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Predation and sediment disturbance effects of the intertidal polychaete *Nereis virens* (Sars) on associated meiofaunal assemblages

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Abstract

A microcosm experiment was carried out to determine the effects of the activity of the burrowing polychaete *Nereis virens* (Sars) on the associated meiofauna. The sediment basin (76 X 41 cm) was filled with 10 cm of sandy sediment previously sieved with a l-mm mesh to remove any undesired macrofauna and macrodetritus. Fifteen 13-cm long polyvinyl-chloride (PVC) tubes (I.D. = 10 cm) were pushed into the sediment to partition treatments. ***Nereis*** were added to the tubes at two densities, low (N = 1) and high ($N = 3$). Five tubes were used as controls (no *Nereis*), while two sets of five tubes were used for the low (L) and high (H) density treatments. respectively. After 14 days, meiofauna was sampled by coring. Cores were cut into three slices: surface (O-l cm), subsurface (l-5 cm), and deep (5–10). High densities of ***Nereis*** (H) significantly affected nematodes, harpacticoid copepods, and nauplii abundance. However, lower abundances were found only in the top cm of the sediment. Moreover, a significant number of dead nematodes found in this sediment layer of treatment H allowed a distinction between sediment disturbance effects and predation effects. Sediment disturbance caused by Nereis may be related to an intensive "ploughing" of surface sediment during food-searching activity. Diversity indices were affected only in the top cm of the sediment with generally lower values in treatment H. Differences in the relative survival of the different feeding groups were found in treatment H, where microvores and deposit feeders respectively showed greater and lower survival. Multivariate analysis (multidimensional scaling) revealed significant differences in nematode species composition among treatments in all sediment layers. It is concluded that N. *virens* significantly affects meiofauna mostly by disturbance of the top cm of the sediment where its predation represents an influent force as well. The structure of nematode assemblages in subsurface and deeper sediment

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layers is also affected. most likely by changes in redox conditions caused by the bioirrigating effects of Nereis burrows.

Keywords: Nereis; Disturbance: Predation: Community structure; Meiohenthos: Nematodes; Microcosm experiment

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1. Introduction

Several studies have shown the importance of infaunal polychaetes in structuring macrofaunal benthic assemblages either by trophic interactions (i.e. competition and predation) or by sediment disturbance (Fauchald and Jumars, 1979; Witte and de Wilde, 1979; Brenchley, 1981; Wilson, 1981; Commito and Shrader, 1985; Ronn et al., 1988). Commito (1982) and Ambrose (1984a,b,c) showed that nereid polychaetes play a significant role in regulating the densities of infaunal amphipods, bivalves, and annelids.

Other studies suggest that nereids may be an important structuring agent of meiofaunal assemblages as well, again through predation or sediment disturbance. Goerke (197 1) defined the polychaete Nereis *diversicolor* (Müller) as an opportunistic omnivore including meiofauna in its diet, and Reise (1979) demonstrated that N. diversicolor can have a significant negative impact on meiofaunal abundance. Ronn et al. **(1988)** stated that this polychaete "must be considered as an important structuring force in brackish-water soft-bottom habitats, either by direct predation or by disturbance". Olivier et al. (1993) showed through gut content analysis of Nereis *virens* (Sars) that adults of this species are almost exclusively carnivores feeding on small macrofauna and meiofauna, whereas juveniles are deposit-feeders. A comparative study between N. diversicolor and N. *virens* showed that these two burrowing species have very similar feeding strategies (Olivier, 1994). Both of them use two different food-searching strategies (Goerke, 1971, 1976; Miron et al., 1992a,b; Olivier, 1994). The first strategy (surface searching) consists of extending a third of their body length from their burrow to search for detritus particles or small macrofaunal prey. The latter are attacked with a rapid bound and seized with the eversible pharynx and large jaws typical of Nereis. Using this same tactic, Nereis can "sweep and plough" the surface of the sediment and swallow almost unselectively organic and inorganic fractions of the sediment with its eversible pharynx. Olivier et al. (1993) reported that 75 to 98% (depending on the year period) of *Nereis* gut content is composed of inorganic matter (sediment grains). The second strategy involves the production of a kind of mucus web at the surface of the sediment which entraps sedimenting particles; subsequently, *Nereis* feeds by swallowing the mucus web and the entrapped particles. The surface food-searching strategy is likely to produce both predation and sediment disturbance effects on the meiofauna living in the uppermost layer of the sediment. Video observations (Goerke, 1976) showed that N. *diversicolor* and N. *virens* heavily disturb the surface of the sediment during their food-searching activity. Meiofauna may also be affected in deeper layers of the sediment by changes in redox conditions caused by the bioirrigating effects of Nereis burrows. Reise (1981, 1985), and Reise and Ax (1979) observed greater meiofaunal abundance in deeper sediment layers near macrofaunal burrows suggesting a promotive effect of these biogenic structures.

In spite of the above mentioned studies, indicating that *Nereis* have an influence on meiofauna, Kennedy (1993) concluded after a 6-day field experiment that meiofauna were unaffected by the presence of N. *diversicolor*.

N. *virens* is one of the dominant macrofaunal species of the soft-bottom intertidal zone of the St. Lawrence Estuary (Canada) (Desrosiers et al., 1980, Desrosiers and Brêthes, 1984), and represents one of the most influential biological components of the local intertidal ecosystem (Caron, 1995).

The aim of the present study was to determine if *Nereis* is an effective determinant of meiofaunal densities and nematode assemblages structure. If it is, two questions must be addressed: (1) Is the effect of *Nereis* limited to the surface layer of the sediment, where it feeds, or does it affect deeper layers as well? (2) Do different densities of *Nereis* result in different degrees of structuring effect on nematode assemblages? In order to answer to these questions, a microcosm experiment was carried out to observe the effects of N. *virens* on the meiofauna.

2. Materials and methods

2.1. Experimental design

A 14-day microcosm experiment was conducted at the Pointe-aux-Peres near-shore station of the Université du Quebec à Rimouski (UQAR) on the south shore of the St. Lawrence Estuary (Canada). On September 10, 1997, the top 10 cm sediment was collected from the mid tidal zone of a sheltered inlet located in the Parc provincial du Bic, 45 km west of Pointe-aux-Peres. The sediment was sieved through a 1 mm mesh in order to eliminate the bulk of macrofauna and macrodetritus, and distributed evenly in a 10 cm layer in a poly(vinyl chloride) (PVC) basin (76 L *X* 4 1 W *X* 35 H cm) after being thoroughly mixed to ensure homogeneity. A sample of the sieved sediment was used for granulometric analysis (median = 90 pm; silt-clay = 14%) and organic matter (1.4% of sediment dry weight; combustion at 500°C for 6 h). Fifteen PVC tubes (internal diameter = 10 cm; length = 13 cm) were inserted into the sediment (Fig. 1). Tubes protruded 3 cm out of the sediment and had four holes (diameter = 5 mm) drilled on opposing walls just above the sediment-water interface to allow water circulation. The holes were covered with a 500-μm mesh gauze in order to prevent *Nereis* individuals from leaving their respective tube. The basin was placed in a room with constant temperature (13°C) and a 12: 12 h L:D photoperiod. The temperature corresponded to the mean summer water temperature in the field, and the photoperiod was an approximation of the natural summer photoperiod. Sea water in the basin had a 10 cm depth above the sediment and was changed every 48 h with water collected directly from the sea by a pumping system of the station and previously brought to the experimental temperature. Water aeration was maintained with six air stones. In order to allow surface sediment to remain undisturbed, water change was made as slow as possible (water level increase/ decrease ≈ 3 mm min^{-1}) from two opposite comers of the sediment basin.

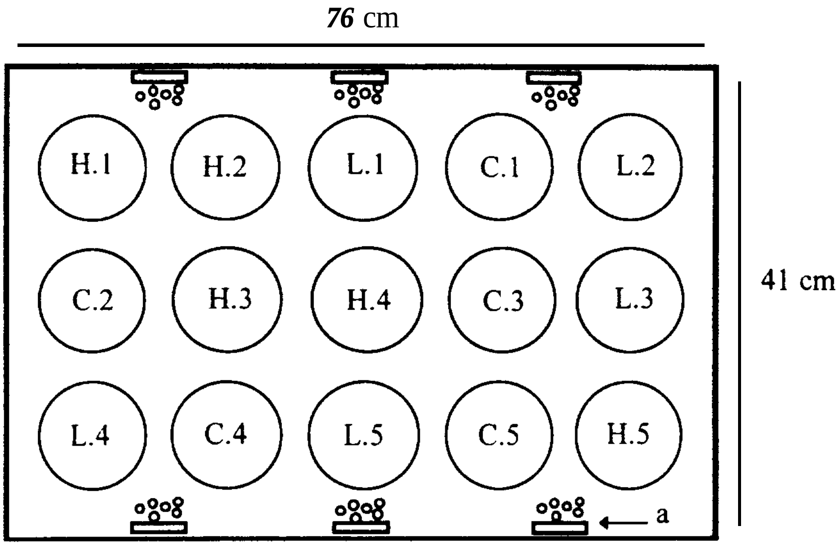

Fig. 1. Experimental design: position of treatments (randomly selected) in the basin; C = controls (no *Nereis*); L = low density of *Nereis* (N = 1); H = high density of *Nereis* (*N* = 3). Internal diameter of treatment tubes = 10 cm. Aeration was insured by six air stones (a) evenly spaced along the side of the basin.

Individuals of ***Nereis*** were collected on September 11, 1997, from the same station as the sediment sampling. At this site, ***Nereis*** individuals have a mean body size intermediate between mature adults, which primarily inhabit the lower tidal zone, and juveniles, which inhabit the upper tidal zone (Caron et al., 1995). Individuals were selected according to body length (7.3 ± 1 .O cm ind.$^{-1}$) and body wet weight (684 ± 15 1 mg ind.$^{-1}$). Two h after collection, the polychaetes were placed in a basin containing aerated marine water located in the same temperature-controlled room. Twenty-four h after polychaete sampling, ***Nereis*** individuals were added to the cores of the sediment basin according to the following design: (i) five control cores (C) with no ***Nereis;*** (ii) five low-density cores (L) with one individual of ***Nereis:*** (iii) five high-density cores (H) with three individuals of ***Nereis.*** Low and high densities of ***Nereis*** corresponded to approximately two- and five-times the normal mean density in the field (75 ±25 ind. m^{-2}, Caron et al., 1995). This was selected following the principle that, at greater experimental densities over a short period of time, the predator should induce a similar effect to normal densities over a longer time (Raffaelli et al., 1989). It is worth noting, however, that densities reported by Caron et al. (1995) are integrated on 1 m^{2}, and that, at smaller spatial-scales, according to its patchy distribution this polychaete may show densities comparable to those used in our experiment (A. Caron, personal communication). In order to avoid any escape of ***Nereis*** individuals, 2-mm mesh grids were fixed to the top of each core including the control cores.

2.2. Sampling

Sampling, was done 14 days after the introduction of ***Nereis*** individuals and was performed using a sharpened circular punch (internal diameter = 26 mm). The water above the sediment was piped out before samples were collected. One sample per core was collected (i.e. five replicates per treatment). Core samples were sectioned from the top into three slices, surface (0- 1 cm), subsurface (l-5 cm), and deep (5– 10 cm), and fixed with 4% formalin. Meiofauna extraction was done by centrifugation with Ludox TM (Heip et al., 1985) after washing samples over a 63-μm mesh sieve. Meiofauna were then counted under a dissecting microscope. Ninety nematodes per core slice were randomly selected and mounted on slides in anhydrous glycerol for identification at genus level, or species when practicable, using higher resolution microscopy. In samples of the O-l sediment layer of treatment H, 90% of individuals were found to be dead at the sampling time (see Results). The whole nematodes (dead + live) of these samples were therefore mounted on slides in order to have an acceptable number of live individuals for statistical analyses. Genus and species identification was based on Platt and Warwick (1983, 1988), and Hopper (1969). Assemblage analysis was restricted to the nematode meiofaunal component only. All individuals of Nereis were recovered alive and in good condition at the end of sampling procedure.

2.3. Data analysis

Abundances of the two main meiofaunal groups (nematodes and harpacticoid copepods) were used as a primary indicator of Nereis influence. Juvenile copepods (nauplii) were counted separately from adults (mentioned as copepods herein) and considered as a third meiofaunal group. Abundance data were In-transformed for comparison among treatments in order to achieve the analysis of variance (ANOVA) assumptions (normality: Kolmogorov-Smimov test; equal variance: Levene Median test). Effects on nematode species diversity was studied using four indices: (1) the number of species, N; (2) the Margalef s species-richness-weighted diversity index, SR (Margalef, 1958); (3) the Shannon index (calculated with Log,), H' (Margalef, 1958); (4) the evenness, J' (Pielou, 1966). Statistical differences between diversities of treatments were studied with untransformed data because ANOVA assumptions were achieved. The Student-Newman-Keuls (SNK) procedure was used for all pairwise multiple comparison between treatments.

The effects of Nereis on the different components of nematode assemblages were determined using a multidimensional scaling ordination (MDS) with different degrees of data transformation. Untransformed data analysis is more sensitive to changes in abundance of the dominant species, while increasingly severe data transformations ($\sqrt{}$ and $\sqrt{\sqrt{}}$) are more sensitive to changes of abundance of intermediate and rarest species (Clarke and Warwick, 1994). The MDS analyses were run on Pearson correlation matrices using the SYSTAT.7 software package (Wilkinson, 1997). One way ANOSIM (analysis of similarities) was carried out to determine differences between nematode assemblages in different treatments and sediment depths. SIMPER (similarity percentages) was used to determine the contribution of individual species towards dissimilarity between treatments. ANOSIM and SIMPER were run using the PRIMER (Plymouth Routines in Multivariate Ecological Research) (M. Austen, Plymouth Marine Laboratory, personal communication).

The Nereis effect on functional aspects of nematode assemblages was evaluated using the feeding groups of Moens and Vincx (1997): microvores, ciliate-feeders, deposit-feeders, epigrowth-feeders, facultative predators, and predators.

3. Results

3.1. *Influence on abundance of meiofauna*

More than 98% of total meiofauna, in all treatments, were represented by nematodes (~ 80%), copepods (~7%), and nauplii (~ 12%). However, in the 0- 1 cm layer of treatment H, almost 90% of the nematodes that were counted under the dissecting microscope were found to be dead at the time of sampling when observed at higher resolution microscopy (Fig. 2). Dead individuals were identified by a relatively advanced decomposition of internal anatomy indicating that death probably occurred several days before sampling. This massive mortality was interpreted as a consequence of *Nereis* sediment disturbance. In the O-l cm layer of treatment H, "live-nematode"

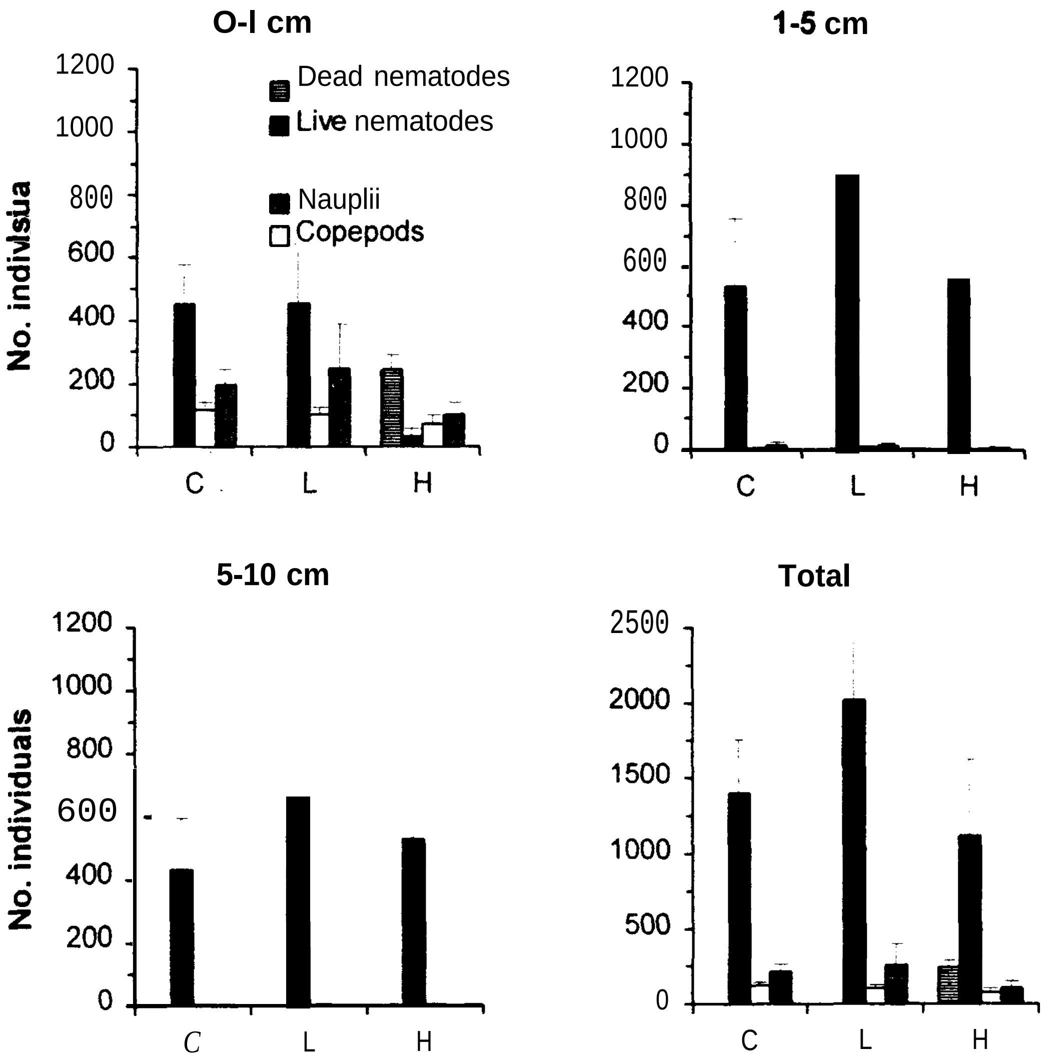

Fig. 2. Abundance (no. individuals/sample) (mean±95% CI) of nematodes. copepods. and nauplii for surface (O-l cm), subsurface (l-5 cm), deep (5-10 cm) sediment layers, and whole cores (O-IO cm). Treatment: C = controls; L = low density; H = high density.

abundance (28± 8 individuals) was significantly lower than “dead-nematode” abundance (278±23 individuals) (r-test, $p < 0.0001$). In the O-l cm layer, abundance of “live” nematodes, total nematodes (live + dead), copepods, and nauplii was significantly lower in treatment H than in controls and treatment L (Fig. 2 and Table 1). Total nematode abundance (dead + live) in treatment H was 39% lower than in the controls. This reduced abundance was interpreted as a gross estimation of *Nereis* predation effect. The resulting estimation of the ratio dead nematodes/consumed nematodes was 6:4. Abundance of copepods and nauplii in treatment H showed a reduction of the same order with 38 and 48% less individuals, respectively, than in the controls. For these two groups it was not possible to distinguish dead from live individuals as they were not studied at higher resolution microscopy.

No significant difference was found for nematode abundances between treatments in the subsurface (1-5 cm: $F = 3.31$, $p = 0.071$) and the deep (5-10 cm: $F = 2.10$, $p = 0.166$) sediment layers. In these two sediment layers, copepods and nauplii had densities too low to allow statistical comparisons between treatments.

The abundances of live nematodes and total nematodes in the whole sediment cores (O-10 cm) was significantly greater in treatment L than in the controls and treatment H (Fig. 2, Table 1). The greater abundance of nematodes in the whole cores of treatment L compared to controls was due to a greater abundance in the l-5 and 5–10 cm sediment layers, though not statistically significant when considered in individual layers.

Dead nematodes in treatment H were not considered for assemblage analysis (diversity indices, MDS, and feeding structure), though species were still identifiable.

3.2. Influence on nematode assemblages structure

3.2.1. Univariate analysis

Univariate measures (diversity indices) did not show any significant differences between treatments when considering the whole cores, except for abundance (Figs. 2 and

Table 1
ANOVA results indicating statistic value (F) and significance level (*p*) of tests for differences in abundance (In-transformation) for the surface sediment layer and the whole cores; SNK test identifies differences among treatments (continuous lines indicate no significant difference)

	One-way ANOVA	Student-Newmann-Keuls test ($p < 0.05$)		
O-1 cm		C	L	H
“Live” nematodes	$F = 49.6$; $p < 0.001$	———	———	
Total nematodes (live + dead)	$F = 5.3$; $p < 0.05$	———	———	
Copepods	$F = 5.2$; $p < 0.05$	———	———	
Nauplii	$F = 10.3$; $p < 0.01$	———	———	
Total		C	H	L
“Live” nematodes	$F = 7.2$; $p < 0.01$	———	———	
Total nematodes (live + dead)	$F = 4.1$; $p < 0.05$	———	———	

3). However, distinct measures of diversity indices for the different sediment layers showed contrasting results. In the O-l cm sediment layer, treatment H had significantly lower values for the number of species (*N*) and the Shannon index (*H'*) (Table 2). Inversely, in treatment H, equitability (J') was significantly greater than in treatment L and tended to be greater, although not statistically significantly, than in controls (Fig. 3 and Table 2).

In the l-5 cm layer, only the Margalef' s species richness (SR) was found to be significantly greater in treatment H than in C and L (Table 2). No significant difference between treatments was found in the 5-10 cm sediment layer.

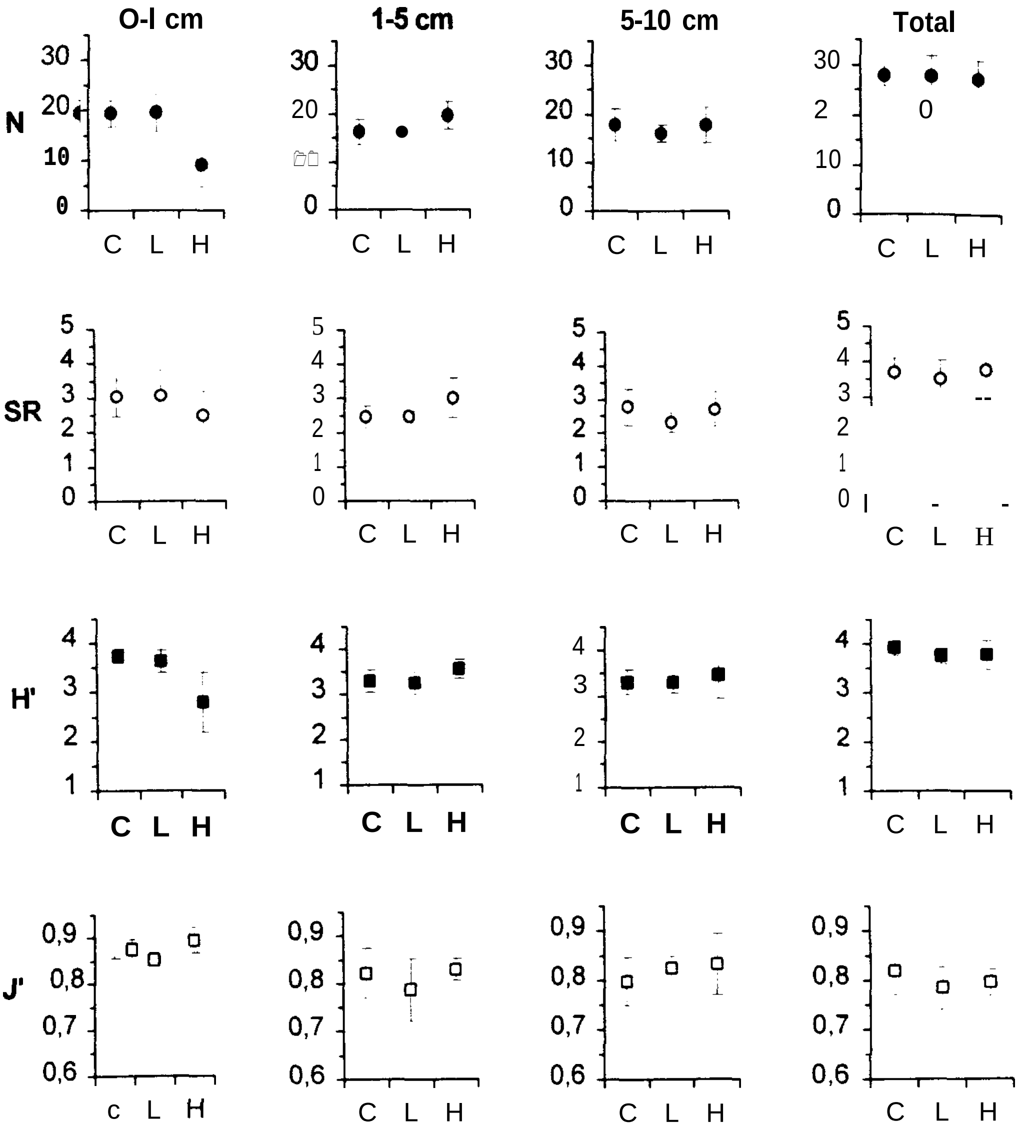

Fig. 3. Diversity indices (mean ±95% CI) for nematode assemblages in specific sediment layers and the whole cores. N = no. of species; SR = Margalef s species richness; *H'* = Shannon's index (calculated using Log_2); *J'* = evenness. Treatment: C = control; L = low density; H = high density.

Table 2
ANOVA results indicating statistic value (F) and significance level (*p*) of tests for differences in diversities (no data transformation) for the surface (0- 1 cm) and subsurface (I -5 cm) sediment layers; SNK test identifies differences among treatments (continuous line indicate no significant difference)

	One-way ANOVA	Student–Newmann–Keuls test ($p < 0.05$)		
O-l cm		C	L	H
N	$F = 20.6$; $p < 0.0001$	————————		
H'	$F = 13.9$; $p < 0.001$	————————		
J'	$F = 6.1$; $p < 0.05$	————————		—
1–5 cm				
SR	$F = 7.34$: $p < 0.01$	————————		

3.2.2. *Multivariate analysis*

The MDS plots with untransformed and d-transformed data differentiated controls and treatments not only when considering the different sediment layers separately, but also when taking into account the whole cores (Fig. 4). With a more severe data transformation ($\sqrt{\sqrt{}}$), samples of all treatments were distributed with no apparent order; for this reason these plots are not reported herein. ANOSIM results show differences between controls and treatments (Table 3). In the O-l cm layer, SIMPER results showed that dominant species in controls and treatment L (*Eleutherolaimus* sp., *Anoplostoma blanchardi*, *Microlaimus* sp. 1, *Sabatieria punctata)* were the most affected when associated to high densities of *Nereis* (Table 4). Species with intermediate abundance (*Paracanthonchus caecus*, *Innocuonema* sp., *Desmolaimus* sp., *Theristus (Daptonema)*

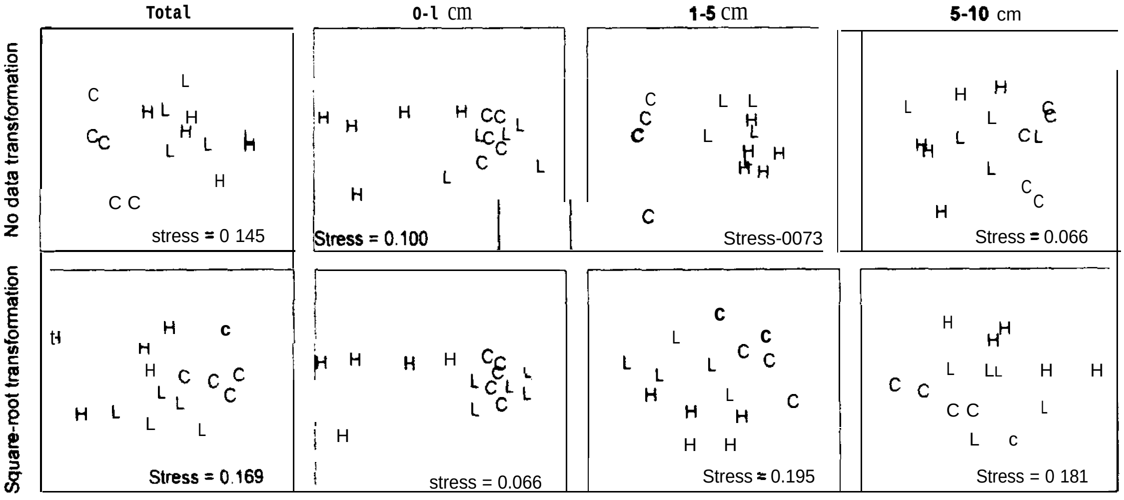

Fig. 4. Multidimensional scaling (MDS) ordinations of nematode assemblages for the different sediment layers and the whole cores with untransformed and V'-transformed data. C = control; L = low density treatment: H = high density treatment.

Table 3
ANOSIM results indicating statistic value (*R*) and significance level (*p*) of tests for differences in nematode assemblage structure between controls (C) and treatments L and H in the different sediment layers and at different levels of data transformation

		Data transformation					
		None		√		√√	
		R	*p*	*R*	*p*	*R*	*p*
O-l cm							
C	L	0.02	0.44	− 0.03	0.56	0.01	0.44
	H	1.00	**	0.96	**	0.86	**
L	H	0.99	**	0.96	**	0.88	**
l-5 cm							
C	L	0.48	**	0.33	*	0.16	0.14
	H	0.37	*	0.14	0.18	0.03	0.43
L	H	0.37	*	0.28	0.56	0.10	0.29
5–10 cm							
C	L	0.40	*	0.43	*	0.36	*
	H	0.42	**	0.35	*	0.30	*
L	H	0.16	0.18	0.27	0.63	0.27	0.71
Total							
C	L	0.48	**	0.42	**	0.19	0.87
	H	0.40	*	0.32	**	0. IO	0.21
L	H	0.48	**	0.55	**	0.46	**

$p < 0.05$ (*)
$p < 0.01$ (**)

procerus) were, however, also affected. In the subsurface (l-5 cm) and deep (5-10 cm) layers, differences between controls and treatments were most evident in the rank of the dominant species, particularly *S. punctata*, *Sabatieria* sp. A, and *Paramonohystera* sp.

3.3. Influence on the vertical distribution of nematode species

The vertical zonation of nematode species was studied using the MDS analysis (Fig. 5). In the controls, samples clearly clustered according to their sediment layer. In treatments L and H, surface samples (S) were also well separated from subsurface (M) and deep (D) samples; however, subsurface and deep samples were not as clearly separated as in the controls. MDS analysis with transformed data gave very similar plots to those with untransformed data. ANOSIM results showed the differences between the sediment layers in the controls and the treatments (Table 5). SIMPER analysis showed the contribution of each species to the mean Bray-Curtis dissimilarity term between sediment layers (Table 6). Bray-Curtis dissimilarity between samples of same sediment layer and treatment was generally smaller than 40%, except for the O-l cm samples of treatment H (53%) where nematode assemblages were more heterogeneous in their composition and structure.

Table 4
Results from SIMPER analysis of untransformed data of nematode abundances indicating the contribution (%) of each species to the mean Bray-Curtis dissimilarity term (between parenthesis) for the O-I cm (a), the I-5 cm (b), and 5–10 cm (c) sediment layers; a cut-off of 70% was employed (i.e. when 70% of the total Bray-Curtis dissimilarity term between treatments has been explained by the species which are listed in order of decreasing contribution).

	Mean abundance (ind. / sample)		%	Cumulative (%)
a)				
Treatments compared	C	L	(37.85)	
Paracanthonchus caecus	41	13	8.96	8.96
Theristus (D.) procerus	24	39	8.46	17.42
Anoplostoma blanchardi	58	65	8.24	25.66
Innocuonema sp.	27	38	7.88	33.55
Sabatieria punctata	37	43	7.43	40.98
Desmolaimus sp.	27	40	7.19	48.17
Eleutherolaimus sp.	76	69	6.74	54.91
Microlaimus sp. 1	42	41	6.02	60.93
Axonolaimus sp.	18	9	3.86	64.79
Leptolaimus papilliger	12	10	3.63	68.42
Halalaimus sp.	13	12	2.79	71.21
Treatments compared	c	H	(89.41)	
Eleutherolaimus sp.	76	3	17.02	17.02
Anoplostoma blanchardi	58	3	12.51	29.53
Microlaimus sp. 1	42	2	9.91	39.45
Paracanthonchus caecus	41	1	9.34	48.79
Sabatieria punctata	37	3	8.06	56.86
Innocuonema sp.	27	0	6.21	63.07
Desmolaimus sp.	27	0.4	5.68	68.75
Theristus (D.) procerus	24	1	5.13	73.87
Treatments compared	L	H	(89.87)	
Eleutherolaimus sp.	69	3	15.34	15.34
Anoplostoma blanchardi	65	3	14.74	30.09
Sabatieria punctata	43	3	10.04	40.13
Desmolaimus sp.	40	0.4	9.03	49.16
Microlaimus sp. 1	41	2	8.33	57.49
Innocuonema sp.	38	0	7.79	65.27
Theristus (D.) procerus	39	1	7.42	72.70
b)				
Treatments compared	C	L	(49.02)	
Sabatieria punctata	91	273	26.50	26.50
Paramonohystera sp.	86	175	14.85	41.35
Sabatieria sp. A	134	74	10.86	52.21
Anoplostoma blanchardi	20	55	5.10	57.32
Innocuonema sp.	27	51	5.10	62.41
Microlaimus sp. 1	30	32	4.13	66.54
Paracanthonchus caecus	8	30	3.43	69.97
Treatments compared	c	H	(45.61)	
Sabatieria sp. A	134	38	19.88	19.88
Sabatieria punctata	91	161	15.19	35.07
Paramonohystera sp.	86	53	10.81	45.87

Table 4. Continued

	Mean abundance (ind./sample)		%	Cumulative (%)
Anoplostoma blanchurdi	20	52	6.61	52.48
Paracanthonchus caecus	8	37	4.76	57.24
Microlaimus sp. 1	30	38	4.25	61.49
Daptonema tenuispiculum	21	16	4.00	65.49
Theristus (D.) procerus	23	20	2.84	68.34
Parachromadorita sp.	14	5	2.61	70.94
Treatments compared	L	H	(44.41)	
Sabatieria punctutu	273	161	18.45	18.45
Parumonohystera sp.	175	53	17.74	36.19
Sabatieria sp. A	74	38	6.43	42.62
Innocuonema sp.	51	28	5.46	48.08
Microlaimus sp. 1	32	38	5.21	53.30
Anoplostomu blanchurdi	55	52	5.19	58.49
Paracunthonchus caecus	30	27	3.49	61.98
Theristus (D.) procerus	26	20	3.48	65.46
Daptonema tenuispiculum	16	26	3.25	68.71
Ptycholaimellus ponticus	26	9	2.67	71.37
c)				
Treatments compared	C	L	(42.20)	
Paramonohystera sp.	13	105	19.25	19.25
Sabatieria punctutu	124	180	16.28	35.53
Anoplostoma blanchardi	47	71	9.27	44.80
Theristus (D.) procerus	44	57	7.51	52.31
Sabatieria sp. A	35	36	4.94	57.25
Ptycholaimellus ponticus	12	18	4.18	61.43
Innocuonema sp.	35	47	4.13	65.56
Daptonema tenuispiculum	14	24	4.03	65.59
Treatments compared	C	H	(44.29)	
Paramonohvstera sp.	13	83	16.67	16.67
Subutieria punctata	124	113	15.90	32.57
Theristus (D.) procerus	44	25	8.01	40.57
Anopiostoma blanchardi	47	39	7.34	47.91
Microlaimus sp. 1	33	47	6.35	54.27
Parachromadorita sp.	3	30	5.42	59.68
Sabutieria sp. A	35	26	5.37	65.06
Innocuonema sp.	35	51	4.44	69.50
Treatments compared	L	H	(42.09)	
Sabatieria punctata	180	113	20.68	20.68
Paramonohvstera sp.	105	83	12.35	33.04
Anoplostoma blanchardi	71	39	8.41	41.45
Theristus (D.) procerus	57	25	6.67	48.11
Microlaimus sp. 1	18	47	6.10	54.21
Parachromadorita sp.	9	30	5.16	59.37
Sabatieria sp. A	36	26	4.45	63.82
Innocuonema sp.	47	51	3.96	67.79
Ptycholaimellus ponticus	28	16	3.82	71.61

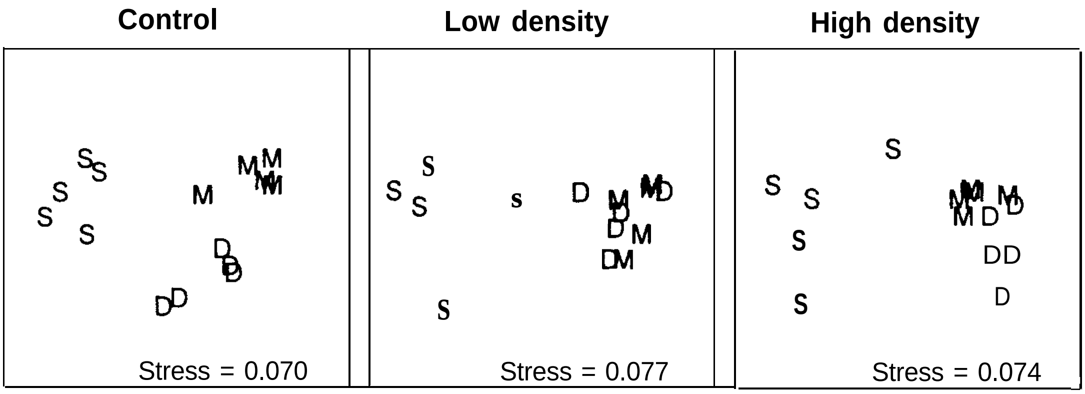

Fig. 5. Multidimensional scaling (MDS) ordinations (untransformed data) of nematode depth-segregated assemblages at the three experimental treatments. S = surface (0–1 cm); M = subsurface (1–5 cm); D = deep (5–10 cm).

3.4. Influence on the feeding structure of nematode assemblages

In the O-l cm layer of treatment H, few individuals survived and a very large variability of the relative abundance of their respective feeding groups (Fig. 6) discouraged statistical comparison between treatments. Nevertheless, a general trend of differential survival was noticeable in this sediment layer. Results suggest that microvores survived better and that epigrowth feeders were more affected (Fig. 6).

In the 5– 10 cm layer. where no abundance significant differences were found between

Table 5

ANOSIM results indicating statistic value (*R*) and significance level (*p*) of tests for differences in nematode assemblage structure between the three sediment layers (S = O-1 cm; M = l-5 cm; D = 5–10 cm) of controls and low and high density treatments at different levels of data transformation

		Data transformation					
		None		$\sqrt{}$		$\sqrt{}\sqrt{}$	
		R	*P*	*R*	*P*	*R*	*P*
Controls							
S	M	0.91	**	0.96	**	0.87	**
	D	0.99	**	0.93	**	0.72	**
M	D	0.46	*	0.28	*	0.12	0.20
Low							
S	M	1.00	**	0.97	**	0.76	**
	D	0.94	**	0.94	**	0.89	**
M	D	0.17	0.16	0.24	*	0.17	0.12
High							
S	M	1.00	**	0.99	**	0.95	**
	D	1.00	**	0.99	**	0.97	**
M	D	0.25	0.06	0.20	0.10	0.13	0.18

$p < 0.05$ (*)
p co.01 (**)

Table 6
Results from SIMPER analysis of untransformed data of nematode abundances indicating the contribution (%) of each species to the mean Bray-Curtis dissimilarity term (between parenthesis) for the controls (a). and the treatments L (b) and H (c): a cut-off of 70% was employed (i.e. when 70% of the total Bray-Curtis dissimilarity term between sediment layers has been explained by the species which are listed in order of decreasing contribution).

	Mean abundance (ind. /sample)		%	Cumulative (%)
a)				
Sediment layers compared	o-1	1-5	(63.36)	
Sabatieria sp. A	2	134	20.43	20.43
Paramonohystera sp.	IO	86	II.78	32.21
Eleutherolaimus sp.	76	8	II.37	43.58
Sabatieria punctata	37	91	9.57	53.15
Anoplostoma blanchardi	58	20	6.15	59.30
Paracanthonchus caecus	41	8	5.60	64.91
Desmolaimus sp.	27	3	4.03	68.94
Axonolaimus sp.	18	2	2.82	71.76
Sediment layers compared	O-l	5-10	(55.70)	
Sabatieria punctata	37	124	18.17	18.17
Eleutherolaimus sp.	76	0	15.57	33.74
Sabatieria sp. A	2	35	7.28	41.02
Paracanthonchus caecus	41	6	7.23	48.25
Anoplostoma blanchardi	58	45	6.95	55.20
Theristus (D.) procerus	24	45	6.21	61.40
Desmolaimus sp.	27	6	4.67	66.08
Innocuonema sp.	27	35	3.66	69.73
Sediment layers compared	1-5	5-10	(45.67)	
Sabutieria sp. A	134	35	22.06	22.06
Parumonohytera sp.	86	13	15.89	37.95
Sabatieria punctata	91	124	12.11	50.06
Theristus (D.) procerus	23	44	6.87	56.92
Anoplostoma blanchardi	20	47	6.06	62.98
Daptonema tenuispiculum	21	14	3.65	66.62
Halalaimus sp. 1	6	18	3.11	69.73
b)				
Sediment layers compared	O-l	1-5	(65.72)	
Sabatieria punctata	43	273	25.72	25.72
Paramonohystera sp.	4	175	18.09	43.81
Sabatieria sp. A	8	74	7.44	51.25
Eleutherolaimus sp.	69	8	6.81	58.06
lnnocuonema sp.	38	51	4.61	62.68
Theristus (D.) procerus	39	26	3.99	66.67
Desmolaimus sp.	40	6	3.88	70.55

controls and treatments, the relative abundance of microvores tended to increase from controls toward treatments with increasing density of *Nereis*, while for deposit feeders it tended to decrease.

Table 6. Continued

	Mean abundance (ind./sample)		%	Cumulative (%)
Sediment layers compared	0-1	5-10	(59.56)	
Sabatieria punctata	43	180	19.54	19.54
Paramonohystera sp.	4	105	14.83	34.38
Eleutherolaimus sp.	69	0	10.53	44.91
Theristus (D.) procerus	39	57	7.19	52.09
Desmolaimus sp.	40	10	4.75	56.84
Innocuonema sp.	38	47	4.75	61.59
Sabatieria sp. A	8	36	4.36	65.95
Ptycholaimellus ponticus	5	28	3.63	69.58
Sediment layers compared	1-5	5-10	(40.11)	
Sabatieria punctata	273	180	20.16	20.16
Paramonohystera sp.	175	105	16.74	36.90
Sabatieria sp. A	74	36	6.64	43.54
Theristus (D.) procerus	26	57	5.41	48.95
Innocuonema sp.	51	47	5.34	54.29
Microlaimus sp. 1	32	18	4.86	59.15
Anoplostoma blanchardi	55	71	4.37	63.52
Paracanthonchus caecus	30	15	3.68	67.20
Microlaimus sp. 2	17	0	2.86	70.06
c)				
Sediment layers compared	0-1	1-5	(92.70)	
Sabatieria punctata	3	161	28.72	28.72
Paramonohystera sp.	0	53	9.45	38.17
Anoplostoma blanchardi	3	52	7.92	46.09
Sabatieria sp. A	0	38	6.59	52.68
Microlaimus sp. 1	2	38	6.25	58.93
Innocuonema sp.	0	28	5.56	64.48
Daptonema tenuispiculum	0	26	5.47	69.95
Sediment layers compared	0-1	5-10	(92.90)	
Sabatieria punctata	3	113	20.50	20.50
Paramonohystera sp.	0	83	17.39	37.88
Innocuonema sp.	0	51	11.68	49.56
Microlaimus sp. 1	2	47	7.79	57.36
Anoplostoma blanchardi	3	39	6.32	63.67
Theristus (D.) procerus	1	25	5.94	69.61
Sediment layers compared	1-5	5-10	(44.54)	
Sabatieria punctata	161	113	17.76	17.76
Paramonohystera sp.	53	83	8.60	26.36
Anoplostoma blanchardi	52	39	7.05	33.41
Microlaimus sp. 1	38	47	6.78	40.16
Paracanthonchus caecus	27	3	5.35	45.55
Innocuonema sp.	28	51	5.30	50.84
Parachromadorita sp.	5	30	4.82	55.66
Daptonema tenuispiculum	26	13	4.45	60.11
Theristus (D.) procerus	20	25	4.41	64.52
Sabatieria sp. A	38	26	4.40	68.92
Desmolaimus sp.	13	0	2.77	71.69

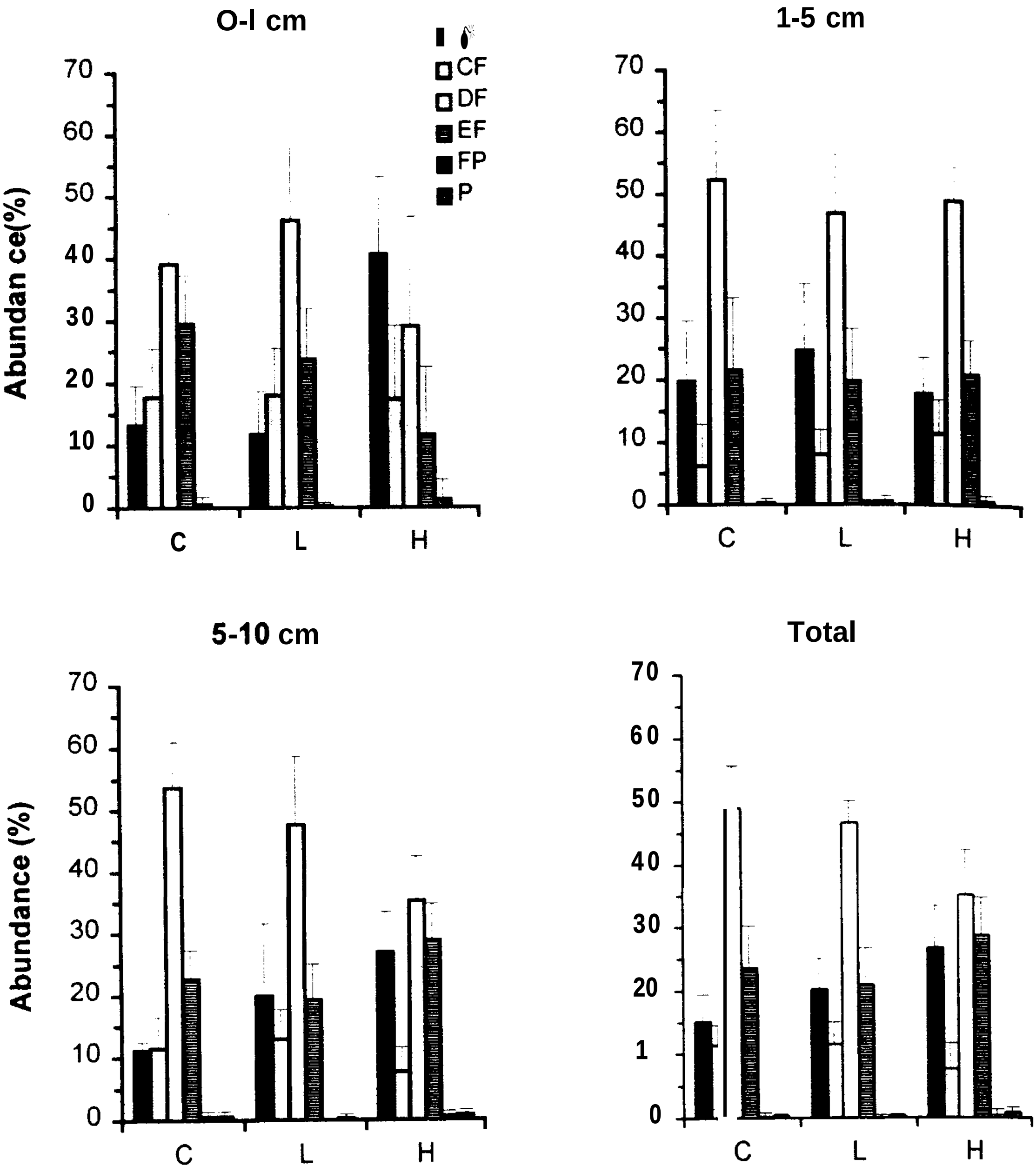

Fig. 6. Mean relative abundance (mean±95% Cl) of nematode feeding groups (Moens and Vincx, 1997) in the different sediment layers and the whole cores: M = microvores. CF = ciliate-feeders. DF = deposit-feeders, EF = epigrowth-feeders. FP = facultative predators, P = predators.

4. Discussion

It is worth noting that a period of 48 h, the time between the placement of the sediment in the basin and the beginning of the experiment, appeared to be sufficient for the reestablishment of a typical meiofaunal vertical distribution. Four sediment cores were collected from the areas within the cores of the sediment basin just before introducing *Nereis* individuals into their respective tubes. Meiofaunal densities and diversities of these samples were studied for the three sediment layers and compared to those of the controls collected at the end of the experiment. No statistically significant difference in these univariate measures was found between the beginning and the end of the experiment (r-test, $p < 0.05$). Multivariate analysis (MDS) did not reveal significant differences as well.

A short term experiment offered three main advantages compared to a long term one. First of all, the data outputs reflected the effects of *Nereis* excluding recruitment responses of meiofauna to predation-disturbance impact. Secondly, it prevented *Nereis* cannibalism that might have occurred if high densities were held for relatively long periods (Clark, 1959; Reish and Alosi, 1968; Caron, 1995). Finally. it allowed the distinction of predation from sediment perturbation effects of *Nereis* on meiofauna.

We are aware that, although our experiment was successful in detecting *Nereis* effects on meiofauna, a pseudoreplication problem could have occurred due to the experimental design. More specifically, microcosm tubes essentially isolated the sediment in each replicate treatment and control. However, water above the sediment surface was able to flow between the different treatment and control replicates through the tubes' holes covered with a 0.5-mm mesh gauze and the Z-mm mesh grids at the top of the tubes. Mobile fauna as nauplii and copepods could have been able to move between treatments and controls through these holes and grids. Although results suggest that mobile fauna migration was negligible, future experiments should be conducted by isolating the fauna of each replicate thus avoiding possible migrations between different microcosm tubes. Moreover, future experiments should be conducted with replicates (or basins) with separate water supply in order to avoid severe treatment effects, e.g., extreme mortality of *Nereis* in the high density treatment. The resulting decay and decomposition effects of the latter would have affected all of the treatments and the controls leading to incorrect experimental interpretations.

The large number of dead nematodes found in the surface sediment layer in treatment H suggested that *Nereis* sediment disturbance was a more influential process on nematode assemblages than predation. Disturbance effect on nematode abundance was greater than the estimated predation by approximately a 6:4 ratio. It can be objected, however, that predation effect may have been overestimated according to the faster decomposition that some nematode species may undergo compared to other species, even in the short time period of the experiment. In other words, the rapid decomposition rates of some species could explain the lower number of total nematodes (dead + live) in treatment H compared to controls and treatment L. As a result, a significant number of individuals of these species may have not been counted even as dead nematodes. In order to answer to this question, dead nematodes in treatment H were identified at species level and integrated with live nematodes in a MDS analysis (2d and 3d) carried out for the O-l cm layer and with different degrees of data transformation. The resulting plots (not reported herein for space constraints) did not show any clustering between samples of same treatments. If H samples had clustered separately from C and L samples, the time-differing decomposition hypothesis would have been supported, but this was not observed.

The decrease in abundance of total nematodes (dead + live individuals) in treatment H was very similar to that observed for copepods. This finding suggests that *Nereis* feeds on meiofauna, though predation may not be selective. Olivier et al. (1993) reported that from 75 to 98% (depending on the year period) of *Nereis* gut content is inorganic matter. Goerke (1971) reported similar amounts (42 to 95%) of inorganic matter in *Nereis* gut. Swallowing large amounts of sediment in the sweep-and-plough food-searching strategy indicates that *Nereis* do not specifically prey on meiofauna. Predation on meiofauna is thus a consequence of swallowing sediment in an almost nonselective way.

Copepods and nauplii were both significantly affected by high densities of *Nereis* suggesting that *Nereis* impacts at least two levels of the copepod life cycle (i.e. adults and juveniles). This must be an important force acting on population dynamics in the field and requires further studies to determine its significance.

It is possible that the observed high mortality was an experimental artifact induced by the high experimental densities of *Nereis.* It seems unlikely that meiofauna could tolerate this high mortality in natural systems, and this question should be investigated in a field experiment. It is worth noting, however, that passive transport of meiofauna in the field may mask eventual high mortalities caused by *Nereis* disturbance. Several studies have shown that in soft bottoms passive transport is the primary dispersal mean of meiofauna and small sessile macrofauna, thus allowing recolonization of small disturbance patches (Fegley, 1989; Palmer. 1988; DePatra and Levin, 1989; Commito, 1995a,b). Passive dispersal in the field may then be an important process in maintaining relatively high meiofaunal abundances in high-density *Nereis* patches.

The surface searching strategy of *Nereis* was probably the main source of sediment disturbance. It is virtually impossible to determine how this sediment reworking may affect nematodes; however we suggest two possible explanations, which are not mutually exclusive. The first one is that, when high densities of *Nereis* occur, this polychaete may cause, by crawling on the sediment surface, a frequent destruction of pathways that nematodes may “trace” and follow in their living activity. Several authors have reported on burrowing nematodes producing an intricate system of more or less permanent tubes in the sediment (Cullen, 1973; Riemann and Schrage, 1978; Platt and Warwick, 1980; Nehring et al., 1990). The frequent destruction of this system may result in a disturbance of food particle interception and thus reduce nematode feeding opportunities. In treatment L, no evidence of mortality was found. suggesting that effects of sediment disturbance was a function of the intensity (i.e. frequency) of disturbance. Schratzberger and Warwick (1998) found that frequency of sediment physical disturbance is an important determinant of meiofaunal assemblages structure. The second explanation may be that *Nereis* transformed the feeding resources available for nematodes in an unfavourable way. As reported by Tenore (1983), several potential food items are not viable for deposit-feeders due to their low nitrogen and calorific content. In these particular conditions, competition may occur on food partitioning. However, if one species dominates competition (e.g. *Nereis*), impoverishment and limited availability of feeding resources occur (Pianka, 1978; Branch, 1984). Tsuchiya and Kurihara (1980), and Chareonpanich et al. (1994a.b) showed how deposit-feeding polychaetes affect some characteristics of the sediment important for meiofauna sustenance (e.g. concentration of chlorophyll a, organic matter content, number of fine organic particles, and microalgae abundance). In our experiment. differences in the relative survival of the different feeding groups suggest that *Nereis* affected nematode trophic processes. In the O-1 cm layer of treatment H, microvores and epigrowth feeders respectively showed greater and lower survival. This was probably due to greater availability (i.e. lower rarefaction) of microvore nematodes food items (bacteria) compared to those of epigrowth-feeding nematodes. In the 5-10 cm sediment layer, the relative abundance of microvores and deposit feeders respectively tended to increase and decrease from controls to treatment H. In this case, the cause may be the oxygenation of the deeper sediment layer resulting from the bioirrigating effect of the pumping movements of Nereis in its burrows (Goerke, 197 1). Through bioirrigation, microbial growth was probably stimulated (Aller and Yingst, 1978; Eckman et al., 1981; Reichardt, 1989; Nehring et al., 1990; Grossmann and Reichardt, 1991) thus providing an increase in food allowing a proportionally greater number of microvores to survive in the deep sediment layer of treatments L and H.

The bioirrigating effect may also explain why vertical zonation of nematode species in subsurface and deep sediment layers was less evident in treatments L and H than in controls (Fig. 5). Vertical redox gradients were probably steeper in C cores causing a more marked vertical zonation of nematode species. Although vertical redox profiles were not measured, it was noted at the time of sampling that below 1 cm the sediment was slightly darker. especially in treatment C. and away from Nereis burrows in treatments L and H. Oxygenation of deeper sediment layers may also explain the greater abundance that nematodes tended to have below 1 cm depth in treatments L and H as compared to controls (Fig. 2). Although nematode recruitment processes are excluded due to the short experiment period, greatest densities in deeper sediment layers may have been a consequence of the promotive effects of Nereis burrows (Reise, 1981, 1985). The most likely of these, the more favourable redox conditions, allowed oxiphilic species to inhabit deeper sediment layers (Reise and Ax, 1979).

Our results clearly indicate that Nereis has an effect on univariate as well as on multivariate levels of nematode assemblages analyses. However, univariate measures were less sensitive than multivariate measures to the presence and density of Nereis. A greater sensitivity of multivariate measures in biological disturbance studies has been reported by other authors (Austen, 1989; Austen and Warwick, 1989; Warwick et al., 1990, 1997; Austen and Widdicombe, 1998). Univariate measures showed a significant difference among treatments only in the surface sediment layer and did not show any significant difference in deeper sediment layers. Assuming random predation of Nereis on meiofauna, which is what our results suggest, differences in diversity were mainly due to sediment disturbance associated with ***Nereis*** feeding activity. As for evenness (J'), it normally has lower values when disturbance occurs (Huston, 1979). However, in our experiment, in the O-l cm layer, in treatment H, J' was significantly greater than in treatment L and tended to be greater, although not statistically significantly, than in controls. This may be due to the short time period of the experiment. Surviving species in the O-l cm layer of treatment H did not have sufficient time to respond with recruitment processes. A longer term experiment would have probably allowed dominance to be established by the most resilient species. Multivariate measures showed that nematode assemblages were affected by the presence of Nereis not only when considering specific sediment layers, but also when considering the whole core. MDS plots showed that the presence of Nereis and its density had an influence on the dominant and intermediate abundance species.

Kennedy (1993) reported that N. *diversicolor*, which has very similar burrowing and feeding habits to those of *N. virens* (Goerke, 1971, 1976; Olivier, 1994). did not affect either meiofaunal univariate structure or their multivariate structure. The contrasting conclusions of Kennedy's study and the present one can probably be explained by considering that (1) Kennedy's experiment lasted about 6 days, which may have not been enough time to produce detectable variations of meiofaunal assemblages, and (2), Kennedy did not investigate meiofaunal abundance in the top cm of the sediment which was the most perturbed by Nereis in the present study.

In conclusion, our study showed that the polychaete *N. virens* affects meiofauna by sediment disturbance and predation at the sediment surface. In deeper sediment layers, however, it may be responsible for a promotive effect as a consequence of bioirrigation caused by its burrowing activity.

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