Vol. 392: 123–132, 2009
doi: 10.3354/meps08202

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published October 19

Factors affecting nematode biomass, length and width from the shelf to the deep sea

Karline Soetaert[1,*], Maria Franco[2], Nikolaos Lampadariou[3], Agnes Muthumbi[4], Maaike Steyaert[2], Leen Vandepitte[5], Edward vanden Berghe[5,6], Jan Vanaverbeke[2]

[1]Centre for Estuarine and Marine Ecology, Netherlands Institute of Ecology, PO Box 140, 4400 AC Yerseke, The Netherlands
[2]Ghent University, Biology Department, Marine Biology Section, Krijgslaan 281/S8, 9000 Gent, Belgium
[3]Hellenic Centre for Marine Research, Gournes Pediados, PO Box 2214, PC 71003, Heraklion, Crete, Greece
[4]University of Nairobi, School of Biological Sciences, PO Box 30197-00100, Nairobi, Kenya
[5]Flanders Marine Institute (VLIZ), InnovOcean Site, Wandelaarkaai 7, 8400 Oostende, Belgium

[6]*Present address:* Ocean Biogeographic Information System, Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, New Jersey 08901-8525, USA

ABSTRACT: The decrease of nematode size with water depth is well documented in the literature. However, many nematode size data sets originate from bathymetric gradients, with strong bias towards deep-water, muddy sediments. This has narrowed our perception of the environmental factors that may influence nematode morphometry. Here we perform a morphometric analysis with data collected from a variety of sampling locations in the Indian Ocean and around Europe at a wider range of depths and sediment types. All nematode size descriptors decreased significantly with water depth, which explained more than 60% of total variation. This trend was most pronounced for mean nematode dry weight, which decreased by ~20% for every doubling in water depth. This coefficient of decrease was smaller than the described decline in food deposition with depth, as estimated from sediment community oxygen consumption rates (~35%), but on the same order of magnitude as the decrease in nematode density. Order of magnitude estimates based on these trends suggest that nematodes contribute about 7.5% to benthic metabolism over the depth range. In contrast to nematode dry weight, the decrease in nematode length and width with water depth was less steep. However, nematode length was also affected by grain size, where shallow-water coarse sediments were inhabited by longer nematodes. Nematodes from the oligotrophic Aegean Sea were characterised by low length values and high width values, probably as an adaptation to sediments poor in organic matter. These observations suggest that local factors can also be very important for shaping the morphometric landscape of the nematode communities.

KEYWORDS: Nematode · Morphometry · Respiration · Size-depth relationship

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The relationship between the size of marine benthic animals and food supply has received considerable attention since the start of the exploration of the deep sea in the 1950s (Le Danois 1948). Animals living in deep-water sediments entirely depend on organic matter produced in the euphotic zone. As this organic matter is degraded during sinking, and as the transit time to the bottom increases with depth, there is a well-documented decrease of organic matter deposition with depth (e.g. Lampitt & Antia 1997, Middelburg et al. 1997, Andersson et al. 2004). Concurrently, a decrease in organism biomass with depth has been regularly observed. Combining these observations led Thiel (1975) to hypothesise that 'associations governed by constantly limited food availability are composed of small individuals on average'. Subsequently, Sebens (1987) and Rex & Etter (1998) showed that the optimal size of an organism decreases as the rate of food input

---

*Email: ksoetaert@nioo.knaw.nl

© Inter-Research 2009 · www.int-res.com

decreases, in order to maximize the net energy gain for a given food input. Since then, size–depth relationships have been assessed for a variety of organisms (e.g. gastropods, McClain et al. 2005).

Nematodes have a ubiquitous distribution and are easily sampled and extracted from the sediment. As their length and width can be measured using non-destructive methods, many size–food studies have focused on this taxon. Results are not always unequivocal: while nematode biomass indeed decreases with depth in certain areas, no patterns or even a reverse pattern is observed elsewhere (see Udalov et al. 2005 and references therein). Studies that compare nematode biomass spectra and individual weights in oligotrophic and eutrophic deep-sea areas of similar depth either reported a smaller individual biomass and fewer larger-sized nematodes in oligotrophic sites (Vanreusel et al. 1995, Sommer & Pfannkuche 2000, Broun et al. 2001) or found no such differences (Gambi & Danovaro 2006).

Whereas in the original hypothesis of Thiel (1975) the food component was the only link between organism size and depth, some authors have postulated that this link could be indirect, via the changes induced in sediment biogeochemistry. For instance, adaptations of nematode length and/or width in response to sediment oxygen gradients can explain the general miniaturisation of nematodes with depth (Soetaert et al. 2002). Others showed that factors other than those related to organic matter input govern nematode individual weight. Based on the analysis of nematode individual biomass from 120 worldwide locations sampled at a depth range from 0 to 8260 m, Udalov et al. (2005) demonstrated that sediment characteristics were a significant factor in explaining the variation in nematode weight in depths shallower than 1000 m, while organic matter input had variable importance, differing between different depth zones and between eutrophic and oligotrophic sites.

Perhaps because of the size–depth hypothesis, many nematode size data sets originate from bathymetric gradients, with strong bias towards deep-water, muddy sediments. This has narrowed our perception of the environmental factors that may influence nematode morphometry. Here we extend the morphometric analysis with data collected over a wider range of depths and sediment types; in addition, we look at temporal (seasonal) differences in the morphometric landscape of nematode communities at 2 stations. We use published and unpublished data on nematode length and width from a variety of sampling locations around Europe, compiled in the largest database on marine nematodes available at present (MANUELA database, Vandepitte et al. 2009). Since we use original data (e.g. all individual length and width measurements for all nematodes in the database) rather than published averages (e.g. Udalov et al. 2005, Rex et al. 2006), our database allows a more thorough analysis of the patterns of nematode biomass, length and width from the shelf to the deep sea. This increased focus on the shelf seas will augment our understanding of the general factors underpinning nematode biomass and morphometry on a large scale. In addition, it will enable us to roughly estimate the contribution of nematodes to sediment metabolism along a depth gradient from the shelf to the abyss.

MATERIALS AND METHODS

Data acquisition and analysis. Data were obtained from the MANUELA database, which contains 83 component data sets on meiobenthos from almost 1300 stations, representing about 140 000 distribution records (Vandepitte et al. 2009). This database was queried for all nematode records for which both length and width measurements were available. The resulting data sets originated from a wide geographic area — the Belgian Continental Shelf (BCS), NE Atlantic, Indian Ocean and Aegean and Mediterranean Seas — from the shelf to the deep ocean (e.g. from 8 to 5951 m depth) and from fine silty sediments to coarser sandy sediments (Table 1, Fig. 1). In addition, seasonal data were available for 2 stations on the BCS: Stns 115bis and 330. When data sets were derived from disturbance studies (e.g. Lampadariou et al. 2005a), we included only data obtained in a pre-disturbance situation. We refer to the original papers for detailed descriptions of the sampling sites.

Suspicious nematode measurements were removed, i.e. where nematode length was smaller than nematode width, where width was not between 5 and 250 µm or where length was not in the interval 100 to 10 000 µm.

Nematode wet weight (WW) was calculated following Andrassy's formula: Biomass (µg WW) = L × W^2/1 600 000, where L is nematode length and W is nematode width (Andrassy 1956). Dry weight (DW) was assumed to be 25 % of WW (Wieser 1960). All values reported here are in µg DW, length and width are expressed in µm.

Data from different sediment slices from the same core were pooled — we refer to Soetaert et al. (2002) and Vanaverbeke et al. (2004) for a discussion of vertical patterns in nematode morphometry in deep-sea and coastal sediments, respectively.

An exploratory analysis showed that the distribution of length, width, L:W ratio and dry weight were highly skewed towards the smaller sizes for all stations. The same was true for all combined sizes (Fig. 2). After log-transformation, the data were approximately normally

Table 1. Location of sampled stations with indication of depth, number of stations, upper sieve size and data source

Area stations	Depth range (m)	No.	Upper sieve (mm)	Source
Belgian Continental Shelf, sand banks	15–25	26	1	Vanaverbeke et al. (2003)
Belgian Continental Shelf, coastal stations	8–20	5	1	M. Steyaert (unpubl. data), M. A. Franco (unpubl. data)
Aegean Sea, Thermaikos Gulf	30–86	6	0.5	Lampadariou et al. (2005b)
NE Atlantic, La Coruña	175–4951	8	1	Soetaert et al. (2002)
NE Atlantic, Vigo	153–2625	5	1	Soetaert et al. (2002)
NE Atlantic, Nazaré Canyon	137–4323	5	1	Soetaert et al. (2002)
NE Atlantic, Goban Spur	206–4460	11	1	Vanaverbeke et al. (1997)
Indian Ocean	57–2179	4	1	Soetaert et al. (2002)
NW Mediterranea, Ligurian Sea	160–1220	6	1	Soetaert & Heip (1989)
Aegean Sea, deep North	153–1271	4	0.5	Lampadariou & Tselepides (2006)
Aegean Sea, deep South	1194–1772	3	0.5	Lampadariou & Tselepides (2006)

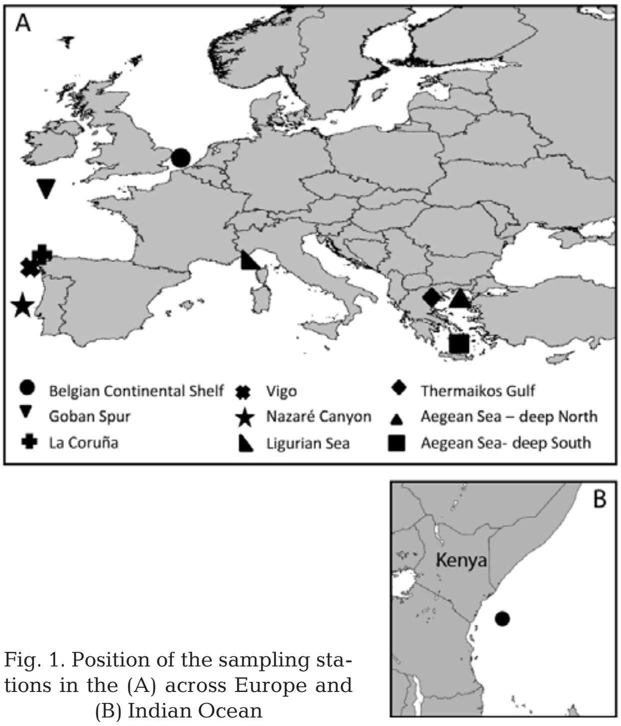

Fig. 1. Position of the sampling stations in the (A) across Europe and (B) Indian Ocean

distributed (Fig. 2). For such skewed data, the geometric mean (based on log-transformed data) can be more robustly derived than the arithmetic mean, which strongly depends on chance occurrences of extremely large individuals. The inclusion of these large individuals in the samples is also influenced by the use of an upper sieve, and this has not always been consistently used in the different studies (see 'Discussion'). To circumvent these chance effects, it is better to perform statistical analyses based on the log-normal distribution and therefore calculate the geometric mean per station. However, the geometric mean of a variable y gives the best estimate for $\ln(y)$, whereas we are generally interested in the mean of the untransformed (i.e. arithmetic) value of y (where y is one of the nematode size descriptors), for instance if we wish to estimate total nematode biomass in a sample. As the back-transformed y is not normally distributed, but skewed to smaller sizes, this skewness needs to be taken into account when estimating the arithmetic mean from the geometric mean. Thus the mean of the arithmetic distribution (μ_a) is estimated as: $\mu_a = \exp(\mu_{\ln y}) \times \exp(0.5s^2_{\ln y})$, where $\mu_{\ln y}$ and $s^2_{\ln y}$ are the estimated mean and variance in logarithmic units, respectively (Finney 1941). The correction factor $\exp(0.5s^2_{\ln y})$, used to convert from geometric to arithmetic mean, was on average 1.15, 1.1 and 2.1 for length, width and individual DW, respectively. In what follows, the term 'mean' is used synonymous with arithmetic mean.

Comparison of nematode biomass, length, width or L:W ratios between sampling dates was done using 1-way ANOVA or *t*-tests. When significant differences were obtained in the case of the 1-way ANOVA, Tukey's Honestly Significant Different (HSD) test for unequal N was applied for pairwise comparisons. When the assumptions for parametric tests were not fulfilled, the non-parametric Kruskal-Wallis test or Mann-Whitney *U*-test was used.

Regressions versus depth and/or sediment median grain size were performed on annual mean values when seasonal data were present, using R (R Development Core Team 2008), which was also used to produce the graphs. Nonlinear fits were performed by linear regression on the log-transformed data.

For exponential fits only, size was log-transformed; for power fits both depth and size were log-transformed. The transformation for the power fit makes the variance constant and independent of the magnitude of the *x*- and *y*-variables (homoscedascity). Similar to the methods described above, we corrected for the skewness when back-transforming, and the arithmetic

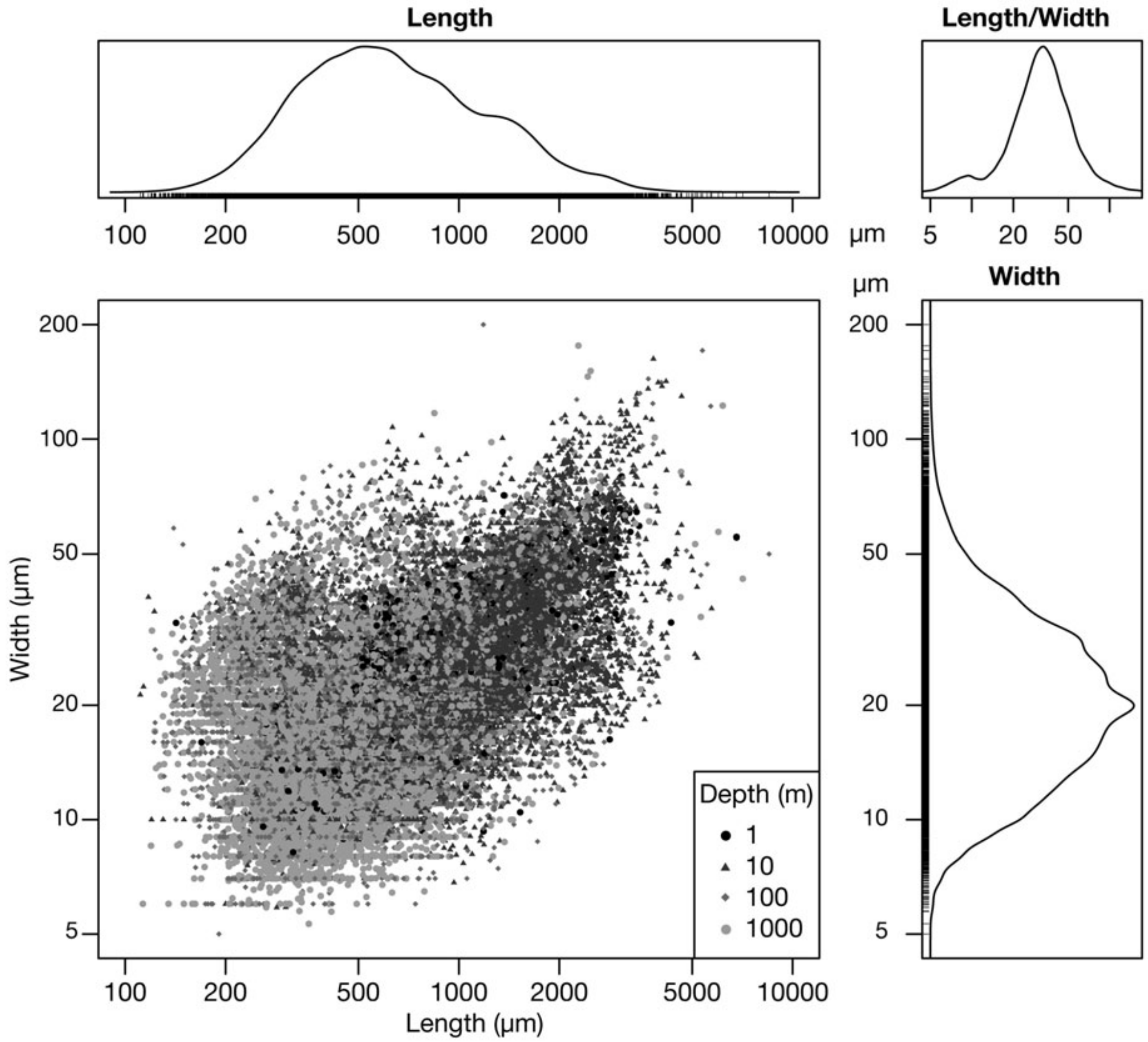

Fig. 2. Length and width of individual nematodes. Large panel shows length–width relationship as a function of water depth. Each data point comprises a single length–width measurement pair per nematode; coloration is a function of water depth. Smaller panels show frequency distributions of length, width and length:width ratio

mean was larger than the geometric mean with a correction factor of $\exp(0.5s^2)$, where s^2 is the estimated variance from the regression, in $\log_e$ units. As this variance was small, this correction factor was negligible for length and width (<1.02) and small for individual biomass (<1.2) (see Table 2).

The variance explained was estimated as the coefficient of determination, i.e.:

$$1-\frac{\sum\left(\hat{y}_i-\bar{y}\right)^2}{\sum\left(y_i-\bar{y}\right)^2}=1-\frac{\text{RSS}}{\text{TotalSS(corrected for mean)}} \qquad (1)$$

where $\hat{y}_i$ is the fitted value and $\overline{y}_i$ is the mean.

The data sets and R-scripts used for analysis are available upon request.

RESULTS

Nematode size

All length and width data are plotted in Fig. 2. The nematodes were on average 782 μm long and 23 μm wide, with a L:W ratio of 36. Ninety percent of all nematodes (i.e. from the 5th to 95th percentile) were between 248 and 1883 μm long, between 10 and 47 μm wide and had a L:W ratio varying between 11 and 70. Individual DW varied between 0.005 and 0.49 μg (5th to 95th percentiles), with a global average of 0.13 μg.

The lowest (0.028 μg DW, deep Ligurian Sea, Mediterranean) and highest (0.4 μg DW, BCS sand bank) mean biomass per station in the data set differed by a factor of about 14. In absolute terms there was more

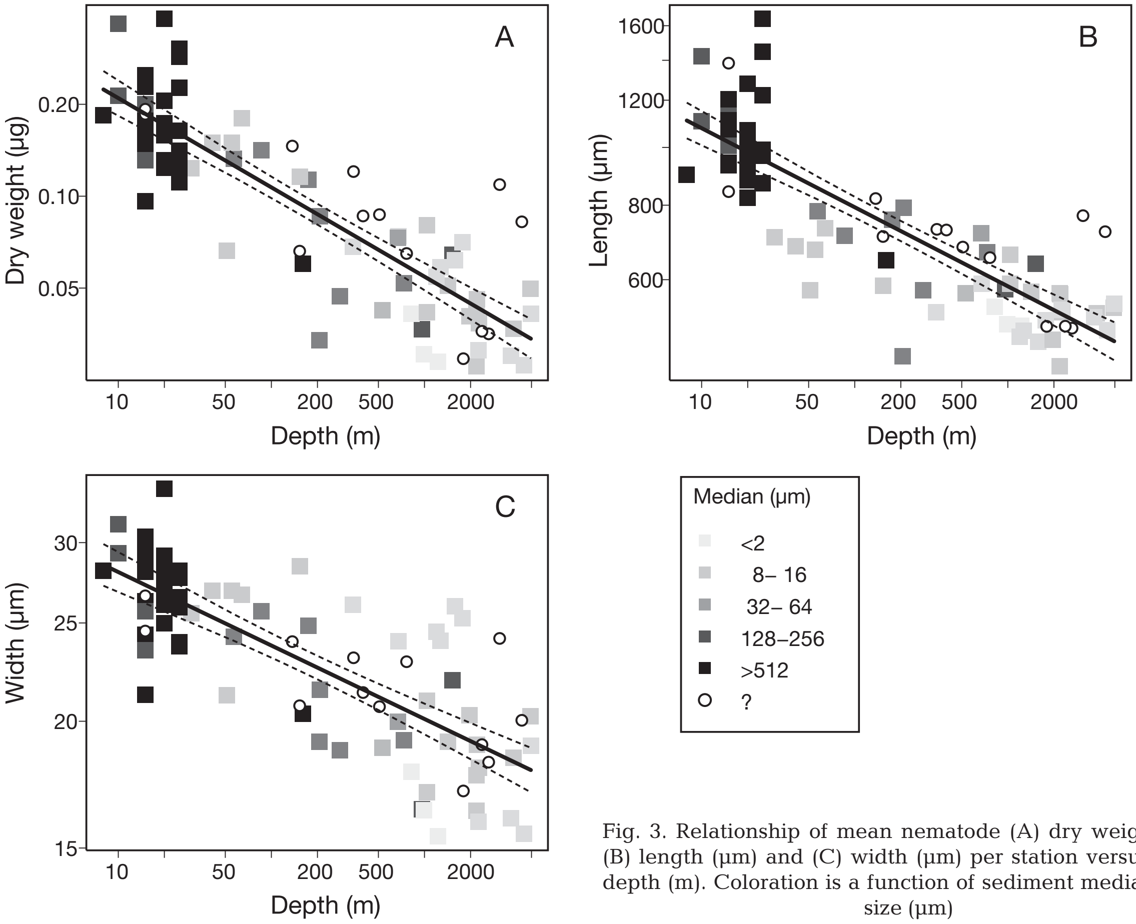

Fig. 3. Relationship of mean nematode (A) dry weight (µg), (B) length (µm) and (C) width (µm) per station versus water depth (m). Coloration is a function of sediment median grain size (µm)

variation in mean biomass in the shelf (depth <200 m, 0.06 to 0.4 µg DW) than in deeper areas (0.028 to 0.12 µg DW) (Fig. 3A). Large variability was also apparent within a limited geographical area (e.g. the BCS: 0.1 to 0.4 µg DW).

Compared to the large range in mean nematode biomass, there was much less variation in mean nematode length and width, which change by factors of 3.8 (429 to 1642 µm) and 2.2 (15 to 34 µm), respectively.

Trends in nematode size

In Fig. 3, the arithmetic mean nematode sizes for each station are depicted as a function of water depth. Average individual nematode DW (Fig. 3A), length (Fig. 3B) and width (Fig. 3C) all decreased with bathymetric depth. This decline was fitted with a linear, an exponential and a power function. In all cases, the decrease was best described with a power function, i.e. of the form $y = aD^b$, where D is depth (m) and a and b are fitting parameters (all regressions: $p < 0.001$, see Table 2). The variance explained by mere depth ($n = 83$) ranged from 62% for mean individual width to 67% for mean individual length (Table 2).

Exponential coefficients of change (b-values of the power fit) were larger for biomass (–0.3) than for length (–0.13) and width (–0.07). The more prominent decrease of biomass is due to the culmination of changes in both the individual length and width measures.

All nematode size measures were also significantly and positively related to median grain size ($n = 70$), although the explained variance was not as high (36 to 64%) as when depth was the independent variable (Table 2).

One confounding factor was the fact that grain size was also significantly related to water depth, the (power-)relationship explaining 56% of total variance, ($r^2 = 0.66$; best-fit: $y = 1795D^{-0.7}$). To test for an effect of grain size, acting independently of its relationship with depth, we regressed the size descriptors on the residuals of the grain size–depth relationship and tested for significance using ANOVA. The relationship was not significant for nematode biomass ($p > 0.7$) or individual width ($p = 0.3$), but was highly significant for nematode

Table 2. Nonlinear regression of the power models $y = aD^b$ (n = 83), $y = cMd^e$ (n = 70) and $y = a'D^{b'}Md^{e'}$ for nematode individual biomass (µg dry weight), length (µm) and width (µm) as a function of depth (D, m) and/or median grain size (Md, µm). The adjusted r^2, variance explained, parameter values and correction factors (CF, to correct for back-transformation, see 'Materials and methods') are also shown. The significance level of the most complex model is relative to the best simple model. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; ns: not significant. Parameter values for non-significant regressions are not given. Due to the strong collinearity of depth and median grain size, the parameters of the combined regression are also not shown

	r^2	Variance (%)	Parameter	CF
Biomass				
aD^b	0.75^{***}	66	$0.41D^{-0.3}$	1.07
cMd^e	0.54^{***}	43	$0.03Md^{0.3}$	1.13
$a'D^{b'}Md^{e'}$	0.79^{ns}			
Length				
aD^b	0.71^{***}	67	$1461D^{-0.13}$	1.02
cMd^e	0.70^{***}	64	$390Md^{0.16}$	1.02
$a'D^{b'}Md^{e'}$	0.80^{***}	74		
Width				
aD^b	0.61^{***}	62	$33.2D^{-0.072}$	1
cMd^e	0.36^{***}	36	$17.5Md^{0.07}$	1.01
$a'D^{b'}Md^{e'}$	0.63^{ns}			

length ($p = <0.001$). Adding median grain size to the depth relationship increased the explained variance (n = 70) from 69 to 74%; ANOVA demonstrated this increase to be significant. Adding sediment grain size to the regression versus water depth did not significantly improve the fit between individual biomass and mean width.

Seasonal trends in nematode morphometry

Compared to the spatial differences, seasonal variation was much less pronounced. Seasonality was investigated in 2 contrasting sediments at the BCS sampled before (February), during (April) and after (October) algal bloom deposition in 2003 (Franco et al. 2007, 2008).

In one fine-sandy sediment (Stn 115bis), with a small fraction of mud and devoid of oxygen below 0.4 cm, nematode individual biomass (Kruskal Wallis: $p < 0.001$), length (1-way ANOVA: $F_{2,3342} = 44$, $p < 0.001$), width (Kruskal Wallis: $p < 0.05$) and L:W ratio (Kruskal Wallis: $p < 0.001$) were significantly different between sampling events (Table 3). Nematode individual biomass, length and width were higher during the phytoplankton sedimentation period compared to before and after this event, but relative differences in nematode width were smaller compared to the changes in nematode biomass and length. Maximum and minimum sizes differed by 40% (DW), 22% (length) and 7% (width).

In a more permeable sediment (Stn 330), located close to Stn 115bis and consisting of medium sand that remains oxic over at least 5 cm sediment depth, significant but small differences in the nematode measurements were observed as well, except for nematode width (Table 3). Tukey's HSD showed that both nematode individual biomass ($F_{2,1626} = 8.97$, $p < 0.001$) and length ($F_{2,1626} = 25.4$, $p < 0.001$) were significantly lower in October compared to February and April. The largest decrease was observed from April to October. The difference between maximum and minimum mean size ranged in between 4% (width) and 34% (DW).

Nematode morphometry

The mean width versus mean length for all stations is plotted in Fig. 4. When ignoring the data from the Aegean Sea, a quasi-linear relationship between width and length tends to emerge, with a L:W ratio near 30; this linear trend tends to level off at a mean body width of about 25 µm. The nematodes from the Aegean Sea significantly deviate from this trend, being much wider for similar lengths.

DISCUSSION

When using observations from different sources, one has to make sure that data are not biased due to methodology. Nematode biomass data can be influenced by sampling devices, fixation method, sieve sizes and weight estimation techniques (Udalov et al. 2005). Weight estimation and fixation methods were the same in all component data sets used. Udalov et al. (2005) found no effects of sampling equipment (boxcorer versus multiple corers) on nematode biomass and we assume this is also the case for the present study. Different upper and lower sieve sizes have been used; lower sieve sizes range from 30 to 38 µm, upper sieve

Table 3. Mean nematode biomass, length from 3 sampling dates at 2 sampling stations on the Belgian Continental Shelf

Location	Biomass (µg DW)			Length (µm)			Width (µm)		
	Feb	Apr	Oct	Feb	Apr	Oct	Feb	Apr	Oct
Stn 115	0.128	0.180	0.156	1114	1362	1307	27.1	29.1	27.6
Stn 330	0.09	0.086	0.067	862	805	675	25.8	26.2	25.2

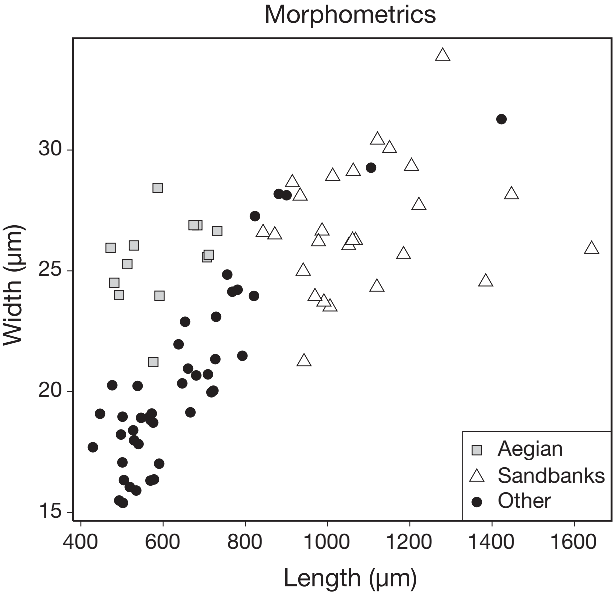

Fig. 4. Nematode length (µm) versus width (µm). Data are station means for the Aegean Sea, sand banks and other stations

sizes include 500 µm and 1 mm (Table 1). Meiobenthologists use an upper sieve mainly to exclude macrobenthos that is not adequately sampled with small cores. Similarly, extremely large nematodes are not adequately sampled, yet inclusion of a few of these giants may strongly increase, and sometimes double, the estimates of mean individual nematode weight in a sample. To avoid these perturbations, we used a more robust estimate of mean weight, based on log-transformed data (see 'Materials and methods').

The use of different lower sieves could result in a selective underestimation of narrower nematodes, but the range of lower sieve sizes is very small (30 to 38 µm). When checking the entire data set, nematodes with a width of 7 to 8 µm were retained on 32 and 38 µm sieves (e.g. in samples from the Ligurian Sea and the BCS), but nematodes with a width of 6 to 7 µm were only found on 32 µm sieves. As only 43 nematodes (of a total of 38 274 nematodes) belonged to this width-class, this did not influence our results.

Based on global databases that span a large range in water depths, it is generally difficult to elucidate which factors affect nematode size, as most environmental conditions somehow relate to water depth. For instance, many sediment biogeochemical (food deposition, oxic mineralisation, oxygen penetration, etc., Middelburg et al. 1996, 1997), biological (Vincx et al. 1994, Heip et al. 2001, Rex et al. 2006) and sediment characteristics (e.g. grain size) are known to change with water depth. For example, in our database, there was a significant negative relationship between water depth and sediment grain size ($r^2 = 0.66$, accounting for 67 % of the variance of grain size). Our results show that all nematode size descriptors can be predicted remarkably well by water depth alone, assuming a power function. The variance explained ranged from 62 % (mean individual width) to 67 % (mean length). Johnson et al. (2007) reported similar coefficients of determination when regressing NW Atlantic macrofaunal biomass against an estimate of food supply. The coefficients of change in the present study varied from –0.3 (DW) to –0.13 (length) and –0.07 (width), denoting that for any doubling in water depth, the average nematode DW decreased by 19 % ($=100[1 - 2^{-0.3}]$), while the length and width only decreased by 9 and 5 %.

However, with depth and grain size so closely related, the primary effect of either on nematode size is not so easy to disentangle. There also existed a significant positive relationship between all nematode size descriptors and median grain size, although for nematode width and weight, the coefficient of determination was smaller than for the depth dependence, indicating that depth has greater explanatory power than grain size. This was not the case for nematode length, where both depth and sediment grain size explained an equal amount of variation. This descriptor was strongly related to the residuals of the grain size–depth relationship, indicating that grain size added explanatory power to depth, and sediment composition itself (i.e. independent from its relationship with water depth) also affects nematode length. It should be noted that the significant improvement of the fit of nematode length was mainly due to a better representation of length in the shallow-water stations, which have rather coarse sediments and whose mean lengths were underestimated when considering only depth as a descriptor (Fig. 3). The shallow sediments comprise a mix of sand bank stations and more fine-grained sediments. Sediments at the sand banks have a median grain size ranging from 214 to 527 µm (Vanaverbeke et al. 2000), while nematodes are roughly only 3 times as long (700 to 1400 µm). The occurrence of longer nematodes here contrasts with earlier findings (Tita et al. 1999) of sandy sediments inhabited by smaller nematodes. However, the results of Tita et al. (1999) were obtained in intertidal estuarine settings, and sediments were finer (median grain size = 182 µm) compared to the sand banks. These authors considered an increase in length and width an adaptation to a predatory life style. Long nematodes in sand bank sediments mainly consisted of *Leptonemella aphanothecae*, several *Chromaspirina* species, *Sigmaphoranema rufum* and *Onyx perfectus* (Vanaverbeke et al. 2002), which, except for *L. aphonothecae* (a selective deposit feeder), are indeed considered to be predators (sensu Wieser 1953). An alternative explanation could be that the larger interstitial space favours longer nematodes.

Nematodes from the Aegean Sea stand apart from those in other locations, in that compared to their length they are much thicker than the nematodes from the other sites. Short and thick nematodes are present in different areas and depths around the world (Soetaert et al. 2002, Vanaverbeke et al. 2004), where they comprise a group well distinguished from the mainstream, slender nematodes by a L:W ratio <15. However, in the Aegean Sea, the stout nematode type (L:W < 15) is entirely lacking; here all nematodes belong to a single morphotype with a narrow range of length and width. The oligotrophy of the Aegean Sea (Psarra et al. 2000) may promote allocation of storage products which leads to increased width, while the short length might be an adaptation to fast reproduction, as was postulated by Soetaert et al. (2002) and Vanaverbeke et al. (2004).

Although the best-fit regression explained 62 to 74% of all variance, this means that 26 to 38% of the variance is left unexplained. This manifests itself by significant variation around the depth regression line (Fig. 3). The remaining unexplained variance can be attributed to a variety of factors, including small-scale spatial and temporal variation or some unmeasured property of the sedimentary environment. The nematode sizes for 2 stations, Stns 330 and 115bis, were estimated on 3 occasions several months apart. Based on these results, it is clear that temporal variation exists, although this variation is low: the maximum and minimum DW differed by at most 40%, whereas on the entire shelf DW varied by more than an order of magnitude.

Correlation does not imply causality. When using depth as an explanatory variable, we assume that it is a surrogate for food supply, which may affect the benthic inhabitants either directly (as a source of organic matter) or indirectly (by altering the oxic conditions). It thus becomes relevant to compare the coefficient of decline of nematode DW with similar trends in estimates of food supply. *In situ* sediment community oxygen consumption (SCOC) rates are amongst the best descriptors of total organic matter mineralisation (e.g. Soetaert et al. 1996), where mineralisation itself is a time-integrated measure of the flux of reactive organic material. Roughly, it can be assumed that about 1 mol O_2 is consumed for 1 mol organic matter mineralised (respired), whether via the oxic or anoxic pathway (Soetaert et al. 1996). In the former case, oxygen is consumed directly by the respiration of organic matter; in the latter case, oxygen is consumed secondarily, when the reduced byproducts (e.g. sulphide) originating from anoxic mineralisation are reoxidised. The relationship between SCOC and water depth has been frequently derived (e.g. Middelburg et al. 1996, Andersson et al. 2004), and is usually expressed as an exponential decay or a double exponential decay (Andersson et al. 2004) with depth, as this formula is consistent with a mechanistic model where organic matter decays while sinking through the water column. For water depths >50 m, we refitted the SCOC data given in Andersson et al. (2004) using a power law. A coefficient of change of −0.62 was obtained (Fig. 5A), i.e. an average decrease of 35% in total SCOC for every doubling in water depth.

Comparing both trends indicates that benthic oxygen consumption decreases faster (35%) with depth than mean nematode body weight (19%). As reported in many studies (e.g. Soetaert & Heip 1995, Vincx et al. 1994), nematode density also tends to decrease with water depth. Based on our samples, the trend of nematode density with water depth is not so clear, mainly because the variation in the shallow stations is very large and density can be relatively low, as many of the sand bank stations are very poor in animal life (Vanaverbeke et al. 2000). If we take into account only the stations deeper than 50 m, we obtain a coefficient of change of −0.33 (Fig. 5B), similar to the value for mean nematode size. Combining the decline of density and individual DW, a coefficient of change of −0.33 to 0.30 = −0.63 for total nematode biomass is obtained, which more or less matches the decline of oxygen consumption with depth. Assuming a C:DW conversion of 0.5, and converting from gram to mol, we arrive at the following relationship between nematode biomass and water depth:

$$Nem_{\mathrm{C}} = \frac{8104 \times 0.41 \times 0.5}{12}\mathrm{D}^{-0.63} = 138\mathrm{D}^{-0.63} \qquad (2)$$

where Nem_{C} is nematode biomass (mmol C m^{-2}) and D is water depth (m). Based on a data compilation by Mahaut et al. (1995), we estimate that nematodes respire on average 7.5% of their biomass per day; assuming an O_2:C ratio of 1, total nematode respiration (Nem_{resp}, mmol O_2 m^{-2} d^{-1}) as a function of water depth can be written as:

$$Nem_{\mathrm{resp}} = 138 \times 0.075 \times \mathrm{D}^{-0.63} = 10.4\mathrm{D}^{-0.63} \qquad (3)$$

Since data sets containing total oxygen consumption rate and standing stocks in the same stations are rare, we merged this estimate of nematode oxygen consumption with the total sediment oxygen consumption rate (SCOC = $140\mathrm{D}^{-0.62}$) to find that only a small fraction (on the order of 7.5%) of the total benthic metabolism is performed by nematodes.

The results presented here are derived from an integrated database, which made available data from wide ranges of bathymetric depth, grain size and season. This increased our understanding of the large-scale factors governing nematode size and shape. As such, we call for similar initiatives that will allow detection of patterns and signals that are not visible from individual data sets alone.

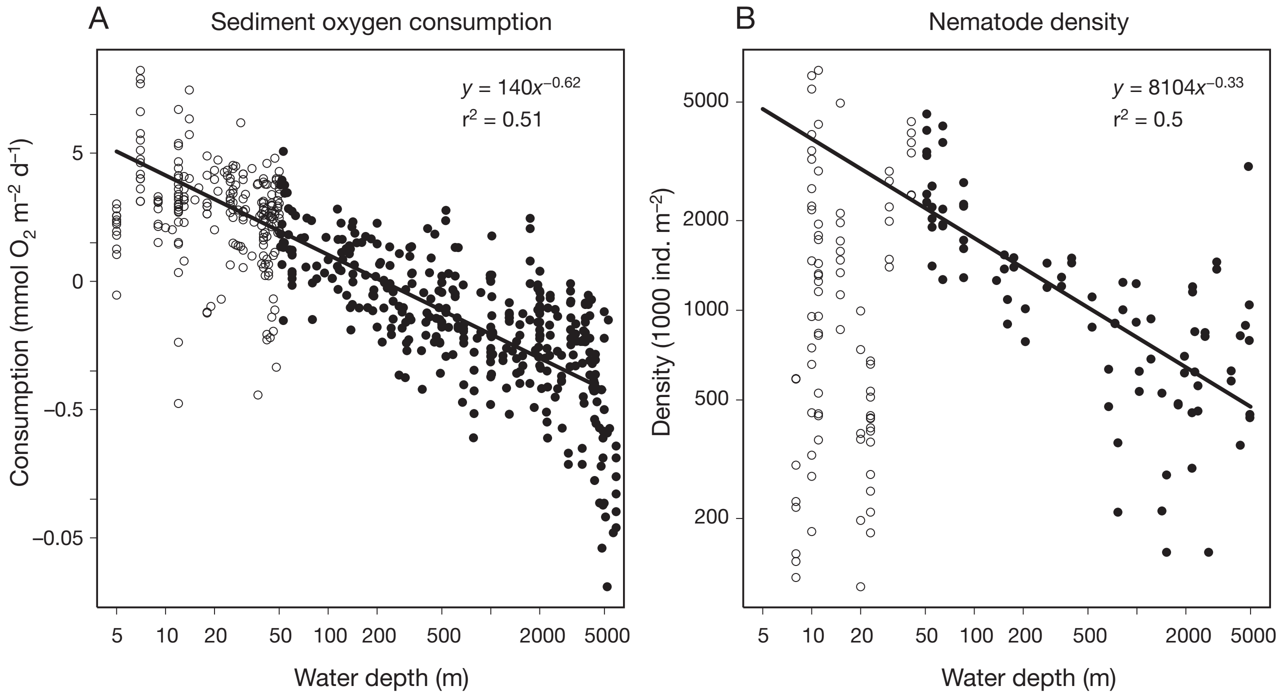

Fig. 5. Power regressions of (A) total sediment oxygen consumption versus water depth (Andersson et al. 2004) and (B) nematode density versus water depth. For both regressions, values at depths below 50 m have been discarded

Acknowledgements. The project has been carried out in the framework of the MarBEF Network of Excellence ‘Marine Biodiversity and Ecosystem Functioning, which is funded by the Sustainable Development, Global Change and Ecosystems Programme of the European Community’s Sixth Framework Programme (contract no. GOCE-CT-2003-505446). This publication is contribution no. 4628 of NIOO-CEME. The authors from Ghent University acknowledge the support from GENT-BOF Project 01GZ0705 Biodiversity and Biogeography of the Sea (2005–2010).

LITERATURE CITED

Andersson JH, Wijsman JWM, Herman PMJ, Middelburg JJ, Soetaert K, Heip C (2004) Respiration patterns in the deep ocean. Geophys Res Lett 31:L03304, doi:10.1029/2003GL018756

Andrassy I (1956) The determination of volume and weight of nematodes. Acta Zool 2:1–15

Broun CJ, Lambshead PJD, Smith CR, Hawkins LE, Farley R (2001) Phytodetritus and the abundance of biomass of abyssal nematodes in the central, equatorial Pacific. Deep-Sea Res I 49:843–857

Finney DJ (1941) On the distribution of a variate whose logarithm is normally distributed. Suppl J R Stat Soc 7:155–161

Franco MA, De Mesell M, Diallo MD, Van der Gucht K and others (2007) Effect of phytoplankton bloom deposition on benthic bacterial communities in two contrasting sediments in the southern North Sea. Aquat Microb Ecol 48:241–254

Franco MA, Soetaert K, Van Oevelen D, Van Gansbeke D, Costa MJ, Vincx M, Vanaverbeke J (2008) Density, vertical distribution and trophic responses of metazoan meiobenthos to phytoplankton deposition in contrasting sediment types. Mar Ecol Prog Ser 358:51–62

Gambi C, Danovaro R (2006) A multiple-scale analysis of metazoan meiofaunal distribution in the deep Mediterranean Sea. Deep-Sea Res I 53:1117–1134

Heip CHR, Duineveld G, Flach E, Graf G and others (2001) The role of the benthic biota in sedimentary metabolism and sediment-water exchange processes in the Goban Spur area (NE Atlantic). Deep-Sea Res II 48:3223–3243

Johnson NA, Campbell JW, Moore TS, Rex MA, Etter RJ, McClain CR, Dowell MD (2007) The relationship between the standing stock of deep-sea macrobenthos and surface production in the western North Atlantic. Deep-Sea Res I 54:1350–1360

Lampadariou N, Tselepides A (2006) Spatial variability of meiofaunal communities at areas of contrasting depth and productivity in the Aegean Sea (NE Mediterranean). Prog Oceanogr 69:19–36

Lampadariou N, Hatziyanni E, Tselepides A (2005a) Meiofaunal community structure in Thermaikos Gulf: response to intense trawling pressure. Cont Shelf Res 25:2554–2569

Lampadariou N, Karakassis I, Teraschke S, Arlt G (2005b) Changes in benthic meiofaunal assemblages in the vicinity of fish farms in the Eastern Mediterranean. Vie Milieu 55:61–69

Lampitt RS, Antia AN (1997) Particle flux in deep seas: regional characteristics and temporal variability. Deep-Sea Res I 44:1377–1403

Le Danois E (1948). Les profondeurs de la Mer. Payot, Paris

Mahaut ML, Sibuet M, Shirayama Y (1995) Weight-dependent respiration rates in deep-sea organisms. Deep-Sea Res I 42:1575–1582

McClain CR, Rex MA, Jabbour R (2005) Deconstructing bathymetric body size patterns in deep-sea gastropods. Mar Ecol Prog Ser 297:181–187

Middelburg JJ, Soetaert K, Herman PMJ, Heip CHR (1996) Denitrification in marine sediments: a model study. Global Biogeochem Cycles 10:661–673

Middelburg JJ, Soetaert K, Herman PMJ (1997) Empirical relationships for use in global diagenetic models. Deep-Sea Res I 44:327–344

Psarra S, Tselepides A, Ignatiades L (2000) Primary productivity in the oligotrophic Cretan Sea (NE Mediterranean): seasonal and interannual variability. Prog Oceanogr 46:187–204

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, available at www.R-project.org

Rex MA, Etter RJ (1998) Bathymetric patterns of body size: implications for deep-sea biodiversity. Deep-Sea Res II 45: 103–127

Rex MA, Etter RJ, Morris JS, Crouse J and others (2006) Global bathymetric patterns of standing stock and body size in the deep-sea benthos. Mar Ecol Prog Ser 317:1–8

Sebens KP (1987) The ecology of indeterminate growth in animals. Annu Rev Ecol Syst 18:371–407

Soetaert K, Heip C (1989) The size structure of nematode assemblages along a Mediterranean deep-sea transect. Deep-Sea Res 36(1):93–102

Soetaert K, Heip C (1995) Nematode assemblages of deep-sea and shelf break sites in the North Atlantic and Mediterranean Sea. Mar Ecol Prog Ser 125:171–183

Soetaert K, Herman PMJ, Middelburg JJ (1996) A model of early diagenetic processes from the shelf to abyssal depths. Geochim Cosmochim Acta 60:1019–1040

Soetaert K, Muthumbi A, Heip C (2002) Size and shape of ocean margin nematodes: morphological diversity and depth-related patterns. Mar Ecol Prog Ser 242:179–193

Sommer S, Pfannkuche O (2000) Metazoan meiofauna of the deep Arabian Sea: standing stocks, size spectra and regional variability in relation to monsoon induced enhanced sedimentation regimes of particulate organic matter. Deep-Sea Res II 47:2957–2977

Thiel H (1975) The size structure of the deep-sea benthos. Int Rev Gesamten Hydrobiol 60:575–606

Tita G, Vincx M, Desrosiers G (1999) Size spectra, body width and morphotypes of intertidal nematodes: an ecological interpretation. J Mar Biol Assoc UK 79:1007–1015

Udalov AA, Azovsky AI, Mokievsky VO (2005) Depth-related pattern in nematode size: What does the depth itself really mean? Prog Oceanogr 67:1–23

Vanaverbeke J, Soetaert K, Heip C, Vanreusel A (1997) The metazoan meiobenthos along the continental slope of the Goban Spur (NE Atlantic). J Sea Res 38:93–107

Vanaverbeke J, Gheskiere T, Vincx M (2000) The meiobenthos of subtidal sandbanks on the Belgian Continental Shelf (Southern Bight of the North Sea). Estuar Coast Shelf Sci 51:637–649

Vanaverbeke J, Gheskiere T, Steyaert M, Vincx M (2002) Nematode assemblages from subtidal sandbanks in the Southern Bight of the North Sea: effect of small sedimentological differences. J Sea Res 48:197–207

Vanaverbeke J, Steyaert M, Vanreusel A, Vincx M (2003) Nematode biomass spectra as descriptors of functional changes due to human and natural impact. Mar Ecol Prog Ser 249:157–170

Vanaverbeke J, Soetaert K, Vincx M (2004) Changes in morphometric characteristics of nematode communities during a spring phytoplankton bloom deposition. Mar Ecol Prog Ser 273:139–146

Vandepitte L, Vanaverbeke J, Vanhoorne B, Hernandez F, Nara Bezerra T, Mees J, Vanden Berghe E (2009) The MANUELA database: an integrated database on meiobenthos from European marine waters. Meiofauna Marina 17:35–60

Vanreusel A, Vincx M, Bett BJ, Rice AL (1995) Nematode biomass spectra at two abyssal sites in the NE Atlantic with a contrasting food supply. Int Rev Gesamten Hydrobiol 80: 287–296

Vincx M, Bett BJ, Dinet A, Ferrero T and others (1994) Meiobenthos of the deep Northeast Atlantic. Adv Mar Biol 30: 1–88

Wieser W (1953) Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Ark Zool 2:439–484

Wieser W (1960) Benthic studies in Buzzards Bay. II. The meiofauna. Limnol Oceanogr 5:121–137

Editorial responsibility: Otto Kinne,
Oldendorf/Luhe, Germany

Submitted: March 27, 2009; Accepted: June 6, 2009
Proofs received from author(s): September 29, 2009