The size structure of nematode assemblages along a Mediterranean deep-sea transect

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(Received 25 November 1987; in revised form 7 July 1988; accepted 21 July 1988)

Abstract—The nematode assemblages along a deep-sea transect in the Mediterranean are composed of individuals that are as small as those found in other areas at much greater depth. This may be related to the low surface primary production since chloroplastic pigment equivalent (CPE) values in the sediments are low as well. A significant decrease of both nematode size and sedimentary CPE values with increasing water depth was found. At all water depths average nematode length increases with depth in the sediment (0–2 cm) due to the decreasing abundance of smaller nematodes.

INTRODUCTION

VARIOUS ecological and physiological characteristics (growth rate, metabolic rate, rate of reproduction, . . .) can be expressed as an allometric function of body weight (BLUE-WEISS *et al.*, 1978; PETERS, 1983; KOOLJMAN, 1986). The size of animals also can determine the outcome of interaction among species (competition, predation) (BROOKS and DODSON, 1965; DODSON, 1974; WILSON, 1975; HALL *et al.*, 1976) and hence has important implications on community structure (HUTCHINSON, 1959).

A useful descriptor of an ecosystem is the size distribution of its living constituents. This idea was first applied to marine pelagic ecosystems by SHELDON and PARSONS (1967). It was extended to benthic assemblages by SCHWINGHAMER (1981), who found a conservative pattern, with three biomass peaks, corresponding to micro-, meio- and macrofauna. Subsequent papers of SCHWINGHAMER (1983, 1985) and WARWICK (1984) confirmed this pattern.

In the deep sea, zonation often is documented in terms of size distributions. Two different types of size–depth patterns exist, reflecting different adaptations to a decrease in food availability with depth (CARNEY *et al.*, 1983). (1) The deeper–bigger type, where the largest species tend to be found in deeper waters. This has been observed in isopods (WOLFF, 1962), cumaceans (JONES, 1969), tanaidaceans (GARDINER, 1975), amphipods (THURSTON, 1979), gastropods (CLARKE, 1960) and foraminiferans (BERNSTEIN *et al.*, 1978). The increase in size has been attributed to an increased mobility, resulting in a larger foraging area (GAGE, 1978; CARNEY *et al.*, 1983). (2) The deeper–smaller type: based on (a) the decrease of size in macrofauna with increasing depth and (b) the slower rate of decrease in meiofauna numbers with increasing depth compared to macrofauna numbers, THIEL (1975) concluded that the average size of multicellular organisms in benthic associations decreases with depth or, more generally, from high to low food

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levels. He formulated the following hypothesis: "Associations governed by constantly limited food availability are composed of small individuals on the average". The decrease in size with increasing depth was attributed to a decreased maintenance cost in small organisms (FENCHEL, 1974), or stated otherwise: food limitation does not allow the higher energy consumption of larger species (THIEL, 1975, 1978; GAGE, 1978; CARNEY *et al.*, 1983).

In the present study, the size distribution of organisms within one taxonomic group, the nematodes, is investigated along a deep-sea transect in the western Mediterranean. Nematodes are the dominant group in the marine metazoan meiofauna and account for about 90% of meiofauna numbers when Foraminifera are excluded (THIEL, 1975).

MATERIAL AND METHODS

Six stations were investigated along a transect in the Ligurian Sea, northwest of the Bay of Calvi (Corsica); depths ranged from 160 to 1220 m (Fig. 1, Table 1). Bottom samples were taken with a small Reineck box-corer (170 cm²), modified to avoid loss of interstitial water when lifting on board. Three cores (10 cm²) for faunal analysis and one core (10 cm²) for granulometric study were taken from the box core. Samples were only retained when there was clear overlying water in the box.

Fig. 1. Location of the six stations, identified by their station number. Bathymetric contours in metres.

Table 1. Position and sediment characteristics of the stations

Station no.	Depth (m)	Latitude (N)	Longitude (E)	Median grain size (μm)	% silt-clay
1	160	42°37.3'	8°40.3'	373	16.3
2	280	42°38.0'	8°40.0'	67	47.8
3	530	42°38.5'	8°39.6'	18	62.7
4	820	42°39.4'	8°39.4'	3	76.6
5	990	42°39.9'	8°39.2'	<3	90.5
6	1220	42°41.1'	8°38.5'	<3	92.0

The benthos cores were split horizontally as follows: the upper centimeter was split in two half centimeters, the remaining sediment column was cut into 1 cm slices. Animals were fixed with a hot (70°C), 4% formaldehyde tapwater solution. In the laboratory, the slices of two subcores were passed through 500, 250 and 38 μm mesh sieves. The fraction remaining on the 38 μm sieve was then centrifuged twice with Ludox to extract the lighter organisms from the heavier sediment grains (HEIP *et al.*, 1985). Macrofauna and soft meiofauna (i.e. excluding hard-shelled foraminiferans) were counted after staining with Rose Bengal. For the fraction smaller than 250 μm , care was taken to allow the settlement of all organisms: enumeration was postponed until about half an hour after pouring into the counting dish (even after several minutes the smallest individuals can still be in suspension and hence overlooked). All nematodes encountered were picked out and mounted in glycerine slides (SEINHORST, 1959). Length (excluding filiform tail part) and width were measured of every unbroken individual; 68–92% of all nematodes counted were measured. Conversion to nematode dry weight was done using the method of ANDRASSY (1956) and assuming a density of 1.13 and a dry weight/wet weight ratio of 0.25 (WIESER, 1960).

The use of a morphometric method instead of direct weighing to estimate nematode biomass has several advantages. As nematodes are too small to obtain an accurate estimate of individual weight, they have to be processed in tens or hundreds at a time. As such, valuable information on the natural variability is lost. This loss can be partly regained by weighing nematodes retained on sieves with successive mesh width. One assumes then that nematodes with corresponding body weight are found on the same sieve. Yet this is not necessarily the case, as shape after fixation (curled or straight), the presence of bristles, etc. . . also play an important role. Another advantage of the morphometric technique is that the nematodes can be preserved and used for other purposes. Disadvantages are the amount of labour required in the making of slides and drawings and the use of conversion factors (see above).

Chloroplastic pigment equivalents (chlorophyll *a* and disintegration products) were measured to estimate the organic input to the sediment: two cores (1 cm²) were drawn from the same box core and the top sediment split into four layers of 1 cm. Measurements were performed fluorimetrically (STRICKLAND and PARSONS, 1972) after scaling with a spectrophotometer (LORENZEN, 1967).

One of the main purposes of this study was to analyse the effect of station depth and depth into the sediment on nematode size. Some critical reflections on the sampling design seem therefore desirable. As HURLBERT (1984) pointed out, if one aims at testing for treatment effects (i.e. depth), some sort of replication is obligatory, and the level of replication is imposed by the hypothesis being tested. Clearly, our sampling design, in

which depth, due to logistic difficulties, could not be replicated (only one box-corer per station), suffers from this lack of adequate replication. Statistics inferred are therefore limited to simple correlations (SOKAL and ROHLF, 1981).

RESULTS

Chloroplastic pigment equivalents

Total chloroplastic pigment equivalents (CPE) values range from $2.44 \mu\text{g cm}^{-2}$ at 160 m depth to $0.48 \mu\text{g cm}^{-2}$ at 990 m depth (Table 2). CPE values decrease with increasing water depth (Fig. 2, Table 2; product-moment correlation coefficient = -0.835 , $P < 0.05$) and with increasing depth into the sediment (Table 2).

Table 2. Mean CPE values ($\mu\text{g cm}^{-3}$)

Sediment depth (cm)	Station depth (m)					
	160	280	530	820	990	1220
0-1	0.72	0.55	0.32	0.35	0.23	0.30
1-2	0.82	0.37	0.20	0.11	0.10	0.09
2-3	0.66	0.17	0.09	0.09	0.08	0.09
3-4	0.48	0.31	0.12	0.13	0.07	0.07
Total ($\mu\text{g cm}^{-2}$)	2.44	1.40	0.73	0.68	0.48	0.56

Fig. 2. Distribution of mean chloroplastic pigment equivalents $\pm$ S.E. and mean nematode lengths $\pm$ S.E. along the transect.

Nematode size

The length–frequency distributions are strongly skewed, with a long tail extending into the larger sizes (Fig. 3, Table 3). The mean nematode length varies from 641 μm at 160 m depth to 507 μm at 1220 m depth. The geometric mean is much smaller: respectively 528 and 422 μm , but still somewhat larger than the median length (498 μm at 160 m depth, 386 μm at 1220 m depth).

The modal size class is 400–500 μm at 160 m depth, 200–300 μm at 1220 m depth. Minimum measured nematode lengths vary from 139 to 113 μm , while the maximum lengths vary from 8501 μm at 160 m depth (i.e. 69 times the minimum length) to 1986 μm at 1220 m depth (i.e. 18 times the minimum length).

Mean nematode dry weights (Table 3) vary from 0.097 μg (geometric mean 0.03 μg) at 160 m depth to 0.037 μg (geometric mean 0.013 μg) at 1220 m. The modal size class is 0.01–0.02 μg for the three shallowest, 0.0–0.01 μg for the three deepest stations.

Nematodes become significantly shorter with water depth (Fig. 2), ($r = -0.97$, $P < 0.01$ for mean, $r = -0.957$, $P < 0.01$ for geometric mean and $r = -0.841$, $P < 0.05$ for median nematode length). Similarly, nematode dry weight is negatively correlated with water depth ($r = -0.909$, $P < 0.02$ for mean, $r = -0.955$, $P < 0.01$ for geometric

Fig. 3. Length–frequency distributions of the nematode assemblages at the shallowest (160 m) and deepest (1220 m) station. The mean is indicated by the small vertical line, indicating a location along the abscissa, total range is shown by the horizontal line, mean $\pm$ S.E. is indicated by the black portion of the bar, mean $\pm$ S.D. is given by the black plus the white bar.

Table 3. Length and weight characteristics of the nematode assemblages along the transect

Station depth (m)	160	280	530	820	990	1220
Length (μm)						
Mean	641.2	593.1	575.8	545.3	516.2	506.9
Geometric mean	528.2	483.8	479.6	455.3	430.6	422.1
Median	498.5	424.7	463.7	414.7	399.3	386.5
% < 300 μm *	13.7	21.2	23.0	25.1	28.1	31.4
% < 300 μm †	10.0	18.8	19.0	22.4	22.3	25.0
Dry weight (μg)						
Mean	0.097	0.074	0.050	0.048	0.040	0.037
Geometric mean	0.030	0.023	0.024	0.019	0.016	0.013
Median	0.025	0.020	0.021	0.016	0.014	0.011
% < 0.01 μg	14.5	24.6	23.2	33.5	40.7	48.6

* Total population.

† Adults only.

Fig. 4. Length distributions of the nematode assemblages at four sediment intervals (0-0.5, 0.5-1, 1-2 and 2-5 cm) for the six stations.

mean, $r = -0.962$, $P < 0.01$ for median dry weight). Nematode length increases with increasing depth into the sediment to 2 cm, but below 2 cm, nematodes can become either shorter (two stations) or longer (four stations) (Fig. 4).

DISCUSSION

Deep-sea benthos is mainly dependent on a supply of food from above. The biological productivity of the Mediterranean is known to be very low and has been compared to the central oceanic gyres (SOURNIA, 1972 in CRUZADO, 1985). Moreover, the temperature of the bottom water (around 13°C) and the overlying waters (>13°C) is very high compared to other deep-sea regions (2–4°C).

As can be expected, CPE values found in this study are very low: the highest value, found in the shallowest station, does not exceed $3 \mu\text{g cm}^{-2}$. In contrast, in an area of low upwelling off North Morocco, PFANNKUCHE *et al.* (1983) found values up to $25\text{--}30 \mu\text{g cm}^{-2}$ at 200 m depth, and $1.3\text{--}2.0 \mu\text{g cm}^{-2}$ between 1200 and 3000 m depth. In the Porcupine Seabight and abyssal plain, values dropped below $3 \mu\text{g ml}^{-1}$ only at depths greater than 4000 m (PFANNKUCHE, 1985).

The decrease of CPE values with depth into the sediment and the decrease with increasing water depth is well known (e.g. PFANNKUCHE *et al.*, 1983; PFANNKUCHE, 1985). The latter has been attributed to an increased efficiency or complexity of the water column food web in deeper, more depauperate water, and the greater probability of food being ingested or broken down with increased exposure distance and travel time (SMITH and HINGA, 1983).

The shape of the length distributions, with a long tail in the larger sizes, suggests that the use of a mean length is not suitable for comparative purposes: the addition of one large individual can easily shift the mean. The geometric mean (mean after log transformation) or the median length is less sensitive to the presence or absence of extremely large individuals and is to be preferred.

The nematode assemblages in the transect are dominated by very small individuals. Based on functional morphology of the pharynx, ROGGEN (1971) calculated that a lower limit of nematode body length is about 300 μm , below which typical nematode morphology becomes functionally inefficient, particularly with respect to locomotion. Atypical ways of locomotion exist in the Desmoscolecidae (STAUFFER, 1924), a family present in low numbers at most deep-sea sites (TIETJEN, 1971, 1976, 1984; VITIELLO, 1976; VIVIER, 1978; DINET and VIVIER, 1979; THISTLE and SHERMAN, 1985). But adult nematodes, not belonging to the Desmoscolecidae and smaller than 300 μm , also are found along the transect (e.g. SOETAERT and VINCX, 1987). The fraction of nematodes smaller than 300 μm in this study, ranges from 13.7% at the shallowest station to 31.4% at the deepest station (Table 3).

Mean dry weights of nematodes in this study are comparable with those observed in other deep-sea areas at greater depth (RUTGERS VAN DER LOEFF and LAVALEYE, 1986: >4000 m depth, $0.023\text{--}0.040 \mu\text{g}$; DINET *et al.*, 1985: >2100 m, $0.072 \mu\text{g}$). They are much lower than dry weights reported from shallow regions with muddy sediments [e.g. WIDBOM (1984) and references herein].

SHIRAYAMA (1983) used six consecutive sieves to estimate total meiobenthos and nematode biomass. He found a significant decrease in the median size index of total meiobenthos with increasing water depth but the median size of the nematodes increased

Fig. 5. Mean abundance of nematodes (<500 µm, >500 µm) 10 cm^{-2} for three sediment layers (0-0.5, 0.5-1 and 1-2 cm)

with increasing depth. This was ascribed to differences in age structure at the different depths, a hypothesis that could not be tested since the material was used for ash-free weight determination. Conversely, PFANNKUCHE (1985) found an increasing number of nematodes in the smaller size fractions with increasing depth.

It is clear from Table 3 that the observed decrease in length with depth is not due to a changing age structure.

Although CPE values decreased with increasing depth, another possibly important factor, sediment texture, also gradually changed, becoming finer with increasing water depth (Table 1). We cannot exclude the possibility that the decrease in nematode size could be influenced by an increasing amount of silt-clay in the sediment. Yet it is questionable whether the presence of 48% (at 280 m depth) compared to 92% of silt-clay (at 1220 m depth) has an influence on interstitial space.

The tendency of nematodes to be longer deeper down into the sediment is not easily understood. One possible explanation is the larger mobility of longer nematodes, enabling them to penetrate into the more compact deeper layers: whereas large individuals (>500 µm) show no preference for any sediment layer, small individuals generally decrease in abundance with increasing depth into the sediment (Fig. 5). In a muddy bottom in the Öresund, JENSEN (1983) distinguished three sediment layers: the upper centimeter was dominated by small nematodes (1.5 nl, i.e. $0.42 \mu\text{g}$ dry wt); the intermediate layer (2-4 cm), corresponding with the redox potential discontinuity layer, was dominated by large nematodes (mean 2.6-3.7 nl, i.e. $0.73\text{--}1.05 \mu\text{g}$); while below 4 cm again small nematodes were found. VIVIER (1978) also noted that nematodes tended to get longer deeper into the sediment.

The possibility of an artifact can not be excluded *a priori*: the time between taking the sample and recovery on deck varies from a few minutes for the shallowest stations to somewhat less than an hour for the deepest station. Perhaps the more mobile nematodes move deeper into the sediment. Yet, the similar findings of other authors strengthen the possibility that the trend is real.

Acknowledgements—This project is funded through grant 2.9007.82 'Ecology and Systematics of Marine Organisms' (C. Heip, principal investigator) of the Belgian National Fund for Collective Fundamental Research. KS acknowledges a grant as 'aspirant' of the Belgian National Fund for Scientific Research. We thank D. Van Gansbeke for the determination of CPE values, W. Gyselinck for the making of slides, D. Van Gansbeke and the crew of the R.V. *Dubuisson* (Station de Recherches Sous-Marines et Océanographiques, Calvi, Corsica) for their help in sampling.

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