1985). Per slice, 120 nematodes were picked out randomly and mounted on Cobb slides for identification and measurements of length and maximal width. When less than 120 individuals were present, all nematodes were picked out. Measurements were performed using an image analyser (Quantimet 500+). From each individual, age, gender and presence of eggs in adult females was recorded. Only nematodes from the March, May and July samples were measured.

Sediments were analysed using a Coulter LS100 Particle Size Analyser. The redox potential of the sediment column was recorded with a mV meter.

Chlorophyll *a* (Chl *a*) values at the sea surface were obtained from Rousseau (2000). The supernatant water in the Reineck boxcorer was carefully siphoned off, and 0.5 l was filtered on Whatman GF/C filters. Filters were stored in the freezer until processing. Chl *a* values were obtained by HPLC (Gilson) using a slightly modified method of Mantoura & Llewellyn (1983).

Results

Study site

Sediments at the sampling station could be 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 reached their highest values on April 29th and May 5th, reflecting the peak phytoplankton bloom (Rousseau 2000). The pattern at the surface was closely followed by the pigment concentrations in the bottom water (Fig. 2), indicating sedimentation of phytoplankton from the end of April. At the date of the first sampling, rather high chl *a* values in the bottom water were observed as well. Redox values remained positive (>100 mV) during the complete sampling period and at all sediment depths.

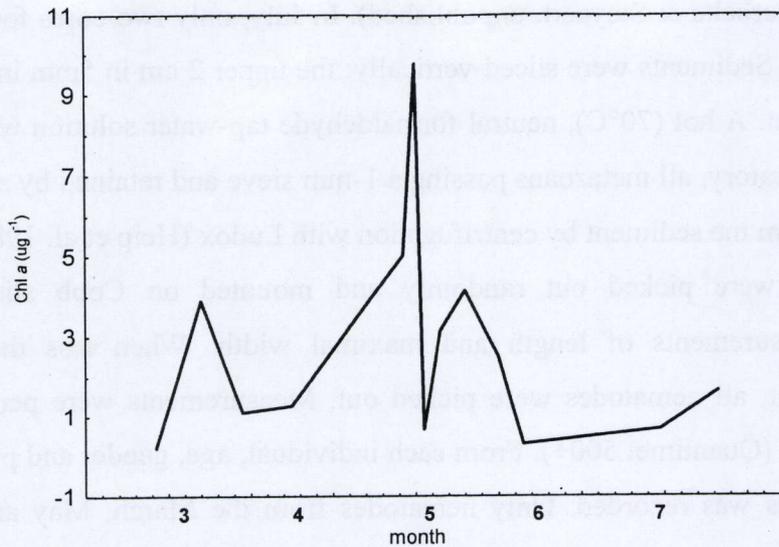


Figure 2. Chlorophyll a concentrations in the bottom water at Station 330 (Belgian Continental Shelf – spring and summer 1999)

Morphological diversity of the nematode communities

All measurements of all replicates and sediment slices per month were pooled before analysing the morphometry of the nematode communities. In March, May and July, respectively 491, 1441 and 528 nematodes were measured.

Figure 3 shows the length-width plots on a log scale per month, and the corresponding length/width frequency distribution. Fig. 4 gives the length distribution for the adult nematode community before, during and after the bloom deposition. At the onset of the bloom in March, nearly all nematodes (>98%) are of the slender type (Fig. 3), with L/W ratios well over 15 and peaking at L/W of 32. One species, *Dichromadora cucullata* dominated the community (18%) and is responsible for the adult peak size at 800-900 µm (Fig. 4). Four other, larger, nematode species (*Neochromadora angelica*, *N. munita*, *Prochromadorella ditlevseni* and *Pomponema multipapillatum*) represent another 12% of the total community.

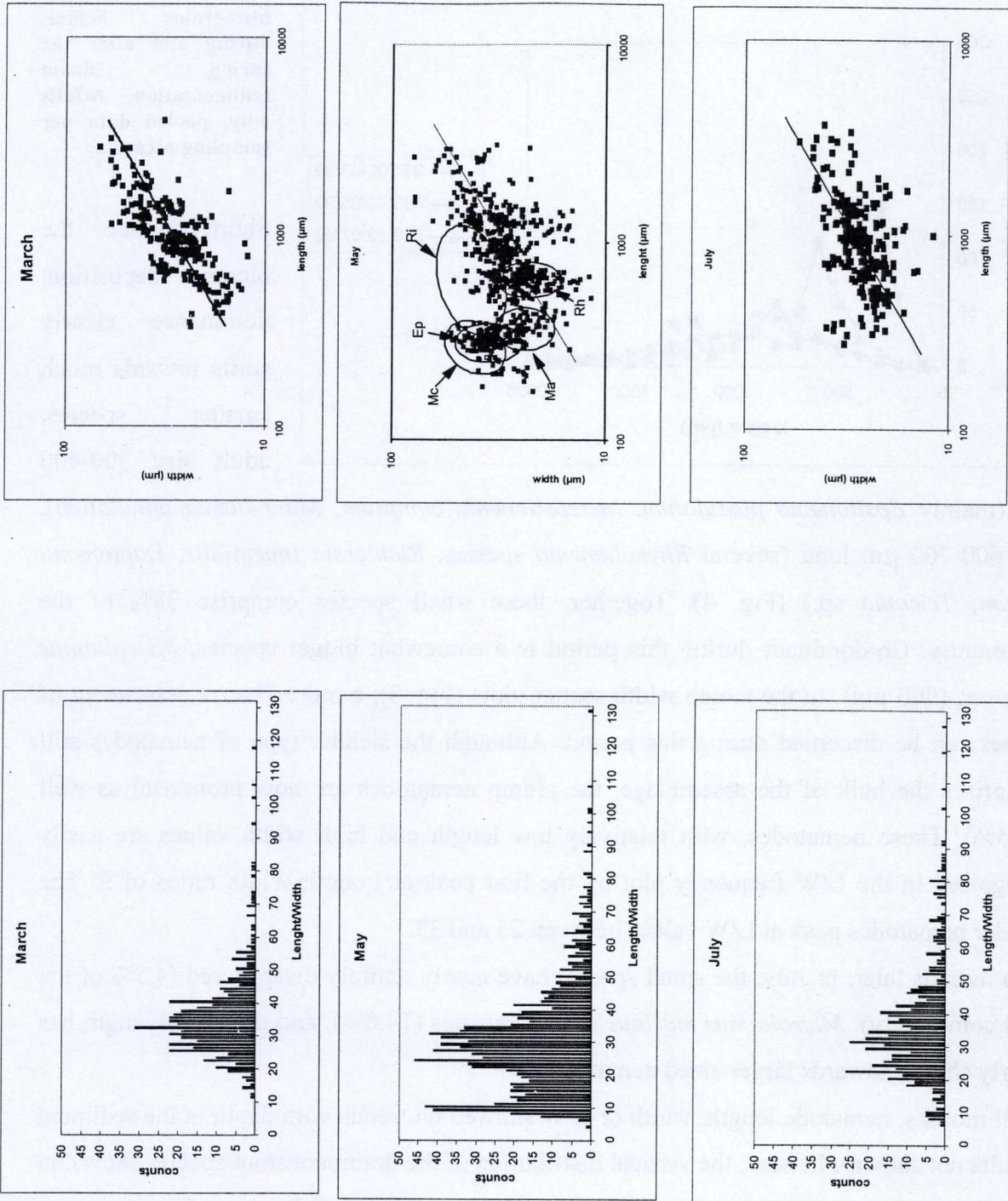


Figure 3. Morphological landscape of North Sea nematodes before, during and after spring bloom deposition. Right panels: Length/Width histograms (Ri: *Richtersia inaequalis*; Ep: *Epsilonema pustulatum*; Mc: *Metepsilonema comptum*; Ma: *Manunema annulatum*; Rh: *Rhynchonema* species). Left panels: body width vs body length on a log scale. All data per month combined. The regression line in the right panels corresponds to the line fitted to the March data in order to facilitate comparisons.

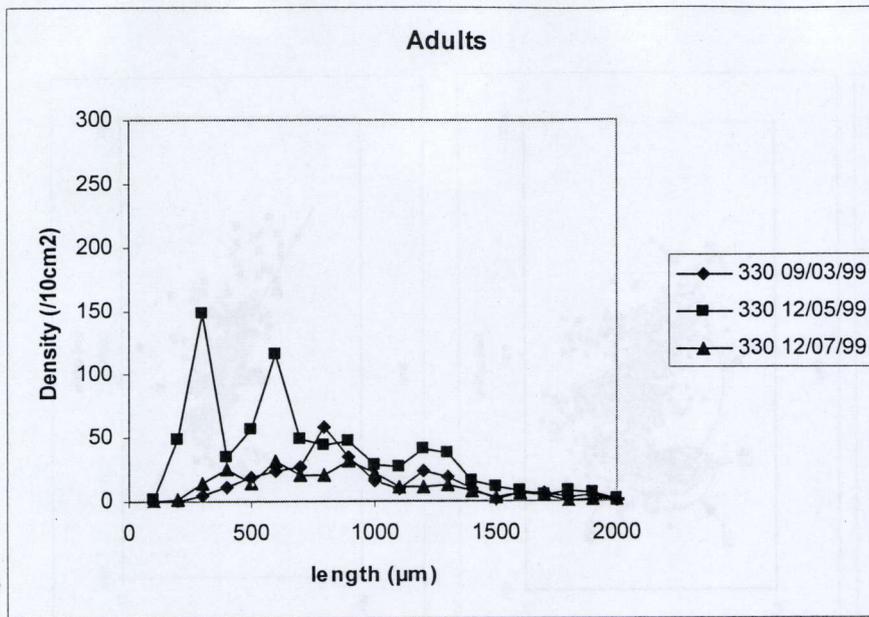


Figure 4. Length histograms before, during and after the spring bloom sedimentation. Adults only, pooled data per sampling occasion.

Shortly after the bloom deposition, dominance clearly shifts towards much smaller species, adult size 300-400

μm (mainly *Epsilonema pustulatum*, *Metepsilonema comptum*, *Mannunema annulatum*), and 600-700 μm long (several *Rhynchonema* species, *Richtersia inaequalis*, *Daptonema nanum*, *Tricoma* sp.) (Fig. 4). Together, these small species comprise 38% of the community. Co-dominant during this period is a somewhat bigger species, *Microloaimus marinus*, (900 μm). In the length width scatter plots (Fig. 3), a more diverse assortment of shapes can be discerned during this period. Although the slender type of nematodes still comprises the bulk of the assemblage, the plump nematodes are now prominent as well (21.5%). These nematodes, with relatively low length and high width values are easily recognised in the L/W frequency plot by the first peak at Length/Width ratios of 9. The slender nematodes peak at L/W values between 25 and 33.

Two months later, in July, the small species have nearly entirely disappeared (4.5% of the total community). *Microloaimus marinus* now dominates (14.8%), and the modal length has clearly shifted towards larger-sized nematodes.

In all months, nematode length, width or L/W showed no trends with depth in the sediment (results not shown). In May, the vertical distribution of the dominant stout species shows no difference when compared to the vertical distribution of the total nematode community (Fig. 5). Except for *M. comptum*, about 40% of the stout species is found in the upper 2 cm of the sediment.

In order to understand the appearance of the stout and small species in May, the distribution of age/sex characteristics of the assemblages (sediment slices and replicates pooled) is depicted in Fig. 6. Since both stout (L/W <15) and small (Length <700 μm) nematodes were virtually absent in March, the distribution for the entire community is shown.

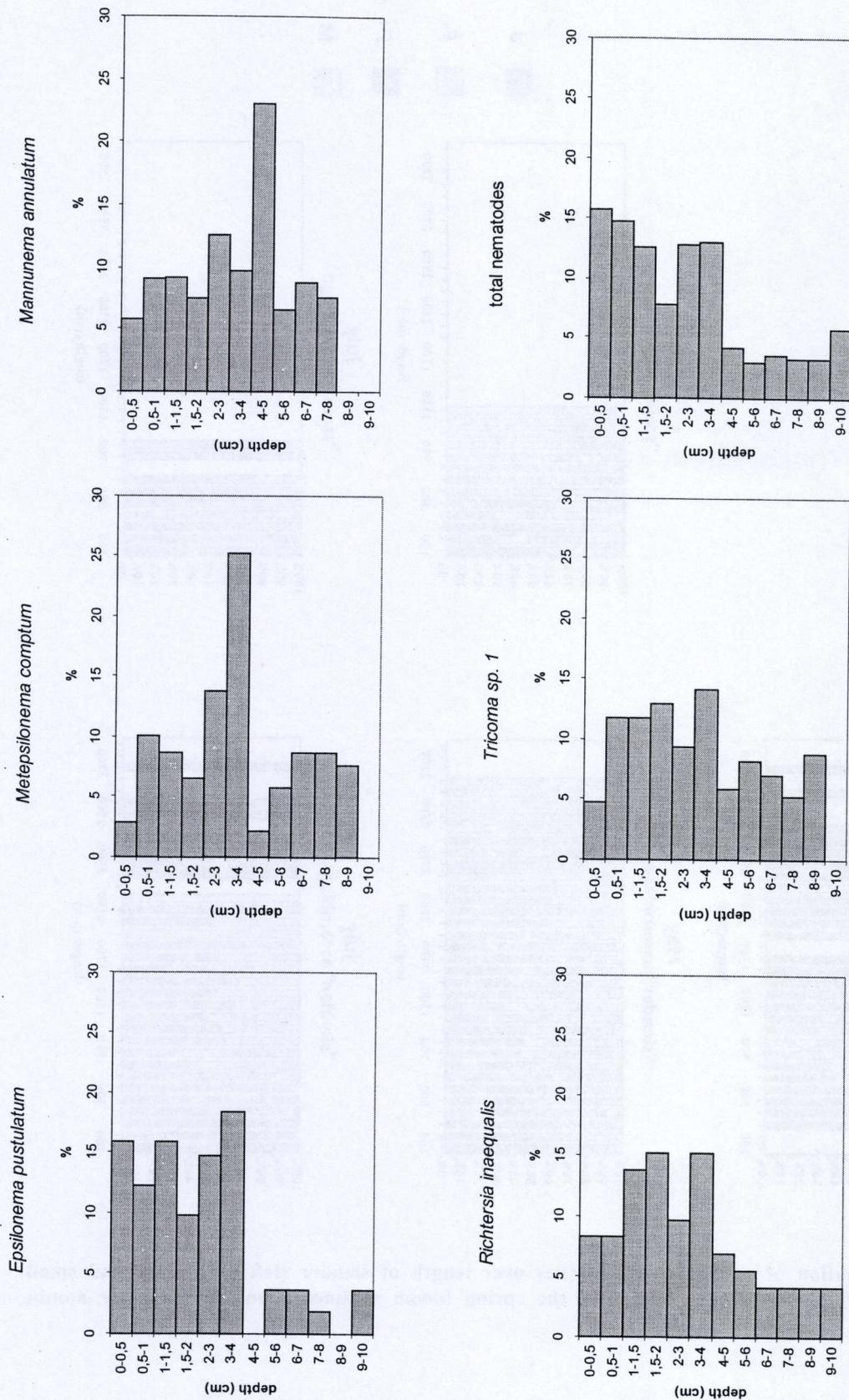


Figure 5. Vertical distribution of dominant stout nematode species and the total nematode community (stout and short nematodes excluded) in May at Station 330. Relative abundances per sediment layer, mean of three replicates.

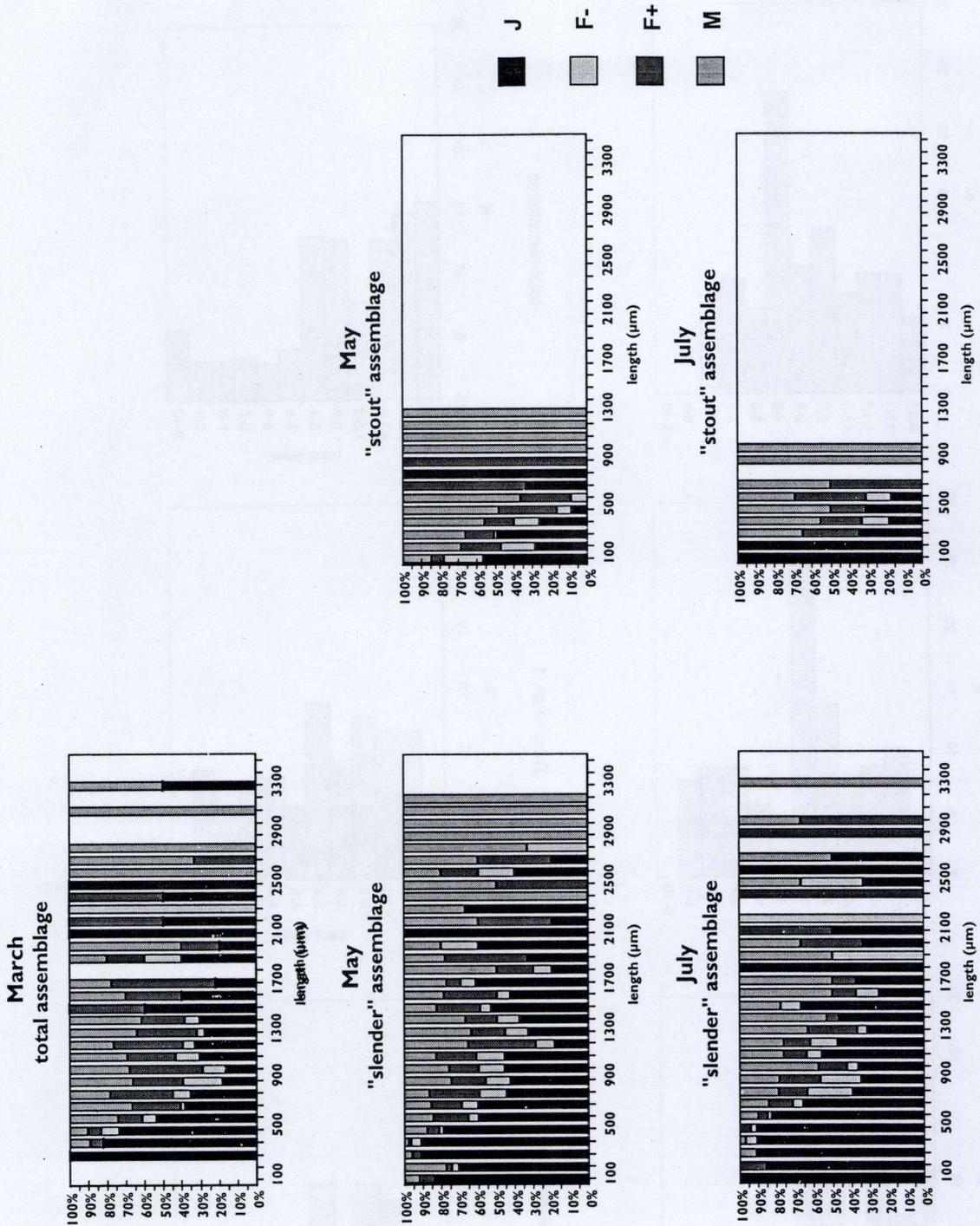


Figure 6. Distribution of age/sex characteristics over length of slender (left) and stout and small nematodes (right) before, during and after the spring bloom sedimentation. All data per month combined.

Comparing the age distribution of stout and small nematodes (individuals identified as *E. pustulatum*, *M. comptum*, *M. annulatum*, *Tricoma* sp., *R. inaequalis* and all *Rhynchonema* sp.) with the slender nematodes in May and July reveals the lower proportion of juveniles

present in the lower size classes of the former assemblage. In May, at least 50% of all stout and short species is adult for lengths $>200 \mu\text{m}$ (except one length class). In July, adults constitute $>60\%$ of the stout and short nematodes when length exceeds $300 \mu\text{m}$. No obvious trends were observed when comparing the slender assemblage throughout the sampling period.

Discussion

Temporal patterns

In coastal areas, a significant fraction of primary production may end up in the sediments, where it is food for the benthic animals (Heip et al. 1995). At our study site, phytoplankton starts to grow in early March; algal densities peak at the end of April after which the algal biomass rapidly declines (Rousseau 2000). As similar temporal patterns are observed for the chlorophyll of the overlying bottom water, at least part of the algal bloom settles on the sediment (Vanaverbeke et al. 2003).

Nematode densities, although generally low, varied almost 4-fold over the 5 month sampling period (March-July). Both small-scale spatial (order of 100 metres) and temporal effects (order of months) contributed to this variability, but the temporal signal explained most of the variation (87%, $F=15.1$, $p=0.0005$). Moreover, the low variability in sediment composition between dates (median grain $330\text{--}360 \mu\text{m}$) and the consistently positive redox over the entire sediment depth ($<10 \text{ cm}$) indicate that the same station was always sampled. Mean nematode densities increased steadily from about 200 individuals 10 cm^{-2} in March to more than 600 individuals 10 cm^{-2} in May after which they decreased sharply again to about 380 individuals 10 cm^{-2} in July (Fig. 7) (Vanaverbeke, this thesis: Chapter VI).

The rapid increase was largely attributed to the emergence of small species, where adult lengths peaked at $300\text{--}400 \mu\text{m}$ and at $600\text{--}700 \mu\text{m}$. In May more than 50% of the adult nematodes were smaller than $700 \mu\text{m}$, whereas this was only 20% in March, 30% in July. One group of thick nematodes (defined with Length /Width ratios < 15) was almost totally absent in March but reached quite high densities ($>130 \text{ ind } 10\text{cm}^{-2}$) in May. In June, few members of this morphotype were present ($17 \text{ ind } 10\text{cm}^{-2}$).

Although our data do not allow estimates of nematode growth rates in the field, we can roughly assess the net rate of increase, from March to May and the net rate of decrease, from May to June, by fitting an exponential growth model:

$$\frac{dN}{dt} = aN$$

which can be solved as:

$$N_t = N_0 e^{at}$$

with N_t : nematode density at time t ; t : time in days and a : the net increase day^{-1} .

Results indicate that stout nematodes ($L/W < 15$) increased their densities at a rate of $6.5\% \text{ d}^{-1}$, which is four times faster, compared to the total community. Short species (length $< 700 \mu\text{m}$) increased densities with a double speed, $3\% \text{ d}^{-1}$ (Table 1).

Rate of net increase	March to May	May to July
Total community	0.015 d^{-1}	-0.007 d^{-1}
Short adults ($L < 700 \mu\text{m}$)	0.03 d^{-1}	-0.017 d^{-1}
Stout community ($L/W < 15$)	0.065 d^{-1}	-0.03 d^{-1}

Table 1. Results of exponential growth model $dN/dt = aN$. All $p < 0.001$; $p = 0.013$

The same differences were observed when densities decreased from May to July. All this indicates that stout and short species are at an advantage when the bloom settles on the sediment surface. Smaller species not only have larger growth rates (Peters 1983), and therefore reach adulthood faster, but they also have higher reproduction rates (Kooijman 1986). This is consistent with the larger rates of increase (Table 1) and the higher dominance of adults in the stout or short species (compare contribution of adults to total assemblages in left and right panels of Fig. 6). The small and stout species therefore have the ability to react in an opportunistic way to a pulsed food supply. On the other hand, they also disappear at a rate much higher than that of the average nematode. Chl a values in the sediment decrease strongly after the peak bloom (Vanaverbeke, this thesis, Chapter VI), indicating that the organic material is remineralised rather fast, and it is probable that the decrease of both stout and short nematodes can partly be attributed to food shortage. Being plump or small *in se* infers that the life span would be rather short. Moreover, small individuals have relatively larger maintenance costs and less storage material, which may make them more vulnerable to food shortages. During summer or late summer, a second diatom bloom occurred in Belgian coastal waters (Rousseau 2000), providing the sediments

again with fresh organic matter when the bloom was terminated. This second input of food sources probably enabled the stout communities to maintain their populations year round.

The stout and small nematode assemblages

Our results confirm the findings of Ratzimbazay et al. (1994) and Soetaert et al. (2002), on the existence of different nematode morphotypes. Soetaert et al. (2002) explained the existence of the stout morphology as the result of evolutionary selection amongst distantly-related taxa rather than resulting from phylogenetic lineage. Our results confirm this. Whereas on the Ligurian shelf and slope (Mediterranean Sea), the stout nematode assemblage consisted of desmoscolecids (*Tricoma*: 26% and *Desmoscolex*: 24%) and *Richtersia* (30%) (Soetaert et al. 2002), at our study site, epsilonematids dominated the stout assemblage, followed by desmoscolids and *Mannunema annulatum*. These belong to three different suborders within the Chromadorida. The predominance of the epsilonematids at our study site is probably due to the rather coarse sediments, in contrast to the finer grained deep-sea sediments of the stations used in the analysis of Soetaert et al. (2002). Members of the epsilonematids are usually found in sandy sediments, on sandbanks (Willems et al. 1982) and in open-sea sediments (Vincx 1986) where hydrodynamic forces can be substantial.

Soetaert et al. (2002) further hypothesized that the stout nematode communities evolved as an adaptation towards reducing predation pressure, as they combined large body width with armored cuticulas. Similarly, the representatives of the stout nematodes at our site combine the plump shape with armor. The ϵ -like body shape of epsilonematids, together with the presence of long setae will make it difficult for a predator to swallow the nematode, while *Manunema annulatum* has stout somatic setae on peduncles all over the body. The somewhat longer *Rhynchonema* species, which also show an opportunistic response to phytoplankton sedimentation, similarly have cuticular ornamentation.

In the deep-sea or continental slope stations, the Length/Width ratio of the nematodes showed consistent patterns with depth in the sediment, with stout nematodes always living in the upper layers of the sediment. Soetaert et al. (2002) argued that their large width precluded them from inhabiting the suboxic and anoxic layers deeper into the sediment. Our results also corroborate this: in the absence of oxygen related gradients no patterns in length, width or Length/Width ratio were observed.

Our findings however contrast with the results of Soetaert et al. (2002) in one important manner. Whereas the existence of the plump nematodes in the continental slope and deep-sea areas appears to be a persistent feature (they were found at all margin sites examined), their presence is clearly a transient phenomenon in our sampling site. Boon & Duineveld (1998) and Boon et al. (1998) showed that, in North Sea sediments comparable with our sampling station, bacterial activity is very much related to the input of organic matter from the water column: it increases drastically after a food pulse and decreases again when the easily degradable fraction of the organic matter is broken down. Such pulses in bacterial activity are probably not as pronounced along continental slopes and at deep-sea sites, where the quality of organic material reaching the sea floor decreases with increasing water depth (Heip et al. 2001) and where the reduced quality and availability of the organic matter, together with the lower temperatures causes a prolonged remineralisation process (Soetaert et al. 1996). Except for the *Richtersia* species, the stout and short nematode species have very small buccal cavities, forcing them to feed selectively on small food items, such as bacteria (Wieser 1953). Moens et al. (1999) showed that even closely related nematode species show clear species-specific preferences for bacterial strains, bacterial densities and bacterial age. This might indicate that the preferential food source for this type of nematode at deep-sea sites is present over a longer time span than in coastal areas.

Conclusions

- In a sandy site in the North Sea, the spring bloom opens a window of opportunity for small nematode species whose densities rise vigorously immediately after the deposition of fresh organic matter. A couple of months later, their densities decline almost as quickly as they rose. This quick response can be explained by the life-history characteristics typical of these species.
- Many of these small nematodes are similar in shape to the 'stout nematode assemblage' as described previously for ocean margin sites. In addition, they share morphological similarities by the presence of armour. However, being dominated by Epsilonematidae, the composition of the stout assemblage in the southern North Sea sediment differs from margin sites where Desmoscolecidae were more prominent.

- Whereas in the southern North Sea sediment, the presence of plump species is a transient feature, in continental slope areas they seem to persist, possibly relating to the continuous presence of suitable food items in these areas.