

Mededelingen van de Koninklijke Academie voor Wetenschappen, Letteren en Schone Kunsten van België

Overdruk uit

VLIZ (vzw)
VLAAMS INSTITUUT VOOR DE ZEE
FLANDERS MARINE INSTITUTE
Oostende - Belgium

Academiae Analecta

2796



Vlaams Instituut voor de Zee
Flanders Marine Institute

AWLSK

Klasse der Wetenschappen, Jaargang 55, 1993, Nr. 2

Paleis der Academiën, Brussel

SIZE SPECTRA
OF NEMATODE ASSEMBLAGES
IN AN EAST AFRICAN MANGROVE

BY

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Keywords : nematodes, biomass, benthic, mangroves, distribution.

ACKNOWLEDGEMENTS

I thank the Belgian Academy for science, Letters and Fine Arts for awarding the Mc Leod prize 1991 to my essay.

This work was financed by the Belgian National Science Foundation (FKFO project 2.0043.88) and the EEC project TS2-0240-C (GDF). I am grateful to the Kenyan Marine Fisheries and Research Institute in Mombasa for providing logistic facilities for the field work and Dr A. Vanreusel and Dr P. Aerts for the technical assistance in Kenya. D. Van Gansbeke, W. Gijssels and D. Schram are thanked for processing the samples, Dr M. Vincx for help with the statistical tests and Prof. Dr A. Coomans, Dr M. Vincx and Dr A. Vanreusel for a critical reading of the manuscript.

ABSTRACT

The size spectra and biomass of the nematode assemblages in the sediments of *Avicennia marina*, *Bruguiera gymnorrhiza*, *Cerriops tagal* and *Sonneratia alba* at Gazi Bay (Kenya), are described. Weighted mean length (resp. dry weight) of the nematodes varies from 0.543 to 1.367 mm (resp. 0.10 to 0.19 μ g) and differs considerably from geometric and median values. Nematodes become longer (around *Avicennia* and *Sonneratia*) or remain similar in length (around *Bruguiera* and *Cerriops*) with increasing depth into the sediment. Body elongation is suggested to be an adaptation to low oxygen and food supply, which are under the impact of *Uca*-burrows.

Nematode production in the mangroves is found to be regulated by an interaction of density and individual biomass, in which the former plays a dominant role.

INTRODUCTION

Body size and biomass spectra of populations and communities, as well as of individual organisms, are related in many aspects to life-history characteristics (generation time, respiration, dispersion) and have important implications for fundamental ecological concepts (size-related competition and predation, diversity) (Roggen, 1970 ; Fenchel, 1974 ; Hall *et al.*, 1976 ; Blueweiss *et al.*,

1978 ; Peters, 1983 ; Warwick, 1984). With regard to the Sheldon spectrum (Sheldon *et al.*, 1972) a large body of literature covers the biomass spectra of a wide range of benthic communities to establish the consistency in the spectra (Gerlach *et al.*, 1985 ; Schwinghamer, 1981, 1983, 1985 ; Warwick, 1982, 1984 ; Warwick & Joint, 1987 ; Warwick *et al.*, 1986). Yet the size distribution of benthic meiofauna organisms, in particular that of nematodes, has not been investigated extensively (Soetaert & Heip, 1989). Little information is also available on vertical distribution of meiofauna in mangrove sediments (Dye, 1983a ; Nicholas *et al.*, 1991 ; Vanhove *et al.*, 1992). Most studies are restricted to the upper sediment layers, usually without preliminary investigation of depth distribution (Gerlach, 1958 ; Decraemer & Coomans, 1978 ; Hodda & Nicholas, 1985 ; Dye & Lasiak, 1986 ; Lalana-Rueda & Gosselck, 1986 ; Alongi, 1987a,b).

This paper reports on the effect of depth into the sediment on nematode biomass. The study on meiofauna densities and diversities in the mangroves of Gazi Bay is presented in Vanhove *et al.* (1992).

MATERIAL AND METHODS

Sampling was carried out in the mixed mangrove at Gazi Bay circa 50 km south of Mombasa (Fig. 1) (Gallin *et al.*, 1989). The sediments of four mangrove species (*Avicennia marina*, *Bruguiera gymnorrhiza*, *Ceriops tagal*, *Sonneratia alba*) were investigated during spring tide, in the Summer (July) of 1989. Samples were obtained by taking handcores (3.6 cm diameter, 30 cm length) to a depth of 20 cm and split horizontally into 1 cm portions for the upper 5 cm, 2.5 and 5 cm intervals for deeper layers. Each core was preserved in a hot (60°C) 4% formaldehyde solution.

Meiofauna. — Extraction of meiofauna from the sediment (38 µm mesh sieve), examination and counting followed the procedures recommended by McIntyre & Warwick (1984). Separation of roots and detritus from the meiofauna was very difficult and time consuming. For this reason the counting procedure could not be repeated.

Sediment analysis. — One core was used for granulometric analysis. Preliminary drying at 100°C was necessary to remove peat. Sediment contained more than 90% sand. A mechanical shaker was used to pass this sand fraction through a graded series of standard sieves (Buchanan, 1984).

Organic matter. — An additional core was divided in the same intervals as mentioned above (meiofauna) for analysis of organic matter. From each fraction, organic nitrogen was measured applying the chemical Kjeldahl-method (Greiser & Faubel, 1988).

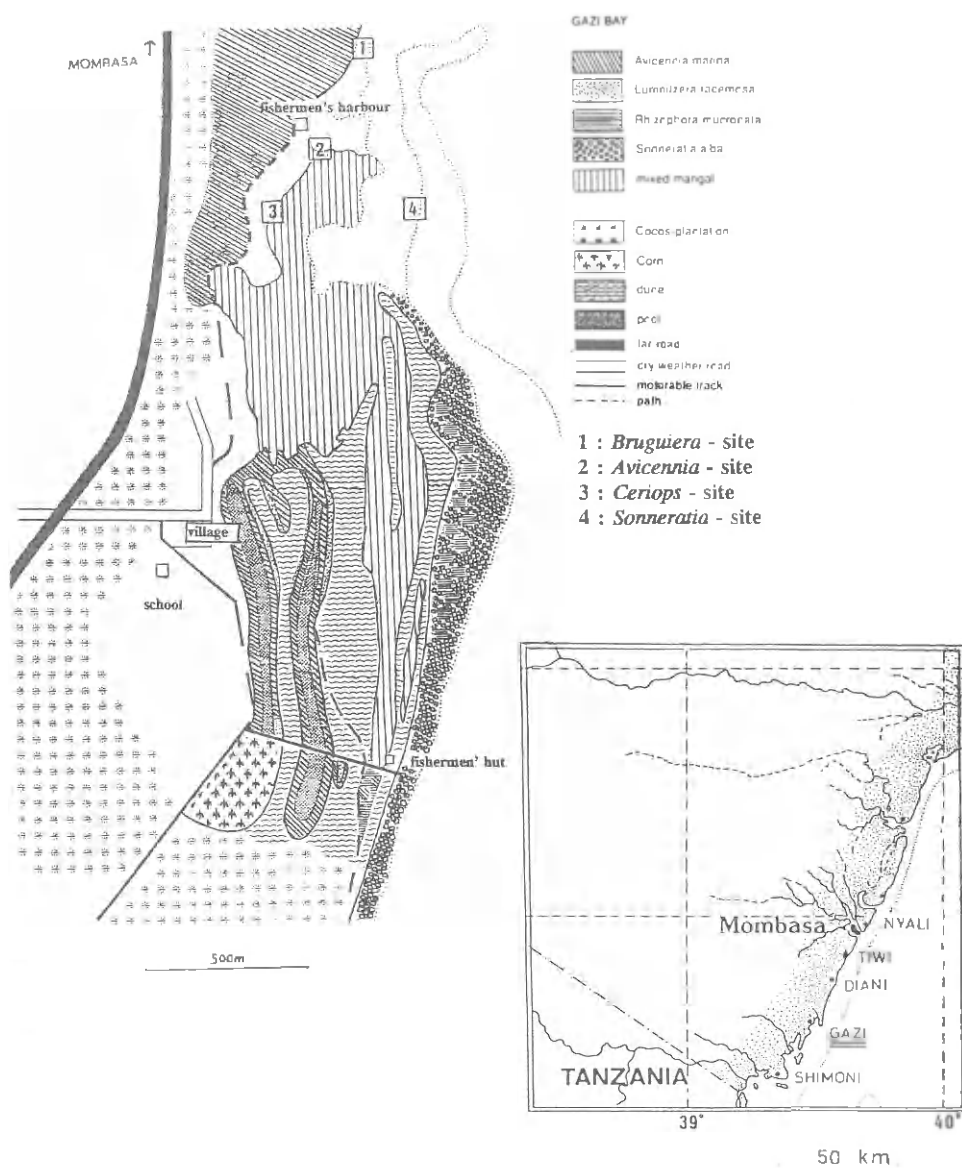


Figure 1. — Location of the four stations in the mangrove of Gazi Bay (after Gallin *et al.*, 1989).

Biomass. — About 50 nematodes encountered in each sediment interval were picked out and mounted in glycerin slides (Seinhorst, 1959). Weights of nematodes were determined from dimensions of length and the square of the maximum width, measured under the camera lucida, using the adjusted method of Andrassy (Soetaert, 1989) and assuming a specific gravity of 1.13 and a dry/wet weight ratio of 0.25.

Data analysis. — The parametric two way ANOVA, combined with a Student's t-test, was used to test length and biomass differences between stations and depths. Correlations were calculated by means of the non-parametric Spearman rank correlation coefficient (Sokal & Rohlf, 1981).

RESULTS

Abiotic factors. — In table 1 granulometric features and concentrations of Kjeldahl-N are shown for the four mangrove stations. Characteristic for *Sonneratia* are the high mud content and organic matter content compared especially to the figures for *Bruguiera*, while *Avicennia* and *Ceriops* occupy an intermediate position. Median grain size shows little variation among the four stations and all sediments are classified as medium sand.

TABLE 1

Characteristics of the sediment and Kjeldahl-N at the four collecting sites.

STATION	<i>Avicennia</i>	<i>Bruguiera</i>	<i>Ceriops</i>	<i>Sonneratia</i>
Median grain size (mm)	0.468	0.324	0.337	0.396
Sediment type	medium sand	medium sand	medium sand	medium sand
% mud	2.46	0.35	1.71	3.37
Kjeldahl-N mg N/100DS	456.11	205.99	450.95	835.51

Meiofauna. — Total densities are high in all four stations varying from 6707 ind. 10 cm⁻² in *Bruguiera* to 1976 ind. 10 cm⁻² in *Ceriops* (Table 2). Nematodes dominate and reach abundances from 53.5% (*Bruguiera*) to 95.1% (*Sonneratia*). Copepod densities, particularly harpacticoids, are low in comparison with nematodes for *Avicennia*, *Ceriops* and *Sonneratia*, but higher densities are recorded in *Bruguiera* (Table 2).

Nematode length. — Weighted mean length of the nematodes varies from 0.543 (*Bruguiera*) to 1.367 mm (*Sonneratia*). Differences between the four stations are significant ($p < 0.05$). *Sonneratia*-nematodes are remarkable larger than other nematodes in Gazi Bay (Table 3).

TABLE 2
Density (ind./10 cm²) and abundance (%) of meiofauna taxa.

STATION	<i>Avicennia</i>	<i>Bruguiera</i>	<i>Ceriops</i>	<i>Sonneratia</i>
TOTAL	3442	6707	1976	2889
NEMATODES				
Density	2329	4205	1709	2555
Abundance	77.9	53.5	85.5	95.1
COPEPODS				
Density	215	1113	61	51
Abundance	6.3	16.6	3.1	1.8
OTHER TAXA				
Abundance	26.1	20.7	10.4	9.8
Ratio c/n (%)	9.2	26.5	3.6	2.0

TABLE 3
Length and weight characteristics of the nematode assemblages at the four stations.

STATION	<i>Avicennia</i>	<i>Bruguiera</i>	<i>Ceriops</i>	<i>Sonneratia</i>
LENGTH (mm)				
Arithmetic mean	0.785	0.612	0.892	1.473
Weighted mean	0.765	0.543	0.857	1.367
Median	0.695	0.502	0.709	1.274
Geometric mean	0.667	0.498	0.733	1.312
DRY WEIGHT (μg)				
Arithmetic mean	0.18	0.10	0.10	0.19
Weighted mean	0.17	0.09	0.09	0.19
Median	0.09	0.04	0.06	0.15
Geometric mean	0.08	0.04	0.06	0.14
TOTAL BIOMASS (mg dwt/10 cm ²)	0.186	0.168	0.103	0.358

As pointed out by Soetaert & Heip (1989) the mean length (resp. individual biomass) is not suitable for comparative purposes. Geometric mean and median length are less sensitive to the presence or absence of extremely large individuals. Geometric mean and median are comparable, but smaller than the first mentioned weighted mean (resp. 0.498-1.312 mm and 0.502-1.274 mm) (Table 3).

— Nematodes tend to be longer with increasing depth into the sediment of *Avicennia* (the depth 2-3 cm not taken into account) and are so significantly at $p < 0.05$, except for the two sediment layers between 4 and 7.5 cm (Fig. 2B). The same, though not significant trend can be seen in *Sonneratia*-sediments (Fig. 3E). For *Bruguiera* and *Cerriops* lengths are rather similar, ranging from about 0.5 mm to a maximum of 1.25 mm. A minimum value is obtained in both stations at 4-5 cm, it is significantly ($p < 0.05$) different from the other sediment intervals (Figs 2E, 3B). Except for *Cerriops*, densities and lengths follow a complementary pattern (Figs 2A & B, 2D & E; 3D & E), with a high negatively significant correlation for *Avicennia* and *Sonneratia* ($r_s = -0.883$ and -0.783 for median length; -0.800 and -0.833 for mean length, df 9) and significant for *Bruguiera* ($r_s = -0.667$ for both mean and median length, df 8).

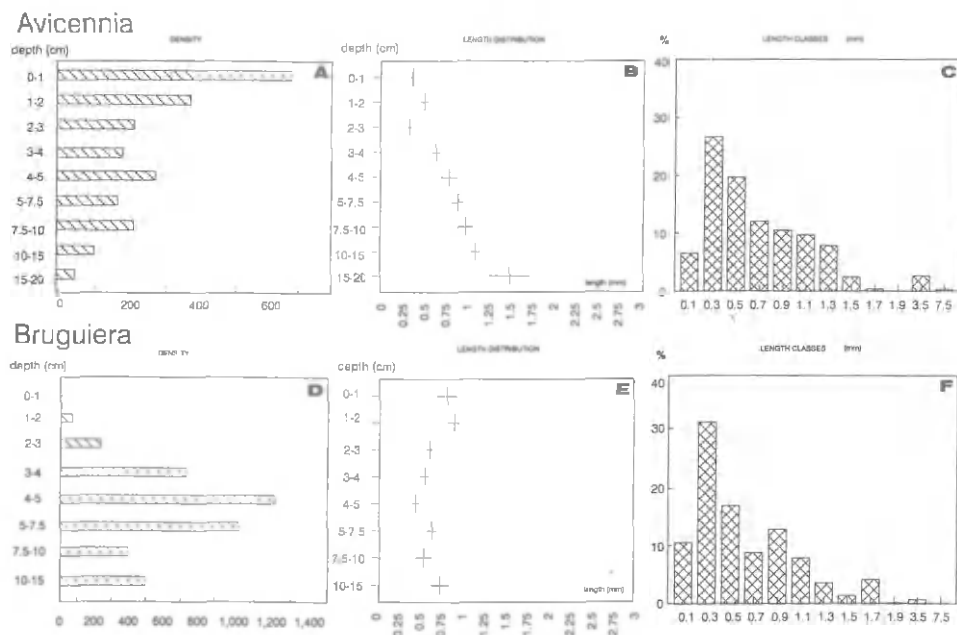


Figure 2. — Characteristics of the nematode assemblages for the sediments of *Avicennia* (A-C) and *Bruguiera* (D-F): A),D) density (ind./10 cm²) and B),E) length (mean $\pm$ S.E.) (mm) distributions at the different sediment intervals; C),F) length-frequency distributions.

— The length frequency distributions (Figs 2C, 2F, 3C) show a clear modal class in *Avicennia*, *Bruguiera* and *Ceriops*, respectively 0.2-0.4 mm for the first two stations and 0.6-0.8 mm at *Ceriops*. A long tail extends into the larger sizes. *Sonneratia* sediments contain larger nematodes, but the length-frequency curve (Fig. 3F) is not strongly skewed as for the other sediments. Consequently no obvious modal class can be discerned.

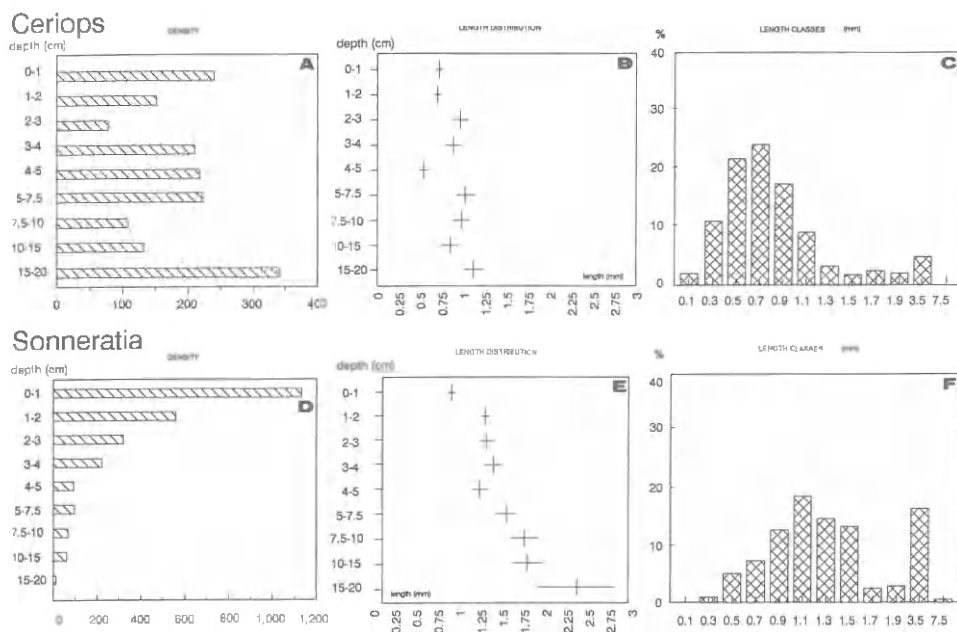


Figure 3. — Characteristics of the nematode assemblages for the sediments of *Ceriops* (A-C) and *Sonneratia* (D-F): A), D) density (ind./10 cm²) and B), E) length (mean $\pm$ S.E.) (mm) distributions at the different sediment intervals; C), F) length-frequency distributions.

Nematode biomass. — Mean nematode dry weights (Table 3) vary from 0.10 to 0.19 μ g. As for the nematode length, geometric mean and median are lower than the weighted mean, though the magnitude of difference is much larger: *Avicennia* and *Bruguiera* data are only half as high. Geometric mean values vary between 0.04 and 0.14 μ g.

Total biomass calculations based on geometric mean individual length vary between 0.103 and 0.358 g dwt/10 cm². Biomass and density are not significantly related.

Relation biotic-abiotic factors. — The main source of variation in meiofauna distributions one would expect, is due to changing sediment characteristics. Therefore correlation tests of nematode length (mean and median) and biomass with mud percentage and organic N were conducted for each depth into the

sediment. Analysis revealed that 1) nematode lengths around *Avicennia* are significantly positively related ($r_s = 0.700$, df 9) to Kjeldahl-N and negatively ($r_s = -0.667$ for median ; $r_s = -0.767$ for mean length) to mud percentage ; 2) nematode lengths around *Bruguiera* are significantly negatively correlated ($r_s = -0.714$ df7) with Kjeldahl-N. Clear trends, however, could not be detected.

In conclusion :

1) *Avicennia*, *Bruguiera* and *Ceriops* sediments have nematodes with comparable length ; *Sonneratia* sediments contain larger individuals. 2) Nematodes (and other taxa) still reach high densities in sediment intervals which are usually not investigated (up to 20 cm deep and more). 3) With regard to nematode lengths there exists a "deeper-longer" relationship in two sediments (*Avicennia* and *Sonneratia*), while for the other sediments (*Bruguiera* and *Ceriops*) there is no clear trend. 4) Except for *Ceriops*, densities and lengths of nematodes follow opposite patterns. 5) The length-frequency distributions are, except for *Sonneratia*-nematodes, strongly skewed, with a long tail towards the larger sizes. 6) Arithmetic mean can be remarkably different from geometric mean and median. 7) Length nor biomass spectra are clearly related to sediment characteristics.

DISCUSSION

Length and biomass of nematodes from Gazi versus these from other regions. — The sediments of Gazi Bay are inhabited by small nematodes, which have a mean individual dry weight of 0.09-0.19 μg dw. This is slightly higher than in deep-sea nematode communities (Soetaert & Heip, 1989 : 0.04-0.10 μg dw), but lower than dry weights measured in temperate, shallow regions (Vanreusel, 1990 : 0.09-2.46 μg dw, mean 0.402 μg).

Total nematode biomass in this study is comparable with other mangrove regions (Table 4). The higher figures obtained by Dye (1983 a,b) probably would lie in the same range when only nematodes had been taken into account.

Production estimates vary from 0.6 to 1.7 g C/m²/year. Since there is as yet no better method to determine secondary production of nematodes of tropical areas, the generally applied P/B ratio 9 is used for production estimates, despite the criticism formulated by Vranken & Heip (1986). Production calculations were based on different mangrove biomass data from the literature, using a P/B = 9 and assuming a carbon ratio of 40% (Table 4). Logically (as production estimates are based on total biomass) the data from Gazi are comparable to those from other mangroves.

TABLE 4

Biomass and production estimates in mangrove communities (see text).

Reference	Locality	Biomass (dwt) (mg / 10 cm ²)	Production (gC / m ² / yr)	Comment
this study	Gazi Bay, Kenya	0.171-0.485 0.103-0.358	0.616-1.746 0.371-1.289	mean biomass geometric biomass
Schrijvers, 1991	Gazi Bay, Kenya	0.367-0.453	1.321-1.631	mean biomass
Nicholas <i>et. al.</i> , 1991	Waterfall creek, Australia	0.019-0.888	0.068-3.197	
Dye, 1983 (a)	Transkei, S. Africa	0.370-2.330	1.332-8.388	based on total meiofauna
Dye, 1983 (b)	Transkei, S. Africa	0.196-1.073	0.706-3.863	based on total meiofauna

Deep-sea benthic communities mainly depend on the detrital fall out ("detritus rain") from above to feed on, which results in the presence of small animals. Mangrove organisms, however, are surrounded by high amounts of organic matter (usually associated with a lot of micro-organisms). Consequently they are not restricted by a limited, "accidental" food supply. Mangrove nematodes may use these mass food resources to enhance production not in terms of individual biomass, which is even below other shallow regions, but in high densities. Moreover, nematode biomass decreases with increasing density in *Avicennia*, *Bruguiera* and *Sonneratia* sediments as mentioned earlier.

Vanreusel (1990) found a negative correlation between chlorophyll-a content and mean individual nematode biomass, confirming the hypothesis of Pearson & Rosenberg (1987), which states that food availability is the most fundamental variable determining biomass, production and diversity of benthic organisms. Such investigations were not considered in this study, but are required to support the results.

Biological variables related to sediment. — In general, sediment characteristics are primary factors affecting the abundance, species composition and body size of meiofauna.

In this context the structure and dimensions of the interstices, the organic content and the available oxygen are of fundamental importance. Although no overall statistical correlation exists between density and biomass of nematodes on the one hand, and sediment characteristics on the other hand, some trends have become clear after comparing both variables. In sediments with high mud and organic matter content, high densities and biomass but low taxon diversity is observed (*Sonneratia*) and vice versa (*Bruguiera*, *Avicennia*) (Vanhove *et al.*, 1992). As in most muddy habitats, copepods do not

withstand high silt fractions whilst nematodes are remarkable tolerant. The differences in length between the nematodes of *Sonneratia* and these from other stations (Table 3) may also be related to the high silt content in the former sediment. Variations in length result from physical restrictions imposed by the sediment interstices on body size.

The characteristic *Sonneratia* nematode density pattern (high densities in the upper layer, followed by a rapid decline deeper in the sediment), the high individual nematode length relatively to other sediments, combined with the increase toward deeper layers (also in *Avicennia*), are probably related to some extent with low oxygen conditions (RPD layer was estimated visually from the colourshift near the surface). This is confirmed by the low copepod/nematode ratio (Table 2), as harpacticoids copepods are known to be one of the most sensitive taxa to decreased oxygen.

The tendency of nematodes to become longer with sediment depth is regularly found in tropical as well as in temperate regions (Boaden 1974, 1975 ; Vivier, 1978 ; Jensen, 1986 ; Soetaert & Heip, 1989), though the factor(s) underlying these observations are not well understood. One possible metabolic explanation can be found in the length/radius ratio, which relates surface relative to volume, discussed by Jensen (1986). Longer individuals have a larger epidermal uptake surface. This results in a higher diffusion of nutrients and oxygen, which allows the nematode to live in deeper, food and oxygen depleted sediment layers.

Increase in length could be, next to ectosymbiosis with sulfide oxidating chemolithotrophs (Giere *et al.*, 1982 ; Ott & Novak, 1989) or the use of specific enzymes (Morril *et al.*, 1988) an adaptation of the so called "thiobios" (Boaden & Platt, 1971) to the unfavourable stress conditions of deeper, sulfide rich, anaerobic layers.

Soetaert & Heip (1989) have demonstrated that bigger nematodes show no preference to particular sediment layers, whereas small individuals ($< 500 \mu\text{m}$) rather avoid greater depths. The observed length increase with depth suggests that smaller nematodes are unable to penetrate into the compact deeper layers.

Biological variables with regard to the macrofauna. — As discussed in Vanhove *et al.* (1992). *Uca*-burrows are a prevalent aspect in the mangroves of Gazi Bay. Densities and biomass in the salt marshes investigated by DePatra & Levin (1989) are affected by these biogenic depressions and seem to be of great importance in the Kenyan mangroves too. The occurrence of still high densities and biomass in deeper layers in the sediments studied, could be explained in this context. Higher numbers of meiofauna probably live in close association with the burrows, which form a structural heterogeneity of oxygen rich pockets in oxygen depleted surroundings. With the density-length relationship in mind (see above), the consistent occurrence of small nematodes at 4-5 cm in all sediments, except for *Avicennia*, might be related to the bottom

of the *Uca*-burrows, which there serves quasi as a surface layer. When *Uca*-burrows are absent (e.g. *Sonneratia* sediments) meiofauna tends to be restricted to the upper layers, as food resources (organic matter and bacteria) are more plentiful in the surface layer than further down.

Conclusion

The relation between nematode length and some possible regulation factors presented in this preliminary study indicates that there exist an optimal nematode size for any given ecological situation. However, we are still far from a size efficiency hypothesis as proposed for zooplankton communities (Hall *et al.*, 1976).

SAMENVATTING

De nematodengemeenschappen in de sedimenten van *Avicennia marina*, *Bruguiera gymnorhiza*, *Ceriops tagal* and *Sonneratia alba* in de mangroves van Gazi Bay (Kenya) werden beschreven aan de hand van biomassa en lengtespektra. De gewogen gemiddelde nematodenlengte (resp. het gewogen gemiddelde drooggewicht) varieert tussen 0.543 en 1.367 mm (resp. 0.10 en 0.19 μ g) en verschilt sterk van het geometrisch gemiddelde en de mediaan. De nematoden van *Avicennia* en *Sonneratia* blijken langer te zijn naarmate ze dieper in het sediment voorkomen; *Bruguiera*- en *Ceriops*-nematoden, daarentegen, hebben een min of meer stabiel lengtepatroon in relatie tot de diepte. Waarschijnlijk is de grotere lengte gecorreleerd met lage zuurstof- en voedselconcentraties, die op hun beurt beïnvloed zijn door de aanwezigheid van talrijke wenkkrabben (*Uca*). De gangen van deze dieren maken het immers mogelijk om nutriënten en zuurstof dieper te laten doordringen, wat een positieve impact heeft op lengte en biomassa van de naburig aanwezige nematoden.

De produktie van nematoden wordt gereguleerd door een interactie van densiteit en individuele biomassa. Hierbij zijn de hoge densiteiten in de mangroves van fundamenteel belang.

Hoewel lengte- en biomassaspektra niet statistisch gecorreleerd zijn met Kjeldahl-N en moddergehalte, blijken deze twee abiotische variabelen toch invloed te hebben op de structuur van de nematodegemeenschappen: hoge gehalten hebben een hoge densiteit en biomassa, maar een lage diversiteit tot gevolg.

BIBLIOGRAPHY

- ALONGI, D. M., *Intertidal Zonation and Seasonality of Meiobenthos in Tropical Mangrove Estuaries*, in : "Mar. Biol.", 95, 1987a, 447-458.
- ALONGI, D. M., *Inter-estuary Variation and Intertidal Zonation of Free-Living Nematode Communities in Tropical Mangrove Systems*, in : "Mar. Ecol. Prog. Ser.", 40, 1987b, 103-114.
- BLUEWEISS, L., FOX, H., KUDZMA, V., NAKASHIMA, D., PETERS R. & SAMS, S., *Relationship between Body Size and some Life History Parameters*, in : "Oecologia", 37, 1978, 257-272.
- BOADEN, P. J. S., *Three New Thiobiotic Gastrotricha*, in : "Cah. Biol. mar.", 15, 1974, 367-378.
- BOADEN, P. J. S., *Anaerobiosis, Meiofauna and Early Metazoan Evolution*, in : "Zool. Scr.", 4, 1975, 21-24.
- BOADEN, P. J. S., PLATT, H. M., *Daily Migration Patterns in an Intertidal Meiobenthic Community*, in : "Thalassia jugosl.", 7, 1971, 1-12.
- BUCHANAN, J. B., *Sediment Analysis*, in : "Methods for the Study of Marine Benthos", N. A. Holme & McIntyre A. D. (eds). IBP No 16, 2nd edition. Blackwell Scientific Publications, 1984, 41-65.
- DECRAEMER, W., COOMANS, A., *Scientific Report on the Belgian Expedition to the Great Barrier Reef in 1967. Nematodes XII. Ecological Notes on the Nematode Fauna in and around Lizard Island*, in : "Aust. J. mar. Freshwat. Res.", 29, 1978, 497-508.
- DEPATRA, K. D., LEVIN L. A., *Evidence of the Passive Deposition of Meiofauna into Fiddler Crab Burrows*, in : "J. exp. mar. Biol. Ecol.", 125, 1989, 173-192.
- DYE, A. H., *Vertical and Horizontal Distribution of Meiofauna in Mangrove Sediments in Transkei, Southern Africa*, in : "Estuar. Coast. Shelf Sci", 16, 1983a, 591-598.
- DYE, A. H., *Composition and Seasonal Fluctuations on Meiofauna in a Southern African Mangrove Estuary*, in : "Mar. Biol.", 73, 1983b, 165-177.
- DYE, A. H., LASIAK T. A., *Microbenthos, Meiobenthos and Fiddler Crabs : Trophic Interactions in a Typical Mangrove Sediment*, in : "Mar. Ecol. Prog. Ser.", 32, 1986, 259-264.
- FENCHEL, T., *Intrinsic Rate of Natural Increase : the Relationship with Body Size*, in : "Oecologia", 14, 1974, 317-326.
- GALLIN, E., COPPEJANS E. & BEECKMAN, H., *The Mangrove Vegetation of Gazi Bay (Kenya)*, in : "Bull. Soc. r. Bot. Belg.", 122, 1989, 197-207.
- GERLACH, S. A., *Die Mangroveregion tropischer Küsten als Lebensraum*, in : "Z. Morph. Ökol. Tiere", 46, 1958, 636-730.
- GERLACH, S. A., HAHN, A. E. & SCHRAGE, M., *Size Spectra of Benthic Biomass and Metabolism*, in : "Mar. Ecol. Prog. Ser.", 26, 1985, 161-173.
- GIERE, O., LIEBEZEIT, G. & DAWSON, R., *Habitat Conditions and Distribution Patterns of the Gutless Oligochaete Phallo-drillius leukodermatus*, in : "Mar. Ecol. Prog. Ser.", 8, 1982, 291-299.
- GREISER, N., FAUBEL, A., *Biotic Factors*, in : "Introduction to the Study of Meiofauna", R. P. Higgins & Thiel H. (eds). , 1988, 79-114.

- HALL, D. J., THRELKELD, S. T., BURNS, C. W. & CROWLEY, P. H., *The Size-Efficiency Hypothesis and the Size Structure of Zooplankton Communities*, in: "Ann. Rev. Ecol. Syst.", 7, 1976, 177-208.
- HIGGINS, R. P., THIEL, H., *Introduction to the Study of Meiofauna*. Smithsonian Institution Press Washington, D.C. London, 1988, 488 p.
- HODDA, M., NICHOLAS, W. L., *Meiofauna Associated with Mangroves in the Hunter River Estuary and Fullerton Cove, South-Eastern Australia*, in: "Aust. J. mar. Freshwat. Res.", 36, 1985, 41-50.
- HOLME, N. A., MCINTYRE, A. D., *Methods for the Study of Marine Benthos*, IBP-Handbook No 16, Blackwell Sci. Publ., Oxford, 1984, 387 p.
- JENSEN, P., *Nematode Fauna in the Sulphide-Rich Brine Seep and Adjacent Bottoms of the East Flower Garden, NW Gulf of Mexico*, in: "Mar. Biol.", 92, 1986, 489-503.
- LALANA-RUEDA, R., GOSSELCK, F., *Investigations of the Benthos of Mangrove Coastal Lagoons in Southern Cuba*, in: "Hydrobiologia", 71, 1986, 779-794.
- MCINTYRE, A. D., WARWICK, R. M., *Meiofauna Techniques*, in: "Methods for the study of marine benthos", N. A. Holme & McIntyre A. D. (eds). IBP No 16, 2nd edition. Blackwell Scientific Publications, 1984, 217-244.
- MORRIL, A. C., POWELL, E. N., BIDIGARE, R. R. & SHICK J. M., *Adaptations to the Life in the Sulfide System: a Comparison of Oxygen Detoxifying Enzymes in Thiobiotic and Oxybiotic Meiofauna (and freshwater planarians)*, in: "J. Comp. Physiol. B.", 158, 1988, 335-344.
- NICHOLAS, W. L., ELEK, W. I., STEWART A. C. & MARPLES, T. G., *The Nematode Fauna of a Temperate Australian Mangrove Mudflat: its Population Density, Diversity and Distribution*, in: "Hydrobiologia", 209, 1991, 13-27.
- OTT, J. A., NOVAK, R., *Living at an Interface: Meiofauna at the Oxygen/Sulphide Boundary of Marine Sediments*, in: "Reproduction, genetics and distribution of marine organisms", J. S. Ryland & Tayler P. A. (eds). Olsen & Olsen, Denmark. Proceedings of the 23rd European Marine Biology Symposium, 1989, 415-422.
- PEARSON, T. H., ROSENBERG, R., *Feast and Famine: Structuring Factors in Marine Benthic Communities*, in: "Organization of communities. Past and present", J. H. R. Gee & Giller P. S. (eds). Blackwell Scientific Publications, 1987, 373-375.
- PETERS, R. H., *The Ecological Implications of Body Size*. Cambridge studies in ecology, 1983, 329 p.
- ROGGEN, D. R., *Functional Aspects of the Lower Size — Limit of Nematodes*, in: "Nematologica", 16, 1970, 532-536.
- SCHRIJVERS, J., *Ecologische Studie van het Benthos van de Mangroves en Aanpalende Stranden van Gazi Bay, Kenia*. Masters thesis, University of Gent, 1991, 161 p. (unpublished).
- SCHWINGHAMER, P., *Characteristic Size Distributions of Integral Benthic Communities*, in: "Can. J. Fish. Aq. Sc.", 38, 1981, 1255-1263.
- SCHWINGHAMER, P., *Generating Ecological Hypotheses from Biomass Spectra using Causal Analysis: a Benthic Example*, in: "Mar. Ecol. Prog. Ser.", 13, 1983, 151-166.

- SCHWINGHAMER, P., *Observations on Size-Structure and Pelagic Coupling of some Shelf and Abyssal Benthic Communities*, in : "Proceedings of the 19th European Marine Biology Symposium", Gibbs (ed.), Cambridge University Press, Cambridge, 1985, 347-359.
- SEINHORST, J., *A rapid Method for the Transfer of Nematodes from Fixative to Anhydrous Glycerin*, in : "Nematologica", 4, 1959, 67-69.
- SHELDON, R. W., PRAKASH, A. & SUTCLIFFE, W. H., *The Size Distribution of Particles in the Ocean*, in : "Limnol. Oceanogr.", 17, 1972, 327-340.
- SOETAERT, K., *Een Ecologisch-Systematische Studie van de Diepzee Meiofauna en Nematodengemeenschappen in de Westelijke Middellandse Zee*. Ph.D. Thesis, University of Gent, 1989, 306 p. (unpublished).
- SOETAERT, K., HEIP, C., *The Size Structure of Nematode Assemblages along a Mediterranean Deep-Sea Transect*, in : "Deep-Sea Research", 36(1), 1989, 93-102.
- SOKAL, R. R., ROHLF, F. J., *Biometry*, W.H. Freeman and Company, San Francisco, 1981, 2nd edition, 859 p.
- VANHOVE, S., VINCX, M., VAN GANSBEKE, D., GIJSELINCK, W. & SCHRAM, D., *The Meiobenthos of Five Mangrove Vegetation Types in Gazi Bay, Kenya*, in : "Hydrobiologia", 247, 1992, 99-108.
- VANREUSEL, A., *Ecology of the Free-Living Nematodes from the Voordelta (Southern Bight of the North Sea). I. Species Composition and Structure of the Nematode Communities*, in : "Cah. Biol. Mar.", 31, 1990, 439-462.
- VIVIER, M. H., *Influence d'un Déversement Industriel Profond sur la Nématofaune (Canyon de Casidaigne, Méditerranée)*, in : "Tethys", 8, 1978, 307-321.
- V Ranken, G., HEIP, C., *The Productivity of Marine Nematodes*, in : "Ophelia", 26, 1986, 429-442.
- WARWICK, R. M., *The Partitioning of Secondary Production among Species in Benthic Communities*, in : "Neth. J. Sea Res.", 16, 1982, 1-16.
- WARWICK, R. M., *Species Size Distribution in Marine Benthic Communities*, in : "Oecologia", 61, 1984, 32-41.
- WARWICK, R. M., JOINT, I. R., *The size Distribution of Organisms in the Celtic Sea : from Bacteria to Metazoa*, in : "Oecologia", 73, 1987, 185-191.
- WARWICK, R. M., COLLINS, N. R., GEE, J. M. & GEORGE, G. L., *Species Size Distributions of Benthic and Pelagic Metazoa : Evidence for Interaction?*, in : "Mar. Ecol. Prog. Ser.", 34, 1986, 63-68.