Nematode Community Structure Along a Mediterranean Shelf-slope Gradient

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Abstract. Nematode assemblages along a Mediterranean depth transect (160–1220 m) and vertically in the sediment were investigated. The station at the edge of the continental shelf (160 m) was distinctly different from those situated on the continental slope (280–1220 m). On the slope, nematode communities in the upper centimetre differed significantly from communities in the deeper sediment layers, which were dominated by fewer and larger species. Vertical segregation could be a factor explaining the coexistence of several species belonging to the genus *Sabatieria*, with larger species penetrating deeper into the sediment. Clear differences in buccal morphology suggest food resource partitioning as the dominant factor promoting coexistence of several species belonging to the other dominant genus, *Acantholaimus*.

Problem

Nematodes constitute the most abundant metazoan organisms in the deep sea, and their relative abundance increases disproportionally with increasing depth (THIEL, 1975). Yet little is known about the composition of the nematode fauna in deep-sea communities. Reasons for this include the relatively large numbers of individuals, taxonomic difficulties caused by the high diversity, the small numbers of species already described, and the small size of the individuals.

Quantitative distributions of nematode species in the deep sea have been reported for the North Carolina continental slope (50–2500 m; TIETJEN, 1971, 1976), the Venezuela Basin (3400 m; TIETJEN, 1984), Hatteras abyssal plain, Puerto Rico Trench (2217–8380 m; TIETJEN, 1989), the Scotian Rise (Hebble, 4626 m; THISTLE & SHERMAN, 1985), the Bay of Biscay (1920–4725 m; DINET & VIVIER, 1979), the Norwegian deep sea (970–3294 m; JENSEN, 1988), the Mediterranean Cassidaigne Canyon (310–650 m; VITIELLO, 1976; 168–580 m; VIVIER, 1978), and Planier Canyon (320–580 m; VITIELLO, 1976) near Marseille.

While there are very few data on the bathymetric distribution of meiofaunal

organisms, data concerning the zonation of nematodes with depth into the sediment are even more scanty. VIVIER (1978) reported on the differential vertical distribution of some species in a Mediterranean canyon; THISTLE & SHERMAN (1985) provided some evidence on the vertical segregation of nematodes based on their tail types; JENSEN (1988) mentioned the occurrence of some larger-sized species in the deeper layers of the sediment in one station of the deep Norwegian Sea; SOETAERT & HEIP (1989) showed that nematodes tended to be longer deeper into the sediment along a Mediterranean slope.

In this paper the nematode taxonomic composition is investigated both along a Mediterranean shelf-slope transect and vertically into the sediment.

The distribution of meiobenthic taxa as well as of nematode size and diversity along the same transect and in an adjacent canyon were described in previous papers (SOETAERT & HEIP, 1989; SOETAERT & HEIP, 1990; SOETAERT et al., 1991a, b). Meiobenthic density was much lower along the transect compared to the canyon sites; nematodes were dominant at all stations (SOETAERT et al., 1991a). Nematodes were very small all along the transect; they became significantly smaller with increasing water depth, but increased in size with depth into the sediment (SOETAERT & HEIP, 1989). There was no clear trend of nematode diversity with water depth; nematode communities along the transect were generally very diverse, although less than in the Bay of Biscay (SOETAERT et al., 1991b). A comparison of the generic composition observed in this study with other sites is the topic of another paper (SOETAERT & HEIP, 1995).

Material and Methods

In September 1985, six stations were sampled along a depth transect (160–1220 m) off Calvi (Corsica) in the Ligurian part of the Western Mediterranean (Fig. 1; Table 1). Bottom samples were taken with a small REINECK box-corer (170 cm^2), which was modified to avoid loss of interstitial water. Because of the bow wave that precedes a box corer, some of the surface-living animals could have been lost. Two cylindrical cores (10 cm^2) were taken for faunal analysis and horizontally split into slices (the upper centimetre into two 0.5 cm thick slices, the remainder of the sediment column into 1 cm slices). The samples were fixed with a hot (70 °C), 4% formaldehyde solution and poured over a sieve with a mesh size of 38 μm. The fauna was extracted by means of centrifugation with Ludox (HEIP et al., 1985). After staining with Rose Bengal, all nematodes were picked out and placed onto slides for identification.

Nematode community structure was analysed by means of the BRAY-CURTIS similarity coefficient, and a dendrogram was made by group-average clustering (HEIP et al., 1988). A detrended correspondence analysis (D.C.A. ordination; HILL, 1979) was used to group similar stations together. Both

Table 1. Position and sampling date of the stations.

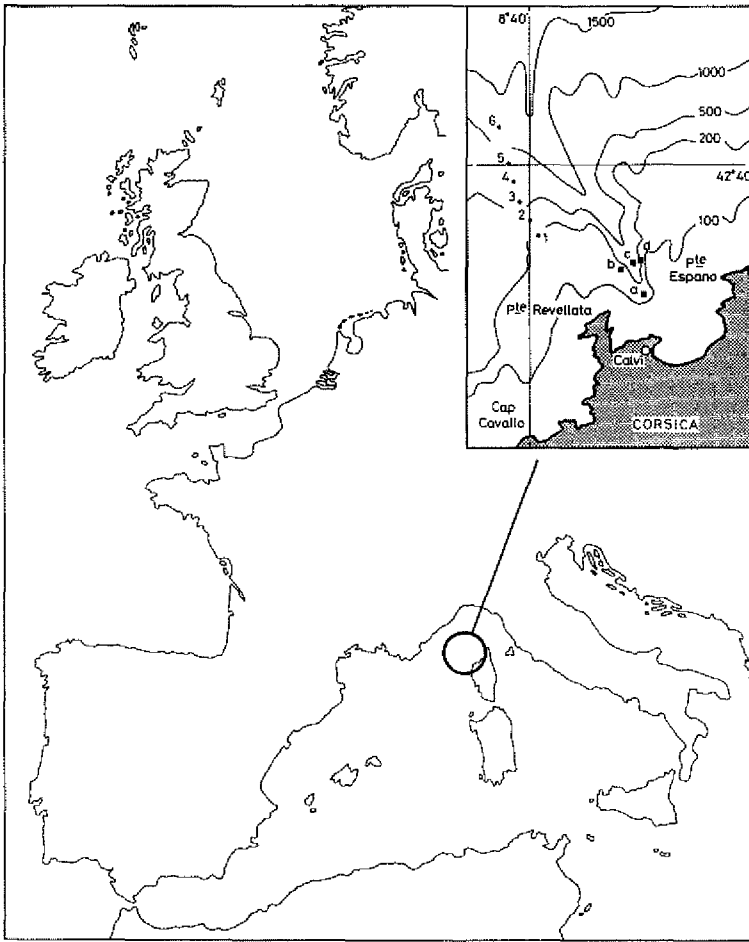| station no	depth m	date (1985)	latitude (N)	longitude (E)
1	160	18.09	42° 37.3′	8° 40.3′
2	280	20.09	42° 38.0′	8° 40.0′
3	530	20.09	42° 38.5′	8° 39.6′
4	820	18.09	42° 39.4′	8° 39.4′
5	990	18.09	42° 39.9′	8° 39.2′
6	1220	18.09	42° 41.1′	8° 38.5′

Fig. 1. Position of the stations. See Table 1 for complete description.

the vertically integrated nematode communities [indiv. $\cdot (10\ cm^2)^{-1}$] and the nematode concentration [indiv. $\cdot (10\ cm^3)^{-1}$] in the different sediment slices were examined. As the number of individuals deeper than 2 cm was limited, the average of the 2–5 cm layer was used.

Results

1. Composition of the nematode fauna

A total of about 4500 individuals belonging to 419 species, 108 genera, and 36 families was identified; 71 groups could only be identified on the genus level. Only 65 species were already described (Tables 2 and 3), either from this transect (21 species), from a Mediterranean canyon, or from other deep-sea sites (36 species).

One species was reported from the Black Sea (SERGEEVA, 1976). The other known species are either ubiquists or poorly described.

2. Community analysis of the vertically integrated samples

The clustering based on the vertically integrated samples separated first the two replicates on the shallowest station (160 m) (Fig. 2). In the remaining group, the stations at 280 m and 530 m and those from 820 to 1220 m formed groups with high similarity. More or less similar results were obtained by means of the detrended correspondence analysis. The 160 m station was distinctly separated from the others. The first D.C.A. axis correlated significantly with station depth (rank correlation coefficient = 0.943, P = 0.02). The eigenvalue of this first axis was much higher than that of the subsequent axes (0.63 versus 0.26, 0.13, and 0.04, respectively), indicating the importance of depth-related environmental factors in explaining the variability in the data set.

3. Horizontal and vertical community patterns

A cluster analysis based on nematode species concentrations per sediment layer [indv. $\cdot (10 \text{ cm}^3)^{-1}$] first separated the entire sediment column of the shallowest station (160 m) (Fig. 3). Most individuals in this station belonged to the species *Comesa* sp.1, *Monhystrella* sp. 1, *Richtersia heipi*, and *Sabatieria* sp. 5. In the remaining group, the sediment layers at 0–1 cm depth were separated from the 1–5 cm layers. Within the upper one-centimetre group, the stations at 280 m and 530 m and those below 820 m formed two distinct clusters. *Sabatieria* sp. 2 was one of the most important species in all the stations below 200 m, but was significantly more abundant in the deeper layers of the sediment. *Monhysteridae* sp. 3 was prominent in the 820–1220 m group at all sediment depths.

As this pattern could have been caused by density differences (density is highest in the upper centimetre) rather than by a different taxonomic composition, the same analysis was done with relative abundances per sediment slice rather than concentrations. The results (not depicted) were very comparable and only four sediment slices were 'misplaced' (*i.e.*, 1220 m A 0.5–1 cm and 820 m A 0.5–1 cm were 'misplaced' in the 280–1220 m 1–5 cm group; 280 m A 1–2 cm and 280 m B 1–2 cm were 'misplaced' in the 280–530 m 0–1 cm group).

The difference in nematode specific composition between the sediment layers for the 280 m–1220 m stations is depicted in Fig. 4 for the most abundant species. In the upper layer, many nematode species are relatively abundant and none is clearly dominant. Deeper than 1 cm some of these species become dominant and can comprise more than 5 % of the nematode community on average (*Sabatieria* sp. 2, *Syringolaimus* sp. 1, *Monhysteridae* sp.3).

Table 2. % abundance of nematode genera and families along the transect, with indication of the mean % abundance and the total number of species (n).

genus	M160	M280	M530	M820	M990	M1220	mean%	n
Acantholaimus	**	***	***	***	***	***	5.01	17
Actinonema	*	*	*	*	*	*	0.83	3
Aegialoalaimus	*	*	*	*	**	***	1.74	3
Amphimonhystrella	*	**	***	***	***	***	3.10	4
Anticoma	—	--	—	—	*	—	0.02	1
Antomicron	*	—	*	*	—	*	0.20	1
Aponema	—	..	*	*	*	*	0.22	2
Araeolaimida indet.	*	*	*	*	*	*	0.35	2
Batheurystomina	—	*	—	....	—	....	0.04	1
Bolbolaimus	**	**	*	—	—	—	0.99	2
Calomicrolaimus	*	*	*	*	*	*	1.70	4
Camacolaimus	*	*	*	—	*	*	0.39	5
Campylaimus	*	*	*	*	*	—	0.76	4
Ceramonema	*	*	*	*	*	*	0.84	9
Cervonema	*	*	*	*	*	*	0.91	5
Chromadoridae indet.	**	*	*	*	....	*	1.04	5
Comesa	*****	*	....	—	....	—	4.51	4
Comesomatidae indet.	—	—	—	—	—	*	0.02	—
Cyatholaiminae indet.	*	—	—	*	*	*	0.30	1
Cyatholaimus	*	*	—	...	—	–	0.19	1
Daptonema	**	*	**	*	**	**	2.15	5
Dasynemoides	*	*	*	....	*	*	0.22	5
Deontolaimus	—	*	*	*	—	...	0.29	1
Desmodora	—	*	—	....	—	....	0.12	3
Desmodorella	*	*	—	....	*	—	0.43	2
Desmodorinae indet.	*	—	—	....	—	..	0.10	1
Desmoscolecidae indet.	—	*	*	*	*	*	0.44	—
Desmoscolex	*	**	***	**	**	*	2.50	33
Dichromadora	*	*	*	***	***	**	2.63	3
Diplopeltoides	...	*	*	*	**	**	1.07	8
Diplopeltula	*	*	*	**	*	*	1.27	12
Disconema	*	—	....	—	...	—	0.14	2
Draconema	*	*	....	*	...	—	0.14	1
Elzalia	*	—	...	—	...	—	0.11	1
Enoplida indet.	—	—	*	*	—	--	0.04	—
Epsilonema	*	—	....	—	...	—	0.04	1
Eubostrichus	*	—	...	—	—	—	0.02	1
Fenestrolaimus	—	—	*	*	—	—	0.04	1
Filipjevia	—	*	—	—	—	—	0.02	1
Gammanema	*	*	—	—	—	—	0.10	1
Glochinematinae indet.	—	...	—	—	*	—	0.02	1
Gomphionchus	—	*	—	—	—	—	0.10	1
Greeffiella	—	...	—	...	—	*	0.04	1
Halalaimus	**	**	***	**	***	**	3.61	38
Halichoanolaimus	*	*	*	*	*	*	0.39	2
Haliplectus	—	...	—	....	*	*	0.19	1
Hopperia	—	*	*	*	*	*	0.64	1
Hypodontolaimus	*	*	*	*	*	...	0.22	2
Innocuonema	—	*	—	...	—	...	0.02	1
Ixonema	*	*	*	*	—	...	0.56	1
Laimella	*	*	*	*	*	*	0.29	3
Ledovitia	*	—	*	*	*	*	0.32	1
Leptolaimoides	*	*	*	*	*	**	0.76	6

Table 2. (*continued*)

genus	M160	M280	M530	M820	M990	M1220	mean%	n
Leptolaimus	*	**	**	**	***	*	2.42	14
Leptosomatidae indet.	*	*	—	—	*	*	0.26	4
Linhomoeidae indet.	**	*	*	*	*	*	0.75	2
Litinium	*	*	*	*	*	*	0.45	4
Longicyatholaimus	*	*	*	*	*	*	0.58	3
Marylynnia	*	*	...	...	*	*	0.14	2
Metacyatholaimus	*	*	*	*	*	*	1.17	6
Metadasynemella	—	*	*	*	...	—	0.16	2
Metalinhomoeus	—	—	...	...	..	*	0.02	1
Metasphaerolaimus	*	*	*	**	*	*	1.02	4
Microlaiminae indet.	**	—	—	...	...	..	0.52	2
Microlaimus	**	***	*	...	*	..	1.77	4
Minolaimus	...	*	*	*	...	*	0.11	2
Molgolaimus	**	****	*	*	*	*	2.78	6
Monhysteridae indet.	***	***	***	****	****	*****	10.05	27
Monhystrella	***	*	—	—	--	...	1.45	1
Namolaimus	...	*	*	*	*	*	0.38	1
Nematoda indet.	**	*	**	**	*	*	2.29	5
Odontophora	*	..	*	—	*	—	0.17	2
Onyx	...	..	...	*	—	—	0.02	1
Oxystomina	*	**	**	*	*	*	1.43	1
Oxystominidae indet.	*	*	*	*	*	**	0.57	4
Paradesmodora	*	.....	..	...	—	—	0.29	1
Paramesacanthion	*	*	*	*	*	—	0.30	5
Paramicrolaimus	*	...	...	..	...	—	0.05	1
Paramonohystera	*	...	...	...	—	—	0.02	1
Pararaeolaimus	--	*	*	*	**	*	0.81	2
Perepsilonema	*	...	...	..	—	—	0.05	1
Pierrickia	*	*	...	...	*	*	0.15	2
Polysigma	*	—	...	...	...	...	0.08	2
Pomponematinae indet.	—	—	*	.....	*	...	0.11	1
Porocoma	—	*	—	...	*	...	0.07	2
Prototricoma	—	*	*	...	*	*	0.42	5
Protricoma	...	*	*	*	*	*	0.37	3
Pselionema	*	*	*	*	*	*	0.79	10
Richtersia	***	**	**	***	**	**	3.94	4
Sabatieria	**	****	*****	*****	****	****	12.92	8
Setoplectus	*	*	*	*	*	...	0.48	2
Siphonolaimus	*	*	—	—	*	...	0.08	2
Southerniella	...	*	*	*	*	*	0.58	5
Sphaerolaimidae indet.	...	...	...	*	*	...	0.12	1
Sphaerolaimus	*	*	*	*	*	*	0.78	4
Spilophorella	*	...	*	*	—	—	0.28	1
Spirobolbolaimus	*	*	*	*	—	—	0.19	1
Synonchiella	*	*	...	--	—	—	0.08	2
Syringolaimus	*	*	*	*	*	**	1.41	2
Tarvaia	...	*	...	...	—	*	0.07	3
Thalassoalaimus	*	*	*	*	—	*	0.35	7
Theristus	*	*	*	*	*	*	0.51	1
Trefusia	*	*	*	*	...	—	0.17	1
Trichotheristus	...	...	*	...	—	—	0.02	1
Tricoma	***	***	*	*	***	**	3.57	21
Tripyloididae indet.	...	*	...	...	...	—	0.03	1
Viscosia	*	*	*	...	...	...	0.18	2
Wieseria	—	...	...	*	—	—	0.02	1
total:								419

Table 2. (continued)

family	M160	M280	M530	M820	M990	M1220	mean%	n
Aegialoalaimidae	*	**	*	**	***	***	2.81	11
Anticomidae	−	−	−	−	*	....	0.02	1
Araeolaimida indet.	*	*	*	*	*	*	0.35	2
Axonolaimidae	*	−	*	−	*	....	0.17	2
Ceramonematidae	**	**	*	*	*	*	2.01	26
Chromadoridae	***	***	****	****	****	****	10.03	32
Comesomatidae	***	****	*****	*****	****	****	14.95	19
Cyatholaimidae	**	**	**	*	**	**	2.59	16
Desmodoridae	***	****	*	*	*	*	3.84	17
Desmoscolecidae	***	****	****	***	****	***	7.35	63
Diplopeltidae	**	**	**	***	***	**	3.42	23
Draconematidae	*	*	−	*	−	−	0.14	1
Enchelidiidae	*	*	*	*	*	*	0.36	2
Enoplida indet.	−	−	*	*	−	....	0.04	...
Enoplidae	−	−	*	*	−	....	0.04	1
Epsilonematidae	*	−	−	−	*	....	0.11	3
Ethmolaimidae	*****	*	*	*	*	*	4.99	6
Haliplectidae	*	*	*	*	*	*	0.67	3
Ironidae	*	*	*	*	*	**	1.41	2
Leptolaimidae	**	**	***	**	***	***	4.06	27
Leptosomatidae	*	*	−	....	*	*	0.26	4
Linhomoeidae	**	*	*	*	*	*	0.91	5
Microlaimidae	****	****	***	**	**	**	5.95	16
Monhysteridae	****	****	***	****	****	*****	11.50	28
Nematoda indet.	**	*	**	**	*	*	2.29	5
Oncholaimidae	*	*	*	....	....	....	0.20	3
Oxystominidae	***	***	****	***	***	***	6.49	57
Paramicrolaimidae	*	..	....	....	....	−	0.05	1
Selachinematidae	***	**	**	***	**	**	4.52	9
Siphonolaimidae	*	*	....	....	*	−	0.08	2
Sphaerolaimidae	*	**	**	**	**	*	1.92	9
Tarvaiidae	....	*	..	....	−	*	0.07	3
Thoracostomopsidae	*	*	*	*	*	−	0.30	5
Trefusiidae	*	*	*	*	−	−	0.17	1
Tripyloididae	....	*	−	−	−	−	0.03	1
Xyalidae	**	**	****	***	***	***	5.91	13
total:								419

−: 0%
*: >0%, <2%
**: ≥2%, <4%
***: ≥4%, <8%
****: ≥8%, <16%
*****: ≥16%

Discussion

1. Gradients related to station depth

Many characteristics of the environment are known to change with water depth (GAGE & TYLER, 1991), and this is also true for the shelf-slope transect under study

Table 3. Systematic list of species already described and their maximum abundance in the transect
$[\cdot(10 \text{ cm}^2)^{-1}]$.

a. Species described from this study.

species	max. abundance	described by:
Protricoma corsicana	3	DECRAEMER & SOETAERT, 1989
P. macramphis	3	DECRAEMER & SOETAERT, 1989
P. microcephala	1	DECRAEMER & SOETAERT, 1989
Spirobolbolaimus bathyalis	3	SOETAERT & VINCX, 1988
Richtersia bathyalis	34	SOETAERT & VINCX, 1987
R. heipi	27	SOETAERT & VINCX, 1987
R. spinosa	14	SOETAERT & VINCX, 1987
R. staresensis	10	SOETAERT & VINCX, 1987
Desmoscolex coronatus	4	SOETAERT, 1989
D. decraemerae	3	SOETAERT, 1989
D. membranifer	13	SOETAERT, 1989
D. parabyssorum	8	SOETAERT, 1989
D. variabilis	7	SOETAERT, 1989
Tricoma apophysis	12	SOETAERT & DECRAEMER, 1989
T. corsicana	1	SOETAERT & DECRAEMER, 1989
T. duopapillata	13	SOETAERT & DECRAEMER, 1989
T. latispicula	3	SOETAERT & DECRAEMER, 1989
T. pygmaea	5	SOETAERT & DECRAEMER, 1989
T. setosa	2	SOETAERT & DECRAEMER, 1989
T. tripapillata	1	SOETAERT & DECRAEMER, 1989
T. vincxae	5	SOETAERT & DECRAEMER, 1989

b. Species described or reported from other deep-sea studies.

species	max. abund.	deep-sea area	reported or described by:
Acantholaimus elegans	5	Norwegian deepsea	JENSEN, 1988
Acantholaimus setosus	2	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Acantholaimus spinicauda	6	Mediterranean	VITIELLO, 1976; VIVIER, 1978
		Biscay	VIVIER, 1985
Acantholaimus iubilus	1	Chilean-Peruvian Trench	GERLACH *et al.*, 1979
		Norwegian deep-sea	JENSEN, 1988
		Biscay,	VIVIER, 1985
		Walvis Ridge	GOURBAULT & VINCX, 1985
Acantholaimus megamphis	15	Biscay	VIVIER, 1985
Ceramonema chitwoodi	1	Mediterranean canyon	VIVIER, 1978
Cervonema jenseni	3	Walvis Ridge	GOURBAULT, 1980
Cervonema tenuicaudatum	8	Mediterranean canyon	VIVIER, 1978
Desmodora conica	4	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Desmoscolex abyssorum	4	Moçambique channel	DECRAEMER, 1984
Desmoscolex asetosus	1	Biscay	DECRAEMER, 1983
Desmoscolex macrophasmata	2	Biscay	DECRAEMER, 1983
Desmoscolex paralongisetosus	2	Biscay	DECRAEMER, 1983
Gammanema mediterraneum	4	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Halalaimus delamarei	1	Mediterranean canyon	VITIELLO, 1976
Halalaimus pachydoroides	4	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Halichoanolaimus lanceolatus	2	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Ledovitia hieta	6	Mediterranean canyon	VITIELLO, 1976
Litinium bananum	5	off N. Carolina	TIETJEN, 1976
Longicyatholaimus cervoides	5	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Metasphaerolaimus crassicauda	10	Iberian deepsea, Biscay	FREUDENHAMMER, 1975

Table 3. (*continued*).

species	max. abund.	deep-sea area	reported or described by:
Minolaimus cervoides	3	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Odontophora fatisca	4	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Oxystomina pulchella	16	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Pararaeolaimus rumohri	10	Norwegian deepsea	JENSEN, 1991
Pierrickia decasetosa	3	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Pselionema deconincki	1	Mediterranean canyon	VIVIER, 1978
Pselionema minutum	1	Mediterranean canyon	VIVIER, 1978
Sabatieria pisinna	43	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Sabatieria vasicola	6	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Setoplectus gerlachi	4	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Southerniella conicauda	1	Mediterranean canyon	VIVIER, 1978
Sphaerolaimus uncinatus	5	Iberian deep sea, Biscay	FREUDENHAMMER, 1975
		Mediterranean canyon	VIVIER, 1978
Tricoma bathycola	5	Iberian deep sea, Biscay	FRUEDENHAMMER, 1975
		Norwegian deep sea	JENSEN, 1988
Thalassoalaimus mediterraneus	2	Mediterranean canyon	VITIELLO, 1976; VIVIER, 1978
Wieseria leptura	1	Mediterranean canyon	VITIELLO, 1972; VIVIER, 1978

c. Species described from non deep-sea sites.

species	max. abund.	area
Actinonema longicaudatum	6	SW Africa, Mediterranean, Red Sea, Bay of Bengal
Aegialoalaimus elegans	1	North Sea, Norway, Atlantic, Oresund
Bolbolaimus murinae	16	Black Sea
Campylaimus gerlachi	6	Bay of Bengal, Kiel Bay
Dichromadora cucullata aff.	24	North Sea, Baltic, etc.
Leptolaimus tritubulatus	6	Manche, Roscoff
Litinium aequale	2	Florida, Madagascar
Metadasynemella macrophalla	4	Mediterranean

(see Fig. 5a and b). The sediment gradually changes from relatively coarse sand on the shelf to nearly pure mud in the deepest stations. Concurrently the content of chloroplastic pigment equivalents in the sediment (an indicator of surface-derived organic matter) decreases more or less exponentially with water depth (SOETAERT *et al.*, 1991a). Because so many factors covary with depth, it is not feasible to attempt to determine the main factor responsible for the observed community gradient. Nevertheless, there is a striking similarity between the change in community composition (Fig. 5c) and in the sedimentary and food environment. On average, the rate of zonation change seemed to decline with increasing depth: the DCA score of the first (main) axis decreased exponentially rather than linearly with depth (Fig. 5c); greatest separation (and hence greatest dissimilarity) was achieved between 160–280 m; the three deepest stations had nearly the same DCA score. Similarly, the clustering analysis revealed a distinct faunal break between the shelf (160 m) and the slope stations (280–1220 m), while a smaller difference
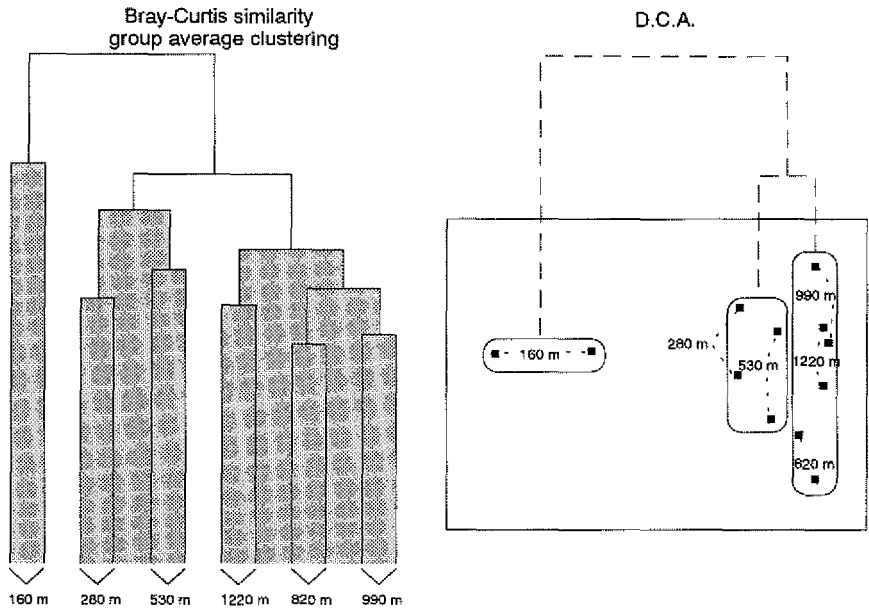
Fig. 2. Clustering (left) and Detrended Correspondence Analysis (right) of the vertically integrated samples [indiv. $\cdot (10 \text{ cm}^2)^{-1}$]. The main divisions imposed by the clustering are also indicated on the DCA plot.

was recorded between the stations on the upper part of the slope (280 and 530 m) and the deeper stations (820–1220 m). These results are consistent with zonation patterns observed in the macrofauna, where the shelf-slope break was shown to be the most important boundary too (review in GAGE & TYLER, 1991).

Amongst the other variables that relate to the nematode community, mean nematode body weight showed a depth-related decrease from about 0.1 μg dry weight on the shelf to 0.04 μg DW in the deepest station (Fig. 5d; data from SOETAERT & HEIP, 1989). Nematode density (Fig. 5e; data from SOETAERT *et al.*, 1991a) and nematode diversity (SOETAERT *et al.*, 1991b, not depicted), on the other hand, were not related to station depth, although total nematode biomass tended to decrease with increasing depth (Fig. 5f).

2. Gradients vertically into the sediment

Compared to bathymetric zonation of the deep-sea fauna, community changes with depth into the sediment have not been similarly addressed. Due to sequential degradation of organic matter by different electron acceptors, there are steep gradients in the sediments of oxygen, nitrogen, sulphate compounds, and other substances (MIDDELBURG *et al.*, 1993) that can affect nematode vertical distribution. Thus, the nematode community was shown to be substantially different in the oxygenated versus sulphide-rich deeper layers of the bottom in the Øresund (JENSEN, 1987). Other sediments exhibit more subtle changes in community com-
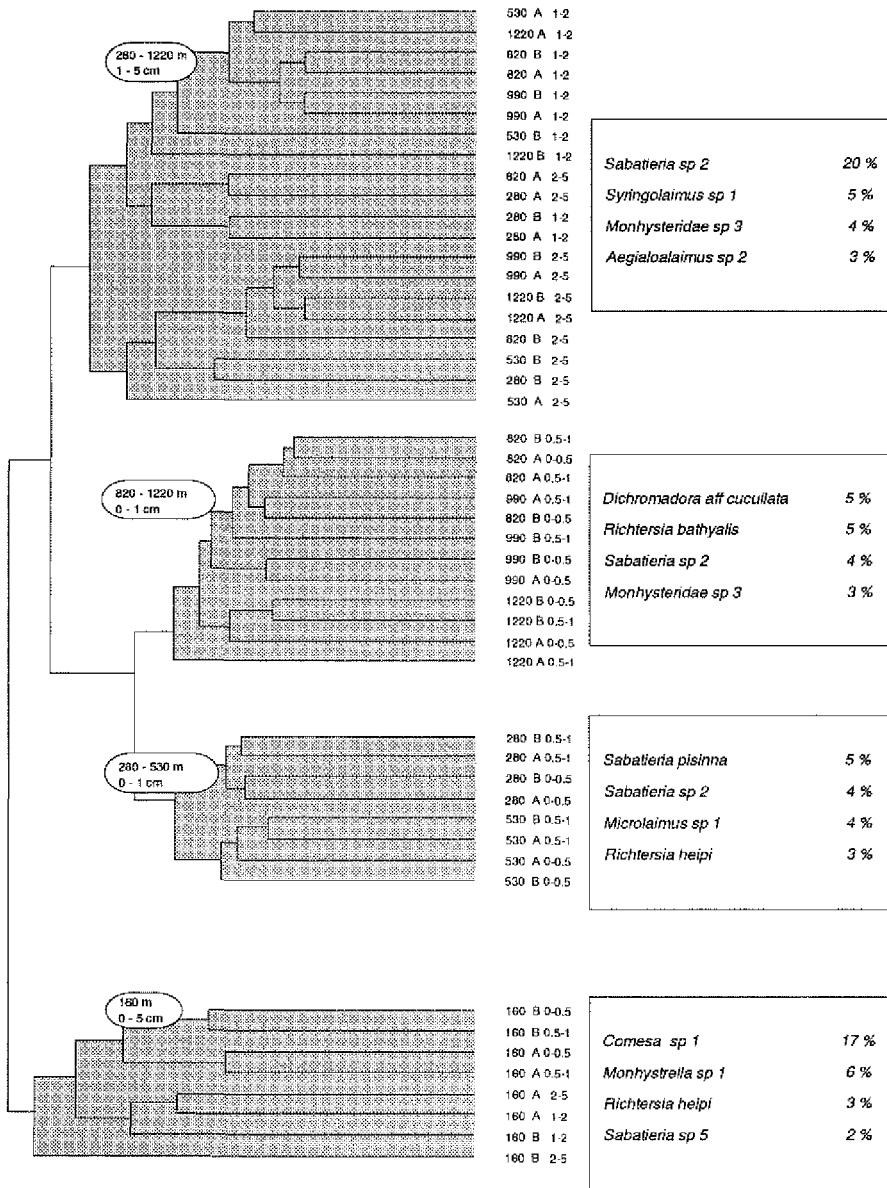
Fig. 3. Clustering based on nematode species concentration [indiv. · (10 cm³)⁻¹] in the different sediment layers. Each sediment slice is referred to by the station depth (in m), replicate (A or B), and the sediment interval (in cm), respectively. The four dominant species and their mean percentual occurrence in each main cluster are represented.

position at relatively small vertical scales (*e.g.*, JOINT *et al.*, 1982; SOETAERT *et al.*, 1994). The vertical structure in the stations along the studied transect is of the second type: the surficial and deeper layers are inhabited by the same species, though with different relative abundances. Although only few species show peak
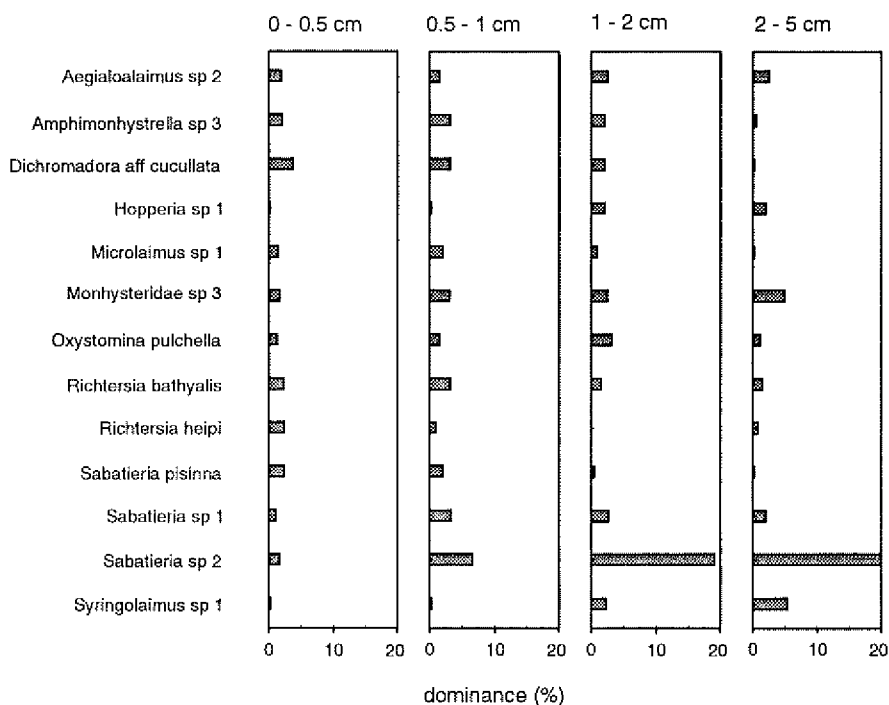
Fig. 4. Mean percentual dominance of the most important species in the different sediment layers of the stations at 280 and 1220 m. Species are arranged in alphabetical order.

abundance at depth, some (mainly larger) species extend deeper into the sediment than others. Thus, the nematode community gradually changes as it becomes dominated by fewer and bigger species deeper down. Two of the dominant genera in the 2–5 cm layer (*Sabatieria, Syringolaimus*) were also reported to be deeper-living in one station in the deep Norwegian Sea (JENSEN, 1988).

3. Taxonomic characteristics

The relationship of the nematode generic composition in this Mediterranean transect with assemblages reported from other studies in the deep sea or on the shelf break were investigated by SOETAERT & HEIP (1995). Our 160 m station had greatest affinities with two shelf-break stations from the Bay of Biscay (VANREUSEL *et al.*, 1992), while the deeper stations harboured a true transitional fauna consisting of genera typical for both the shelf break (*Sabatieria, Richtersia*) and abyssal or hadal sites (*Acantholaimus, Halalaimus*).

With regard to nematode specific composition, a comparative study is not feasible since most deep-sea species are as yet undescribed. Nevertheless, nearly 10% of all (419) species have already been described (Table 3); another 5% were described in this study. Most of the known species at our study site were reported from a nearby Mediterranean canyon, from the Iberian deep-sea, or the deep Bay
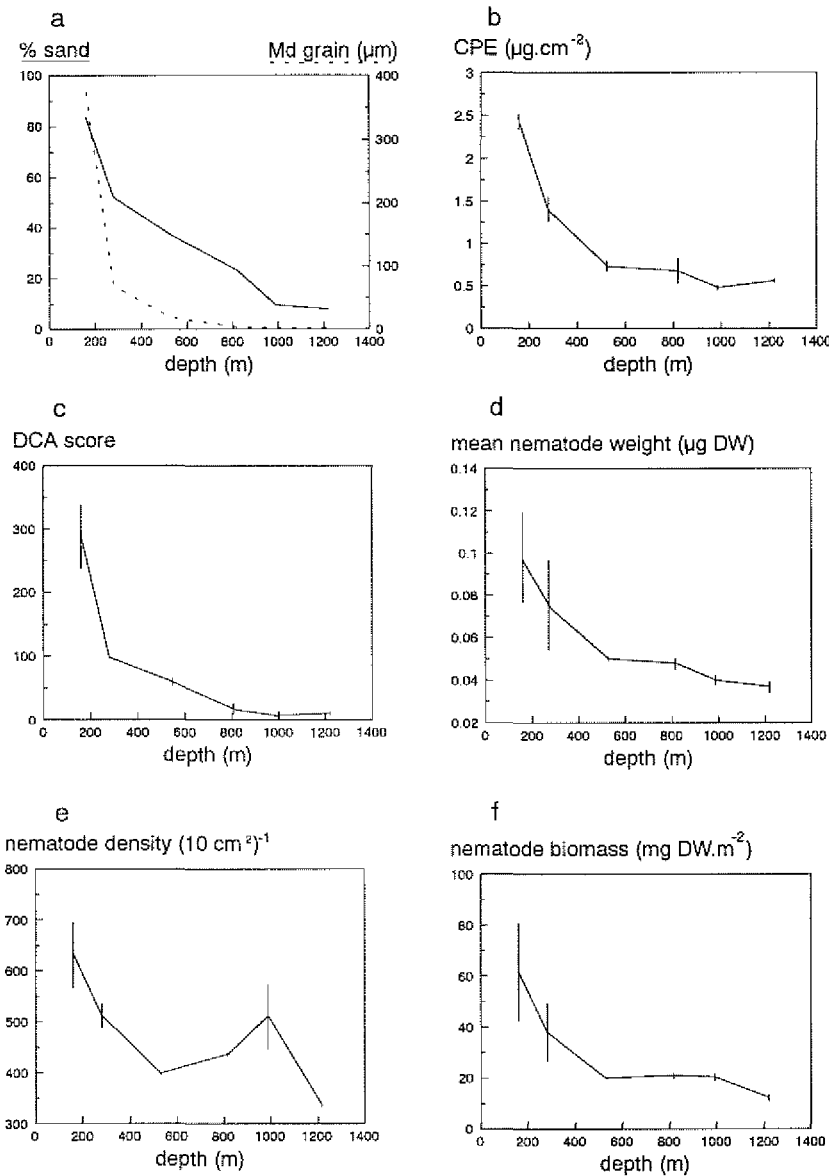
Fig. 5. Depth-related gradients in sediment composition (a), chloroplastic pigment equivalents (b; CPE, $\mu g \cdot cm^{-2}$), nematode community structure (c; DCA score of the main axis), mean nematode weight (d; μg DW), density (e; [indiv. $\cdot (10 \ cm^2)^{-1}$]), and nematode biomass (f; mg DW $\cdot m^{-2}$). The data indicate the mean and total range. Data from SOETAERT et al. (1991a: Fig. 5a, b, e), SOETAERT & HEIP (1989: Fig. 5d), or from this study (Fig. 5c, f).

of Biscay. More surprisingly, four Mediterranean species were common to deep-sea assemblages in the Norwegian Sea, despite the fact that both areas are physically isolated from the vast deep-sea regions (GAGE & TYLER, 1991) and the large

temperature differences ($-0.7\,°C$ in the Norwegian deep sea; JENSEN, 1988; about $13\,°C$ for Mediterranean deep waters).

4. Patterns promoting coexistence

Spatial segregation in the vertical plane can help to explain the high number of nematode species commonly found in marine and estuarine sediments (JOINT *et al.*, 1982). Species diversity patterns along our transect were investigated in SOETAERT *et al.* (1991b). There were 50 to 63 species per 100 individuals, but this high diversity was mainly caused by generic differences ($> 75\%$) rather than within-generic diversity. Of the 108 genera encountered in the transect, only eight were represented by at least 10 species; 30 % of all genera were monospecific. The genera *Halalaimus*, *Desmoscolex*, "*Monhysteridae gen.*", and *Tricoma* were represented by the largest number of species (Table 2), which more or less confirms findings from other studies (TIETJEN, 1989; THISTLE & SHERMAN, 1985; DINET & VIVIER, 1979). The genus *Sabatieria*, although numerically dominant, was represented by eight species only. Within the genera *Sabatieria* and *Acantholaimus*, specific densities were high enough to warrant searching for evidence of competitive avoidance that could allow these closely related species to coexist in the sediment. The structure of the mouth cavity in the genus *Sabatieria* is cup-shaped, unarmed, and reasonably uniform among species (Fig. 6). Thus, partitioning of food resources by mere morphological differentiation of the mouth seems unlikely in this genus. There are, however, differences in the vertical repartition, with successively larger animals being observed deeper in the sediment (one-way ANOVA, $P < 0.001$). The smallest species (*S. pisinna*) is a true surface dweller, while the largest species was not observed in the upper one-half centimetre. Within the genus *Acantholaimus*, vertical segregation is less obvious, and most species seem to prefer the upper sediment layers. However, members of this genus exhibit a wealth of buccal morphologies, from a minute mouth cavity, apparently without teeth (*A.* sp. 3), to larger mouth cavities with one or three large teeth. This is consistent with earlier observations by JENSEN (1988) that competitive interference within this genus could be minimized by resource partitioning among these microbial-feeding nematodes. On the other hand, variation in mouth structure in this Mediterranean transect seems to be much larger than in the Norwegian deep sea.

Summary

In six stations along a Mediterranean depth transect, 419 species of nematodes were found, of which 10 % were already described.

Nematode assemblage structure showed a distinct faunal break between the continental shelf (160 m) and deeper stations (280–1220 m).

On the slope, communities from the upper centimetre differed significantly from those in deeper layers, which were dominated by fewer and larger species.
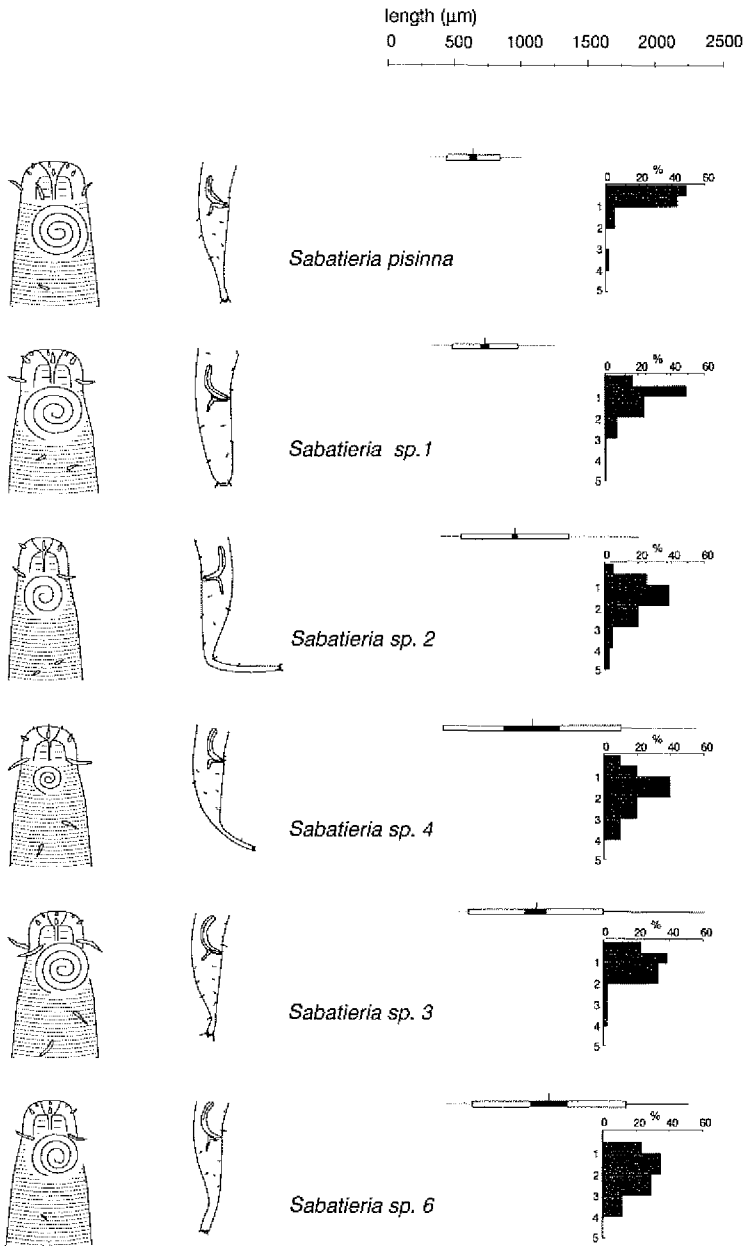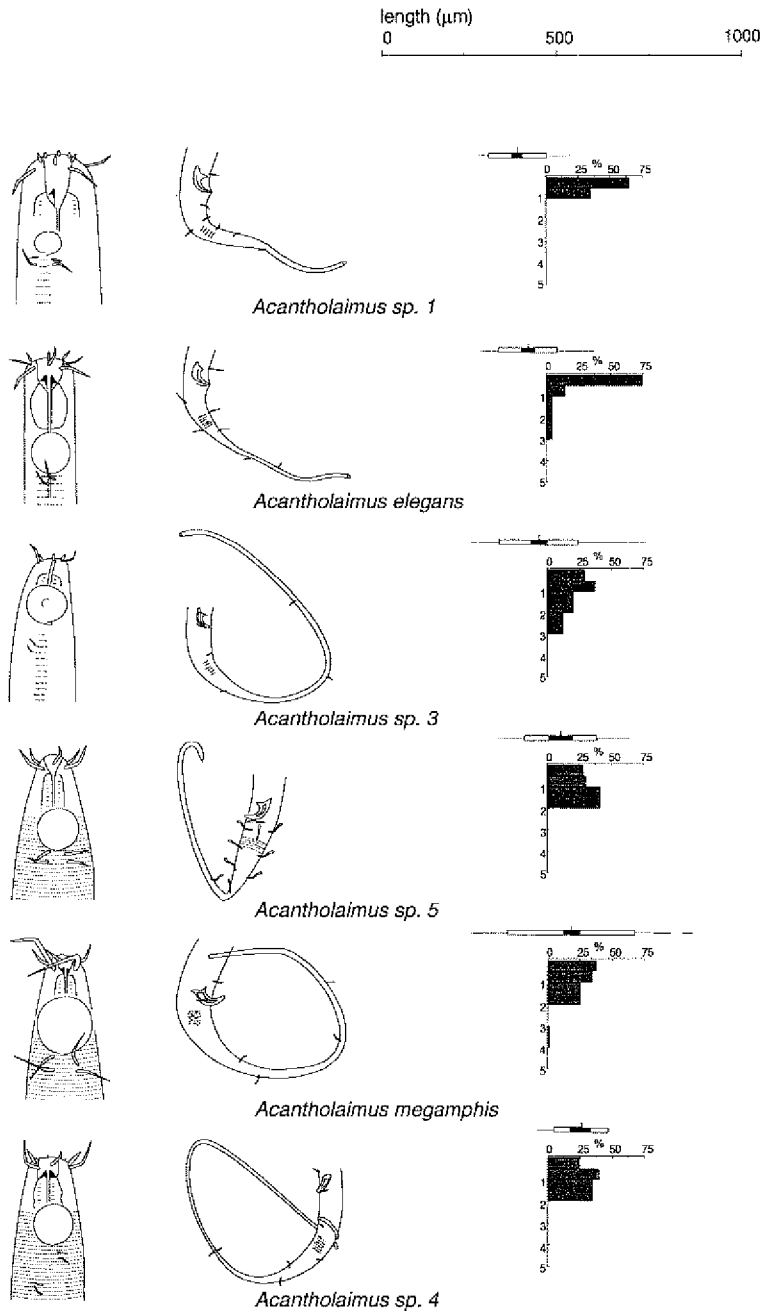
Fig. 6. Vertical distribution into the sediment and length characteristics of the most abundant species of *Sabatieria* in the transect. The vertical distribution (vertical bars) consists of % occurrences in the different sediment layers; length characteristics (of juveniles + adults) are represented by means of dicegrams indicating total range (horizontal line), mean (small vertical line), the mean ± standard deviation (horizontal unfilled bar), and the mean ± standard error (horizontal dark bar).

Fig. 7. Vertical distribution into the sediment and length characteristics of the most abundant species of *Acantholaimus* in the transect. For more details see the legend of Fig. 6.

It is argued that spatial segregation in the vertical plane can explain coexistence of several species belonging to the genus *Sabatieria*, while food resource partitioning (as witnessed by different buccal morphology) can explain coexistence of species belonging to the genus *Acantholaimus*.

Acknowledgements

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