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Spatio-temporal structure of the nematode assemblages of the Brouage mudflat (Marennes Oléron, France)

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Abstract

The density and species composition of the nematode assemblage was investigated in the Brouage mudflat (Marennes-Oléron, France) at three stations over four seasons in relation to environmental parameters (organic matter percentage, chlorophyll *a* and heavy metal content). From the 43 species recorded, six dominant genera represented 75% of the assemblage. Fluctuations of these species were mainly in response to the observed temporal patterns. Over the course of a year, epigrowth feeders were the most important trophic group (43%) with three dominant species *Metachromadoroides remanei*, *Chromadora macrolaima* and *Ptycholaimellus jacobii* but some non-selective deposit feeders, notably *Daptonema oxycerca*, also contributed to the utilisation of primary production. The feeding strategies of the dominant species particularly for epistrate feeders are discussed. An assessment of the influence of nematodes grazing on microphytobenthos biomass and production was then performed. Comparison of nematode species grazing rates based on nematode abundance and ingestion rates and microphytobenthic production are discussed. Using the trophic structure of nematode populations to extend those results, grazing rates represent a significant part of microphytobenthic production in springtime.

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Keywords: nematode; mudflat; diversity; trophic groups; heavy metals; grazing rate

1. Introduction

In mudflats, microphytobenthos, and especially diatoms, are essential sources of food for numerous benthic species (Herman, Middelburg, Van de Koppel, & Heip, 1999; Herman, Middelburg, Widdows, Lucas, & Heip, 2000). While numerous studies document nematodes feeding on diatoms (Admiraal, Bouwman, Heekstra, & Romeyn, 1983; Blanchard, 1991; Bouwman, Romeijn, Kremer, & Van Es, 1984; Middelburg et al., 2000; Montagna et al., 1995; Riera, Richard, Grémare, & Blanchard, 1996), their relative importance in the trophic web remains uncertain. Some studies

indicate nematodes having a grazing rate high enough to influence microphytobenthos biomass or production (Blanchard, 1991; Montagna, 1984; Montagna, 1995; Montagna & Yoon, 1991). Some others show that nematode carbon utilisation probably never constitutes more than a small percentage of primary production (Moens, Luyten, Middelburg, Herman, & Vincx, 2002).

The buccal morphology and some observations of gut content used to be the only tool to investigate trophic structure according to the classification of Wieser (1953, 1960). In many cases, while morphological evidence suggests that diatom feeders do not largely dominate in mudflats, isotopic studies show that intertidal nematode communities largely thrive on microphytobenthos (Middelburg et al., 2000; Moens et al., 2002; Montagna et al., 1995; Riera et al., 1996). Middelburg et al. (2000)

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suggested that nematode species, *Enoploides longispiculus*, considered as a predator according to buccal morphology and results from laboratory feeding experiments, may also directly graze on the microalgae or consume their photosynthetic products. Thus, species considered as predators may not be obligatory predators. Some recent studies (Middelburg et al., 2000; Moens, Verbeeck, de Maeyer, Swings, & Vincx, 1999; Moens & Vincx, 1997; Moens et al., 2002; Riera et al., 1996) have stressed the complexity of nematode nutrition and have provided arguments to refine further the existing knowledge on nematode trophic structure in intertidal mudflats.

The purpose of this study is an investigation of the nematode community of Brouage mudflat (West coast of France, Fig. 1). In such a productive environment like a mudflat, nematode community can play an important role in the energy budget of the benthic system (Kennedy & Jacoby, 1999; Leguerrier et al., 2003; Warwick, Joint, & Radford, 1979) and thus any model of the structure of the food web should take into account nematode density, biomass and trophic structure.

The present study first describes species and trophic structure of the nematode communities according to Wieser (1953, 1960). That information is used to provide an insight into the nematode compartment function in the trophic web. Nematode communities and their

spatio-temporal variations were studied in relation to some environmental variables such as sediment organic matter, chlorophyll *a* content and some heavy metals.

An assessment of the influence of nematodes grazing on microphytobenthos biomass and production was then performed. Calculations of a nematode species grazing rates based on nematode abundance in the mudflat, measured in the present study and ingestion rates from Tietjen and Lee (1973) were performed. These grazing rates related to the proportion of trophic groups are compared to microphytobenthic production in order to evaluate the effect of the nematode assemblage on primary production.

2. Materials and methods

The intertidal mudflat of Brouage is located in Marennes-Oléron Bay, between the French Atlantic coast and Oléron Island (Fig. 1). The area is a macrotidal system influenced by continental inputs mainly from the Charente River and occasionally the Gironde River. The mudflat extends over 60% of the whole bay area. It is characterised by a high microphytobenthic production ca. $400 \text{ g C m}^{-2} \text{ yr}^{-1}$. Molluscs dominate the macrofauna (Sauriau, Mouret, & Rincé, 1989; Sauriau, personal communication) while *Scrobicularia plana*,

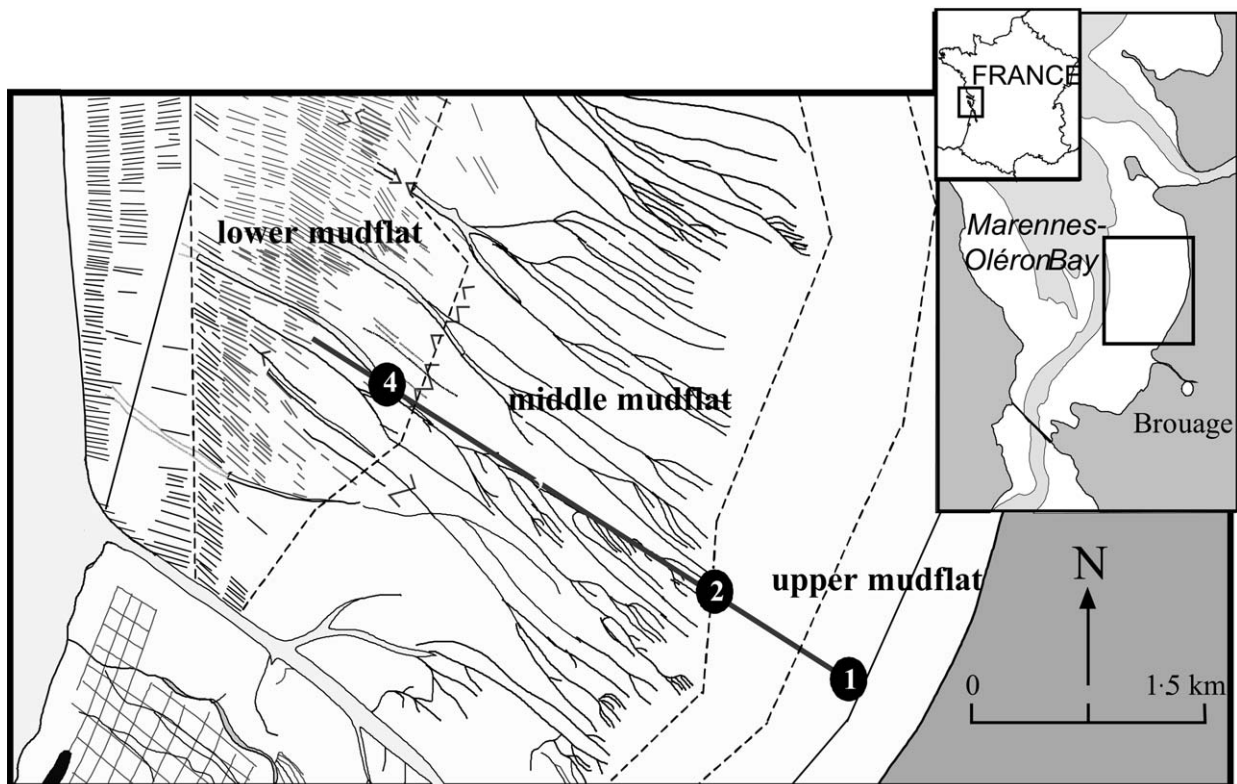


Fig. 1. Position of sampling sites along the cross-shore transect in Brouage mudflat (modified from Gouleau et al., 2000).

Hydrobia ulvae, *Abra nitida*, *Macoma balthica*, the amphipod *Corophium volutator* and the annelid *Nephtys hombergii* represent 80% of the macrobenthic biomass.

Samples were collected at three stations along a 4-km transect (Fig. 1). All stations were sampled four times between 2000 and 2001 at intervals of 3 months: April, June, October and January. Most of the parameters, except chlorophyll *a* content, were obtained from sediment cores collected with a plastic syringe corer of 11.3 cm surface area.

Organic matter content (weight loss after incineration) was estimated by weight loss at 450 °C for 24 h of the top 2 cm of the sediment (Wollast, 1989) from three replicated cores (deep frozen for later analysis). Chlorophyll *a* content was measured on the top 2 cm of five replicated cores (deep frozen at 80 °C for later analysis). The top 2 cm of the five cores were sampled and deep-frozen at –80 °C. Chlorophyll extraction was obtained by sediment agitation during 12 h in the dark with acetone 90%. Chlorophyll *a* content was measured by a fluorimetric method (Neveux, 1976).

Three replicated cores were taken at random in a square metre area for heavy metal analysis. The top 2 cm of sediment was collected for the analysis of Cd, Cu, Pb and Zn concentration. Heavy metal concentrations were obtained as follows: 500 mg of dry sediment samples were acid-digested into a mixture of nitric and perchloric acids (HNO₃ 14 N; HClO₄ 17 N) at 80 °C for 48 h. After evaporation, the dry residues were dissolved in 0.3 N HNO₃ and stored at 4 °C until analysis. Metal concentrations were determined by flame or furnace atomic absorption using a Varian spectra AA250 atomic absorption spectrophotometer.

Meiofauna density (ind 10 cm⁻²) and taxonomic composition were obtained from three replicated cores taken at random in a square metre area. The top 5 cm of sediment from each core were preserved in 4% formalin solution. Meiofauna was extracted from sediment using Ludox TM (Heip, Vincx, & Vranken, 1985). A sample splitter, Motoda-box (Motoda, 1959) was used to obtain an aliquot containing at least 500 individuals for the abundance estimation. From each sample, 100 nematodes were haphazardly removed and mounted on slides and examined microscopically. Faunistic lists were established by species determination of 100 haphazardly picked individuals per sample. The feeding types of the nematodes were determined according to the classification of Wieser (1953, 1960). The density of other meiobenthic taxa was too low to evaluate on split samples and they were checked on a whole sample only during springtime. The granulometric parameters used in the present work were determined by Gouleau, Jouanneau, Weber, and Sauriau (2000).

Normality of the data was checked by Kolmogorov–Smirnov test. Homogeneity of variance was checked

using Bartlett test and Levene test. All hypotheses were tested at $p < 0.05$ level. Two-way ANOVA were applied to assess the significance of differences between stations and seasons. A Fischer (F) test was used to evaluate significant differences between stations and seasons and their interactions. Multiple comparison tests (Bonferoni, T) was used to check the significance of the differences between the principal factors. Structure of the species assemblage with environmental parameters was investigated by principal components analysis (PCA), Bravais–Pearson correlation. BioDiversity Pro beta (1997) was used to calculate diversity parameters, i.e. index of diversity-Shannon H' (\log_2) and index of equitability-Shannon J' . A jack-knife model was computed for estimating the number of species from the region and to predict how many species would have been discovered if sampling had been more intensive.

3. Results

3.1. The environmental parameters

Silt content represented from 90 to 95% (Gouleau et al., 2000). The sand content decreased from the lower part to the upper part of the mudflat and the carbonate content of the sand fraction increased in the upper part of mudflat. At the water sediment interface (0–1 and 1–2 cm), density was more variable due to episodic deposit of fluid mud.

The variations of environmental parameters along the transect are shown in Fig. 2. The mean content of chlorophyll *a* in sediment at the three stations was $56.8 \pm 20.5 \text{ mg m}^{-2}$. The minimum value (33 mg m^{-2}) was measured in January. The seasonal fluctuations were not significant over the duration of the year (for stations $F = 0.86$ and $p = 0.469$; for seasons $F = 2.73$ and $p = 0.136$).

The mean of most of the parameters had station–season interactions (Table 1). The mean percentage of organic matter was $9.17 \pm 1.2\%$. Stations 1 and 2 have a slightly higher percentage of organic matter in April than station 4 ($F = 26.04$ and $p = 0.000$). Mean heavy metal concentration per gram of dry sediment was: $30.1 \pm 4.6 \text{ } \mu\text{g Pb g}^{-1}$, $10.7 \pm 1.9 \text{ } \mu\text{g Cu g}^{-1}$, $108.9 \pm 15.9 \text{ } \mu\text{g Zn g}^{-1}$ and $0.2 \pm 0.04 \text{ } \mu\text{g Cd g}^{-1}$. Spatio-temporal fluctuations of Zn ($F = 4.22$ and $p = 0.005$) and Pb ($F = 4.44$ and $p = 0.004$) were observed, concentrations being slightly higher at station 1 in April than at the two other stations in October. Spatio-temporal fluctuations of Cd ($F = 4.72$ and $p = 0.003$) were higher in January at stations 1 and 2. Mean concentrations of Cu were not significantly different at the three stations ($F = 2.60$ and $p = 0.095$). Cu concentration in the sediment was significantly higher in January than in July ($T = -2.960$ and $p = 0.0409$).

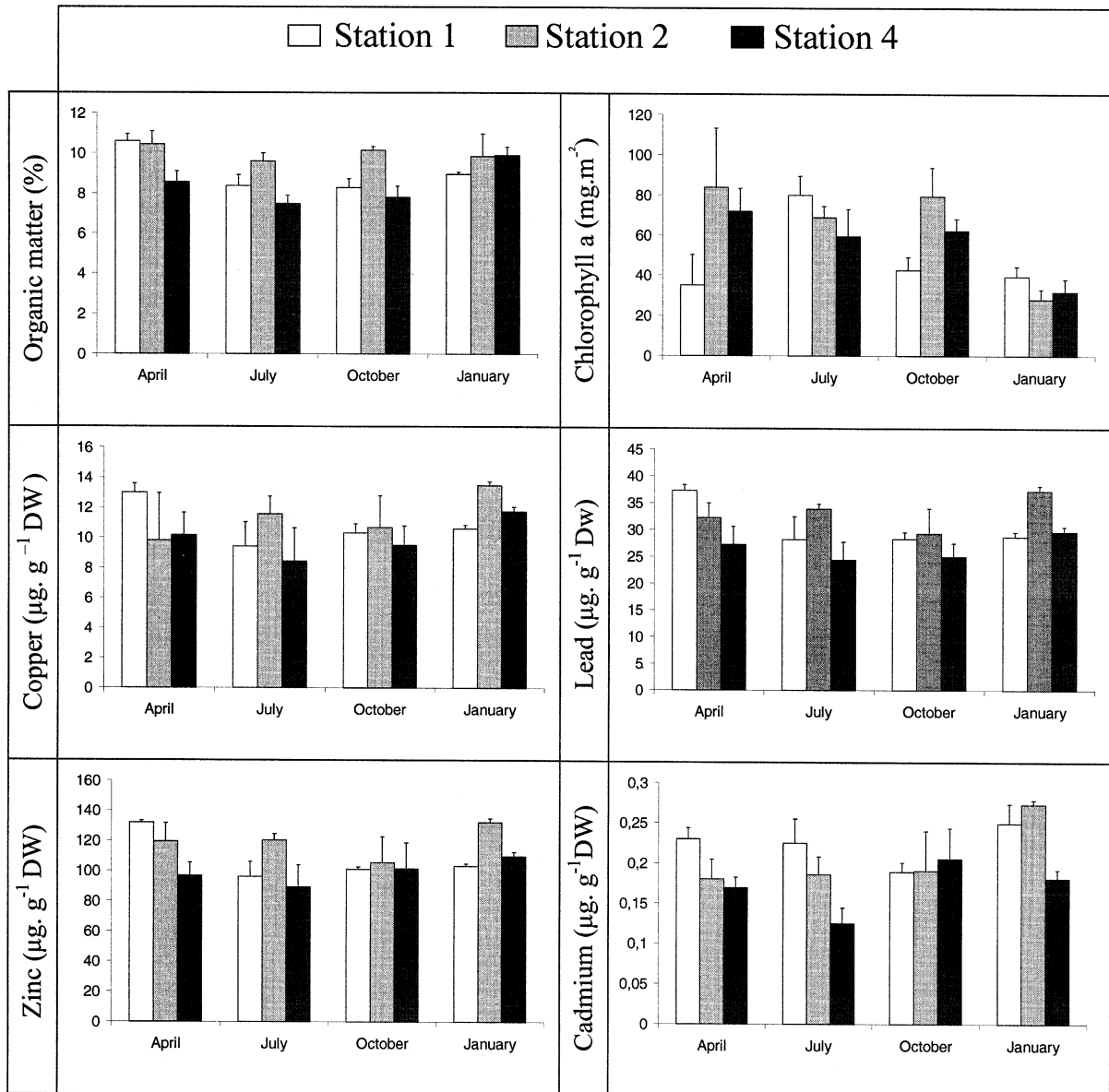


Fig. 2. Organic matter content (%), microphytobenthic biomass (mg m^{-2}) and heavy metal concentrations ($\mu\text{g g}^{-1}$ DW) along the transect.

3.2. Meiobenthic abundance

Six meiofauna taxa were identified in the Brouage samples: nematodes (dominance = 95%), harpacticoid copepods (2%), turbellaria (0.5%), ostracoda (1%), oligochaeta (0.5%) and polychaeta (1%).

The nematode population densities at each station are given in Fig. 3. The mean density of the whole data set was 2112 (± 1250) individuals per 10 cm^{-2} . Station–season interactions were observed ($F = 9.53$ and $p = 0.000$). The higher density ($3849 \text{ ind } 10 \text{ cm}^{-2}$) was observed in April at station 1 and was significantly higher than the densities in January ($T = -4.861$ and $p = 0.0039$), July ($T = -7.027$ and $p = 0.0000$) and October ($T = -6.037$ and $p = 0.0002$) at station 1 and in July ($T = -4.323$ and

$p = 0.0153$) at station 2, and in July ($T = -6.879$ and $p = 0.0000$) and October ($T = -6.802$ and $p = 0.0000$) at station 4. The lowest densities were found in July at stations 1 ($600 \text{ ind } 10 \text{ cm}^{-2}$) and 4 ($669 \text{ ind } 10 \text{ cm}^{-2}$), at levels significantly lower than the densities in January ($T = 5.546$ and $p = 0.0007$; $T = 6.2833$ and $p = 0.0001$) in April ($T = 4.2046$ and $p = 0.0207$; $T = 4.132$ and $p = 0.0336$) at stations 2 and 4, respectively, and in October ($T = 5.9426$ and $p = 0.0003$) at station 2.

3.3. Taxonomic composition

Three thousand six hundred nematodes were determined at generic and species level. A total of 43 species, belonging to 38 genera and 19 families were

Table 1
F- and p-values for the factors station and season and station–season interaction

Parameter	Value	Station	Season	Station–season
Organic matter	F	26.04	13.45	5.90
	p	0.000	0.000	0.001
Chlorophyll content	F	0.86	2.73	–
	p	0.469	0.136	–
Cu concentration	F	2.60	3.49	2.58
	p	0.095	0.031	0.045
Cd concentration	F	14.10	8.10	4.72
	p	0.000	0.001	0.003
Zn concentration	F	12.48	5.43	4.22
	p	0.000	0.005	0.005
Pb concentration	F	19.32	6.74	4.44
	p	0.000	0.002	0.004
Nematode density	F	10.62	22.78	9.53
	p	0.000	0.000	0.000

Bold values indicate significant differences at $p > 0.05$.

found at the Brouage site (Table 2). Twenty-seven species had an abundance lower than 1% and these were considered as rare species. Six genera represent 75% of the population: *Metachromadoroides* (24%), *Terschellingia* (13%), *Sabatieria* (12%), *Ptycholaimellus* (11%), *Chromadora* (8%) and *Daptonema oxycera* (7%).

The total number of families was similar at the three stations, ranking from 15 to 19. Desmodoridae (mean general dominance = 25%), Chromadoridae (19%), Linhomoeidae (19%) and Comesomatidae (15%) dominated the family assemblage.

Species diversity indices were calculated on 100 individuals at the three stations for the four seasons (Table 3).

Species number varied from 27 to 37, Shannon diversity from 3.6 to 4.3 and index of equitability from 0.64 to 0.83. None of these indices were significantly different between the stations and the seasons ($F = 1.3$ and $p = 0.296$). An estimated collector’s curve using the Jack-knife 1 model shows a theoretical number of 50 species (Fig. 4). Eighty-six percent of the potential species were thus identified in the samples, a proportion which suggests that the three stations were quite similar.

3.4. Feeding types and ratio 1B/2A

The proportion of feeding types is shown in Table 4. Epigrowth-feeders (2A) and non-selective deposit-feeders (1B) were dominant in the mudflat accounting for 43 and 35% of the total nematode abundance, respectively. Selective deposit-feeders (1A) and omnivores/predators represented 16 and 4%, respectively. At stations 2 and 4, epigrowth feeders and non-selective deposit feeders were the first and the second most abundant trophic groups. At station 1, the situation was reversed.

Species such as *Ptycholaimellus jacobii*, *Chromadora macrolaima* and *Metachromadoroides remanei* dominated the epigrowth feeders (2A). These were the first two species picked up in April. In contrast, *Sabatieria pulchra*, *Sabatieria punctata* and *Daptonema oxycerca*, non-selective deposit-feeders (1B); *Terschellingia longicaudata*, selective deposit-feeders (1A) were picked up in January.

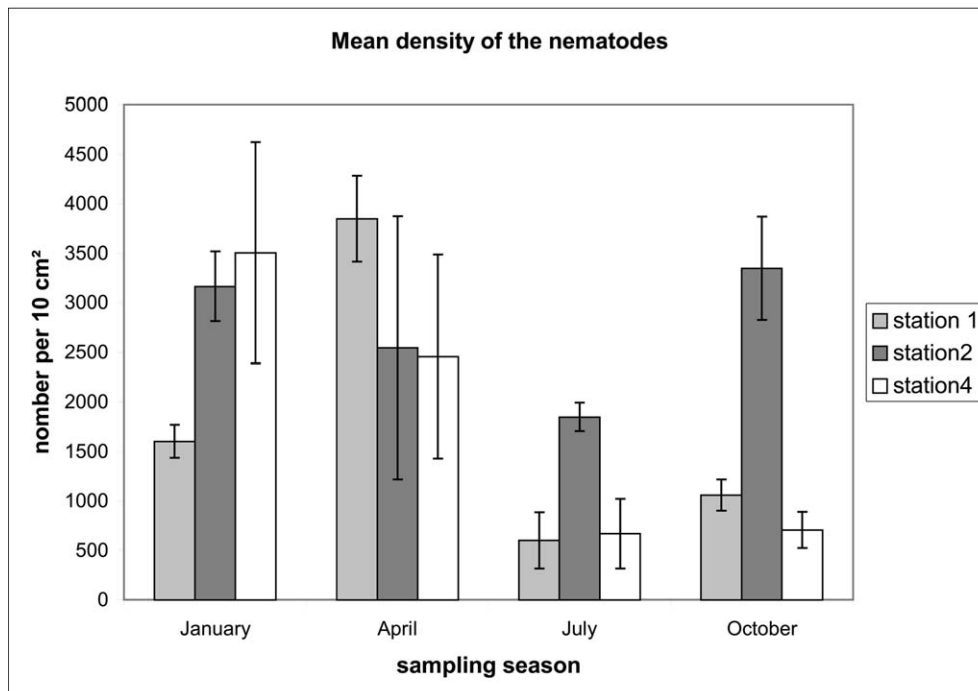


Fig. 3. Nematode population density (ind 10 cm⁻²) per month, at stations 1, 2 and 4. Error bars represent the 95% confidence interval of the mean.

Table 2
List of species ranked by dominance (feeding types after Wieser (1953, 1960))

Genera species	Feeding type	Number of nematode identified			Abundance relative (%)	Abundance cumulate (%)
		Station 1	Station 2	Station 4		
<i>Metachromadoroides remanei</i>	2A	149	427	274	23.6	23.6
<i>Terschellingia longicaudata</i>	1A	174	164	138	13.2	36.8
<i>Ptycholaimellus jacobi</i>	2A	76	172	134	10.6	47.4
<i>Chromadora macrolaima</i>	2A	133	51	103	8.0	55.4
<i>Sabatieria pulchra</i>	1B	137	33	105	7.6	63.0
<i>Daptonema oxycerca</i>	1B	121	63	63	6.9	70.0
<i>Sabatieria punctata</i>	1B	111	62	8	5.0	75.0
<i>Axonolaimus paraspinosus</i>	1B	28	30	59	3.3	78.3
<i>Metalinhomoeus filiformis</i>	1B	27	4	81	3.1	81.4
<i>Desmolaimus zeelandicus</i>	1B	22	58	8	2.4	83.5
<i>Sphaerolaimus gracilis</i>	2B	34	28	9	2.0	85.5
<i>Odontophora setosa</i>	1B	18	6	46	1.9	87.4
<i>Calyptonema maxweberi</i> ^a	?	12	15	26	1.5	88.9
<i>Tripyloides marinus</i>	1B	13	21	20	1.5	90.4
<i>Metacomosoma</i> sp.	1B	45	1	2	1.3	91.7
<i>Aegialolaimus</i> sp.	1A	6	4	32	1.2	92.9
<i>Metachromadora vivipara</i>	2A	4	21	9	0.9	93.8
<i>Parodontophora marina</i>	1B	18	0	7	0.7	94.5
<i>Pierrickia</i> sp.	1A	8	5	10	0.6	95.1
<i>Praeacanthochus punctatus</i>	2A	6	15	2	0.6	95.7
<i>Syringolaimus</i> sp.	2B	1	8	12	0.6	96.3
<i>Viscosia viscosa</i>	2B	6	3	14	0.6	96.9
<i>Halalaimus 1</i>	1A	14	0	9	0.6	97.5
<i>Elzalia</i> sp.	1B	17	0	6	0.6	98.1
<i>Thalassoalaimus</i> sp.	1A	2	0	4	0.2	98.3
<i>Sphaerolaimus</i> sp.	2B	1	4	2	0.2	98.5
<i>Paracomesoma dubium</i>	2A	4	0	0	0.1	98.6
<i>Setosabatieria</i> sp.	1B	2	0	1	0.1	98.7
<i>Cyatholaimidae</i> sp.	2A	0	2	1	0.1	98.8
<i>Latronema</i> sp.	2B	0	0	2	0.1	98.9
<i>Anoplostoma</i> sp.	1B	1	1	0	0.1	99.0
<i>Halalaimus 2</i>	1A	1	1	2	0.1	99.1
<i>Oxystomina</i> sp.	1A	3	0	0	0.1	99.2
<i>Cyartonea germanica</i>	1A	0	0	3	0.1	99.3
<i>Antomicron</i> sp.	1A	1	0	2	0.1	99.4
<i>Terschellingia communis</i>	1A	3	0	2	0.1	99.5
<i>Spilophorella</i> sp.	2A	0	1	0	0.0	99.6
<i>Paracomesoma</i> sp.	2A	1	0	0	0.0	99.6
<i>Anticoma</i> sp.	1A	0	0	1	0.0	99.7
<i>Daptonema hirsutum</i>	1B	0	0	1	0.0	99.8
<i>Linhystra</i> sp.	1A	1	0	0	0.0	99.9
<i>Paramonohystra</i> sp.	1B	0	0	1	0.0	99.9
<i>Pandolaimus</i> sp.	1B	0	0	1	0.0	100
Total		1200	1200	1200	100	

1A, selective deposit feeders; 1B, non-selective deposit feeders; 2A, epigrowth feeders; 2B, omnivores/predators; number of nematodes identified at the three stations and relative abundance.

^a Intermediary type between 2B and 1A.

Table 3
Number of nematode taxa, index of diversity-Shannon H' (\log_2) and index of equitability-Shannon J'

	Station 1				Station 2				Station 4			
	January	April	July	October	January	April	July	October	January	April	July	October
Species number	24	21	22	22	19	18	19	17	24	21	23	22
Shannon H' log base 2	3.4	2.8	3.2	3.0	2.7	2.8	2.9	2.4	3.4	3.1	3.5	2.8
Shannon J'	0.8	0.7	0.8	0.7	0.7	0.8	0.8	0.7	0.8	0.8	0.8	0.7

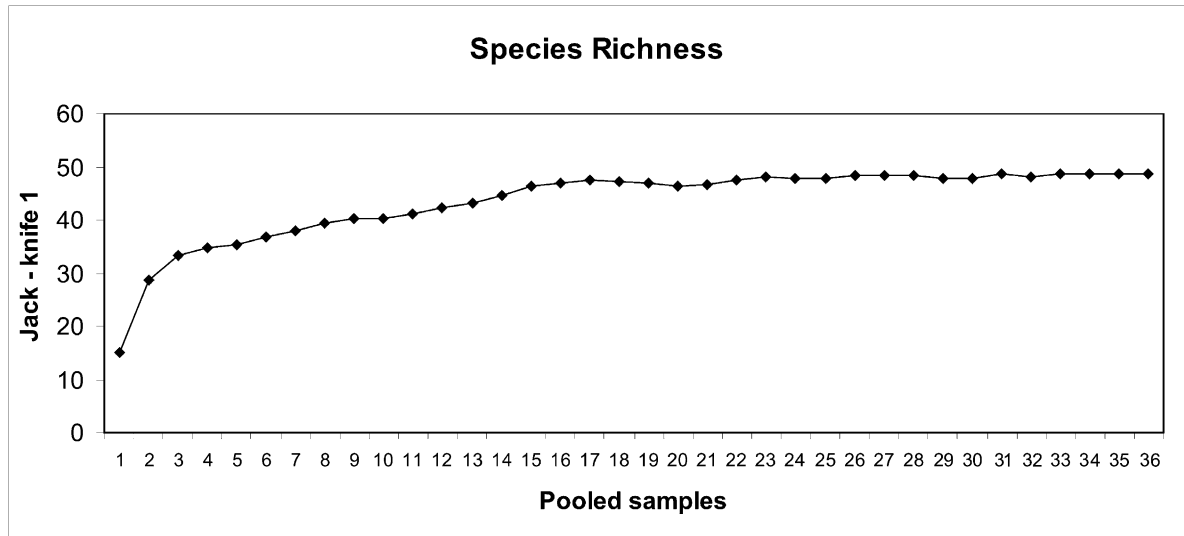


Fig. 4. An estimated collector’s curve to predict how many species would have been discovered had the sampling been more intensive (BioDiversity Pro beta, 1997).

3.5. Relationships between environmental variables and trophic structure of nematode assemblage

Fluctuations in species abundance at the three stations for the different seasons were investigated in relation to environmental parameters (organic matter, chlorophyll content and heavy metals). Only the six dominant species representing about 75% of the nematode assemblage were considered in PCA to allow a focus on the main trends (Fig. 5).

The two main components represented 68% of total inertia. The first axis of inertia separated summer and spring from winter and autumn samples. The more abundant species in the first part of the year were species that

break or pierce the frustules of diatoms to suck out their contents (*Chromadora macrolaima*, *Ptycholaimellus jacobii*) or those which swallow the whole diatom cell (*Daptonema oxycerca*). Species abundant during the second part of the year were those that feed on derived products of primary production (*Metachromadoroides remanei*) or other sources of food (*Terschellingia longicaudata* and *Sabatieria pulchra*).

Some parameters were positively correlated (Table 5) such as heavy metals (Cu, Pb, Zn) with organic matter content (0.71, 0.81, 0.81, respectively) as well as with *Terschellingia longicaudata* (0.78) and *Sabatieria pulchra* with Cd (0.75). Those genera are known to live in reduced sediments with high organic content. All species

Table 4 Percentage of nematode feeding types for each of the samples (feeding types after Wieser (1953, 1960))

Station	Sampling date	Feeding types (%)				Intermediary type
		1A	1B	2A	2B	
1	January	17	59	18	6	0
1	April	15	34	48	1	1
1	July	10	60	27	3	0
1	October	28	32	31	5	3
2	January	18	17	53	11	1
2	April	11	26	60	3	0
2	July	14	27	53	4	1
2	October	14	20	59	4	2
4	January	9	42	42	5	1
4	April	9	16	67	7	2
4	July	17	34	42	3	4
4	October	32	43	23	1	1
	Total	16	35	43	4	1

1A, selective deposit feeders; 1B, non-selective deposit feeders; 2A, epigrowth feeders; and 2B, omnivores/predators.

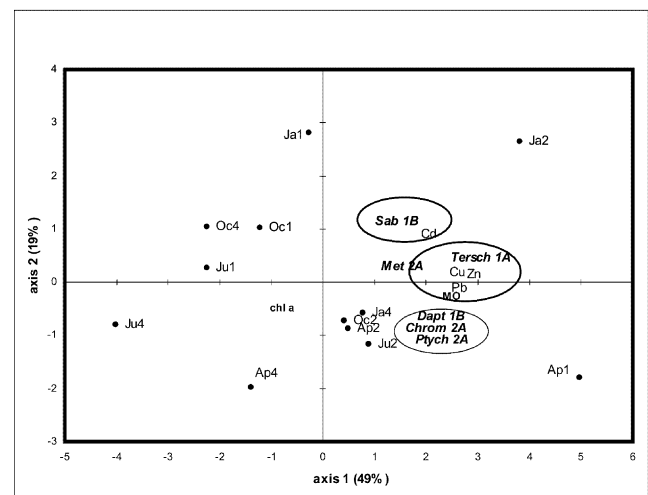


Fig. 5. PCA performed on the six main nematode species identified from 36 replicates sampled at 3-monthly intervals at the three stations in the mudflat of Brouage.

Table 5

Correlations between environmental variable such as organic matter (%MO), chlorophyll *a* content (Chl *a*), heavy metals concentration (Cu, Zn, Pb, Cd) and nematode species abundances

	%MO	Pb	Cu	Zn	Cd	Chl <i>a</i>	<i>Met.</i>	<i>Sab.</i>	<i>Tersch.</i>	<i>Chrom.</i>	<i>Ptych.</i>
Pb	0.81										
Cu	0.71	0.88									
Zn	0.82	0.96	0.87								
Cd	0.34	0.57	0.63	0.55							
Chl <i>a</i>	-0.13	-0.36	-0.64	-0.38	-0.45						
<i>Met.</i>	0.55	0.29	0.37	0.32	0.13	0.02					
<i>Sab.</i>	0.16	0.32	0.32	0.35	0.75	-0.50	-0.15				
<i>Tersch.</i>	0.69	0.76	0.76	0.79	0.53	-0.36	0.59	0.23			
<i>Chrom.</i>	0.40	0.47	0.43	0.42	0.12	-0.19	-0.19	-0.05	0.29		
<i>Ptych.</i>	0.58	0.51	0.39	0.51	-0.20	0.07	-0.05	-0.19	0.09	0.59	
<i>Dapt.</i>	0.61	0.52	0.56	0.49	0.13	-0.26	0.05	-0.16	0.44	0.79	0.51

M. remanei (*Met.*), *S. pulchra* (*Sab.*), *T. longicaudata* (*Tersch.*), *C. macrolaima* (*Chrom.*), *P. jacobi* (*Ptych.*) and *D. oxycerca* (*Dap.*). Bold values indicate correlation significant at $p > 0.05$ ($n = 12$).

were positively correlated with organic matter, with the exception of *S. pulchra* whose correlation was not significant. Other parameters had a strongly negative correlation such as chlorophyll content with Cu (-0.69) and *S. pulchra* (-0.5).

Metachromadoroides remanei was correlated with *Terschellingia longicaudata* (0.6). The abundance of *M. remanei* was not significantly correlated with the abundance of other epigrowth feeders such as: *Ptycholaimellus jacobi*, *Chromadora macrolaima* and non-selective deposit feeder such as *Daptonema oxycerca* (correlations of -0.04, -0.18, -0.16, respectively). Abundance of those three last species was inter-correlated (correlation from 0.51 to 0.58). *Sabatieria pulchra* was not significantly correlated with other species (correlation between -0.19 and 0.23).

Seasons strongly contributed to inertia: stations 1 and 4 in April and station 4 in July (89% to first axis) and stations 1 and 2 in January (54% to second axis). The two first inertia axis did not properly explain the fluctuations of *Metachromadoroides remanei* and chlorophyll content (\cos^2 : 0.14 and 0.44).

4. Discussion

Meiofauna were an important component of the benthos in Brouage mudflat with peak abundance reaching 4051 ind 10 cm⁻². Nematodes represent about 95% of total meiofauna with mean densities of 2112 ind 10 cm⁻². Similar abundances have been already observed by Montagna et al. (1995) in Marennes Oléron Bay and by other authors in European estuaries such as Gironde, Tagus and Westerschelde (Soetaert, Vincx, Wittoeck, & Tulkens, 1995) or the estuarine mudflat of the Lynher Estuary in Cornwall (Warwick & Price, 1979).

The parameters measured in this study do not seem to have a direct influence on the variations in nematode population structure; the metal concentrations were low and the sediment properties and micro-

phytobenthic biomass were homogenous along the cross-shore transect and rather constant over the sampling period. The concentrations of Cd, Cu, Pb and Zn measured at three stations showed that the sediment in Brouage was not heavily polluted compared to similar biotope such as the Fal Estuary in Cornwall where Somerfield, Gee, and Warwick (1994) found values of two to three orders of magnitude higher than in the present study.

In Brouage, the correlation of Cu, Zn and Pb with organic matter was high (Table 5) making it impossible to distinguish between heavy metal contamination effects and organic matter effects. Many heavy metals are bound to organic matter in sediment (Bryan & Langston, 1992) and their variations can be attributed to fluctuations in organic matter stock. At the Brouage site, the poor correlation of Cd with organic matter is probably due to the different chemical behaviour of this metal which is known to be more mobile. At the concentrations observed in this study, Cd is unlikely to be toxic for nematodes as experimental data (Austen, McEvoy, & Warwick, 1994; Austen & Somerfield, 1997) proved that estuarine nematodes are robust to heavy metal contamination.

The strong negative correlation of copper with chlorophyll *a* could result from the metal's impact on benthic algal development as correlation of chlorophyll *a* with organic matter is not significant. Experiments conducted on the marine pennate diatom *Haslea ostrearia* (Joux-Arab, Berthet, & Robert, 2000) have shown that copper can reduce the size of diatom cells and inhibit their development. Those mechanisms identified on planktonic diatoms may also apply to benthic diatoms. Hence, the abundance of nematode species feeding on the diatoms could be indirectly affected by the copper concentration in the sediment.

In the Brouage mudflat, the nematode community is mainly composed of *Metachromadoroides remanei*, *Ptycholaimellus jacobi*, *Chromadora macrolaima*, *Daptonema oxycerca*, *Terschellingia longicaudata*, *Sabatieria*

pulchra and *Sabatieria punctata*, which constitute 75% of nematode abundance. Such dominance of a few species has been recorded from other estuaries (Eskin & Coull, 1987; Soetaert et al., 1995; Warwick, 1971). *Sabatieria*, *Daptonema* and *Terschellingia* were the most common genera for tidal estuarine mudflats and *Metachromadora* was one of the dominant genera in the Tamar estuary (Warwick & Gee, 1984).

The PCA showed that the community was not structured spatially but temporarily. Summer depression of meiofauna observed in the Brouage mudflat, is common in intertidal ecosystems (Warwick & Price, 1979). Rudnick, Elmgren, and Frithsen (1985) suggested that the decline of meiobenthic organisms during summer and autumn could be attributed to a combination of factors, including food and oxygen availability, but other authors also suggest an enhanced macrofauna predation (Coull, Greenwood, Fielder, & Coull, 1995; Feller, 1984; Platt & Warwick, 1980; Sogard, 1984). In Brouage, the influence of physical factors might partly explain the summer decrease in nematode abundance. Temperature and salinity of emerged sediments are more extreme during summer tidal cycle as pointed by Guarini, Blanchard, Gros, and Harrison (1997).

It appears very likely that the variations in nematode abundance reflect the different trophic requirements of the population over the 1 year. In autumn and winter, a non-selective deposit feeder such as *Sabatieria pulchra* and a selective deposit feeder such as *Terschellingia longicaudata* were very abundant.

A strong correlation of *Terschellingia longicaudata* with organic matter suggests an environmental relation between the two. A large amount of organic matter often results in organic matter decay, anoxic conditions and high bacteria development. As *T. longicaudata* is usually found in anoxic conditions and feeds on bacteria (Wieser, 1953, 1960), the correlation found here might reflect these situations. *T. longicaudata* is generally found in the deeper layers of the substrate (Eskin & Palmer, 1985).

Similarly, *Sabatieria pulchra*, classified as non-selective deposit feeder, is known from muddy sediments independent of water depth. The species is found in the redox potential discontinuity layer and can be considered to be a facultative anaerobic animal (Jensen, 1981). The food requirement of this species is unknown except in particular biotopes where the species is attracted by roots of *Potamogeton* meadows in the Baltic Sea (Jensen, 1981). Boucher (1974) noted the presence of small organic particles derived from plants and bacteria in gut contents of different *Sabatieria* species. No satisfactory explanation for the correlation of Cd with *S. pulchra* could be found.

One species, *Metachromadoroides remanei*, was present during the four seasons in notably high abundance (up to 1743 ind 10 cm⁻²). According to buccal

morphology, *M. remanei* was considered as an epistrate feeder (Wieser, 1960). Strangely, the occurrence of *M. remanei* is correlated with *Terschellingia longicaudata* and organic matter but is not correlated with the species *Chromadora macrolaima* and *Ptycholaimellus jacobi* that are supposed to belong to the same trophic type. Moreover, *M. remanei* was more abundant in autumn and winter, as were *Terschellingia* and *Sabatieria*. Recent experimental results concerning the nematodes suggest that carbon derived from microphytobenthos could be conveyed to them via other pathways than direct grazing on microphytobenthos (Moens et al., 2002). Applying this result to the genus *Metachromadora* (*Metachromadoroides*) and interpreting the observed correlation of *M. remanei* abundance and organic matter as a possible environmental relation, *M. remanei* could consume organic matter derived from microphytobenthos.

Three species, i.e. *Chromadora macrolaima*, *Ptycholaimellus jacobi* (epigrowth-feeders) and *Daptonema oxycerca* (non-selective deposit feeder) dominated the Brouage nematode community, during spring diatom bloom and temperature rise. These species probably drive the population dynamics since they have a short generation time of about 2–4 weeks (Heip et al., 1985; Hopper & Meyers, 1966; Tietjen, 1967; Tietjen & Lee, 1973; Warwick, 1981). This means the population can rapidly adapt to the spring conditions of their high relative abundance. However, those three species whose abundances are strongly correlated, do not present similar feeding strategies.

Daptonema oxycerca, initially classified as a non-selective deposit feeder is able to swallow particles of different sizes and large frustules of diatoms (Boucher, 1974; Jensen, 1979; this study). Boucher (1974) noted the large frustules of *Navicula* and *Gyrosigma* in the intestine of *Theristus* sp., a genus close to *Daptonema*. As observed by Moens and Vincx (1997), diatoms are clearly an important food, since freshly sampled individuals of *Daptonema setosum*, commonly have up to 40 or more diatom frustules in their intestine. It is, however, still impossible to evaluate the proportion of diatoms and other particles in the diet.

Feeding habits of *Ptycholaimellus* are close to those of *Hypodontolaimus*, which has a similar buccal cavity. *H. balticus* has been reported to use the dorsal tooth to puncture the diatom frustules after which the cell content is removed (Jensen, 1984). However, some specimens of *Ptycholaimellus jacobi* found in Brouage (about 2%) had a strange cup shaped funnel on the apical part of the head. The function of this structure remains unknown; it could be employed as a means of gathering diatoms.

While most of the information on other nematode diets are not so readily available and remain quite qualitative, *Chromadora* feeding habits are well documented. Feeding habits and ingestion rate of some genera close

to *Chromadora* which feeds on pennate diatoms are known from culture experiments: *Chromadorita tenuis* (Jensen, 1987) and *Chromadora macrolaimoides* (Tietjen & Lee, 1973). Laboratory experiments performed at 20–25 °C and 26‰ S (Tietjen & Lee, 1973) showed that the latter species selects its food and regulates its ingestion rate according to the food source (14 µg of *Nitzschia acicularis* per day and 27 µg of *Nitzschia closterium* per day). As the feeding experiment lasted 72 h, it integrates the eventual daily feeding cycles.

Considering that these conditions may be compared with a field situation in late spring and summer and a mean July abundance in the present study of 5.8×10^4 *Chromadora macrolaima* per square metre, a population of this species could ingest between 0.8 and 1.6 g diatoms $m^{-2} d^{-1}$, i.e. 1.6–3.0 mg Chl $m^{-2} d^{-1}$ or 62–120 mg C $m^{-2} d^{-1}$ in the mudflat. The ratio of dry biomass of diatoms/chlorophyll content in the present study was 522 ± 276 (Fichet, personal communication) and the ratio C/Chl *a* was estimated 40 (Chardy & Dauvin, 1992). While ingestion rates were obtained in laboratory conditions, this estimation compares reasonably with the consumption of microphytobenthos by the whole meiofauna previously measured by Montagna et al. (1995) in July, i.e. 58–189 mg C $m^{-2} d^{-1}$.

In April and July, as *Chromadora* population amounts to 3.6×10^5 per square metre, the grazing rate could be estimated between 385 and 744 mg C $m^{-2} d^{-1}$ or 16 and 31 mg C $m^{-2} h^{-1}$. In Guarini, Blanchard, Gros, Gouleau, and Bacher (2000), the maximum photosynthetic capacity in April and the maximum biomass of the photosynthetic biofilm are estimated, respectively, as 11.2 mg C (mg Chl *a*) $^{-1} h^{-1}$ and 25 mg Chl *a* m^{-2} . Thus, the maximum photosynthetic production should amount to 280 mg C $m^{-2} h^{-1}$. The grazing rate of *Chromadora* amounts to 6–11% of the maximum photosynthetic production.

According to Guarini et al. (2000), microphytobenthos production only occurs during mudflat emersion in the daytime. With an average of 7 hours of daytime emersion, the daily microphytobenthos production can be estimated to be 1960 mg C $m^{-2} d^{-1}$. The grazing rate of *Chromadora* can represent 20–38% of microphytobenthos production. This result should be considered as a maximum as the specimens *Chromadora* used in the experiment by Tietjen and Lee (1973) were starved for 24 h.

In spring and summer samples, the nematode community is dominated by epigrowth-feeders (50%) of which *Chromadora* constitutes 36%. In this season, the diatom community is largely dominated by pennate diatoms, particularly *Navicula* sp., *Gyrosigma*, *Pleurosigma* and *Nitzschia* (Haubois, personal communication) that epigrowth-feeders prefer (Admiraal et al., 1983; Bouwman, 1983; Jensen, 1984; Trotter & Webster, 1984) as those diatoms are an adequate size to be used as a food source. Assuming that epigrowth-feeders have

grazing rates similar to *Chromadora*, the nematode grazing on microphytobenthos may have a significant impact on primary production in spring approximately half of the daily production.

Such a high grazing rate makes it important to take nematodes into account when building a model for trophic relations. The high number of nematodes found in the mudflat represents nearly 2 million potential grazers per square metre that feed on microphytobenthos, labile organic carbon derived from microphytobenthos or bacteria. Nematodes constitute an important energy pathway from primary production to higher trophic levels. Even if they represent only about 10% of total macrofaunal biomass of Brouage, throughput is 1.6 times higher and production twice the macrofaunal production (Leguerrier et al., 2003).

There is an on going debate about the relative importance of meiofauna grazing and microphytobenthic production. These results suggest very high meiofauna grazing compared to primary productivity. Studies suggesting that nematode carbon assimilation does not constitute more than a few percent of primary production based on assimilation rather than grazing (Moens et al., 2002). The ratio assimilation to ingestion amounts to 6.2% for *Chromadorina germanica* (Tietjen, 1980). So, a carbon assimilation of a few percent of microphytobenthos appears compatible with a high ingestion rate. Admiraal et al. (1983) describe a situation where meiofauna only uses about 10% of microphytobenthic production in the Eems-Dollard Estuary. The results show much dependence on the local and seasonal structure of nematode population, their grazing rates and local microphytobenthic production. Considering results from previous studies, it appears that further investigations are needed to assess nematode grazing rates at species level in order to obtain reliable data of carbon flux in benthic ecosystem. Experiments are in progress to assess the ingestion rates of some dominant epistrate-feeders (*Metachromadoroides*, *Daptonema*) and one omnivore–carnivore (*Sphaerolaimus*).

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