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Intertidal meiofauna of the St Lawrence estuary (Quebec, Canada): diversity, biomass and feeding structure of nematode assemblages

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The meiofauna of the St Lawrence estuary was investigated in the intertidal zone of the Parc du Bic (Quebec, Canada). Five nematode assemblages were distinguished by a cluster analysis: A1 and A2 (upper-tide level); A3 (mid-tide level); A4 and A5 (low-tide level). Discriminant function analysis showed that exposure time during low tide was the most important environmental factor in determining differences between assemblages. Chlorophyll-*a*, phaeopigments, sediment water content, and per cent of silt followed in the same order. Nematode densities (400–1500 ind $10\,cm^{-2}$) were found to be lower than those generally reported for other estuarine intertidal zones of the eastern Atlantic coast. Mean nematode biomass in the five assemblages ranged between 96 ± 14 and $248 \pm 86\,\mu g\ C_{org}\ 10\,cm^{-2}$. Deposit feeders were generally the dominant nematode feeding group in terms of abundance and biomass. Correlation of epigrowth-feeders with chlorophyll-*a* and phaeopigments, respectively, suggested that in the upper-tide level, old or partially degraded phytodetritus contribute more to the diet of this nematode feeding group; and in the low-tide level epigrowth-feeders may rely more on 'fresher' phytodetritus.

INTRODUCTION

Estuarine meiofaunal assemblages of the eastern coast of the North Atlantic have been intensively investigated (Warwick & Price, 1979; Warwick & Gee, 1984; Heip et al., 1985; Austen, 1989; Austen & Warwick, 1989; Li & Vincx, 1993; Hall & Frid, 1997). As for the western coast, investigations were limited to US estuaries (Tietjen, 1969; Coull, 1973, 1985), and no study has been carried out in the more northerly Canadian estuaries where climatic conditions are more severe. The present study has examined for the first time the intertidal meiofauna of the St Lawrence estuary (Quebec, Canada). The great length (~360 km) of this estuary is matched by widths as large as 60 km and depths of over 350 m. Two main regions are generally distinguished: the Upper estuary, with a turbidity maximum and strong salinity gradients, and the Lower estuary, which is more homogeneous and has a more oceanic character (El-Sabh & Silverberg, 1990). Another typical aspect of this sub-arctic estuary is a long winter with an ice cover lasting 4–5 months along the shore.

The study area was the Anse-à-l'Orignal of the Parc du Bic in the Lower estuary where the tidal regime has a semi-diurnal pattern with a mean tidal range of 3 m (El-Sabh & Murty, 1990). The surface water temperature of the Lower estuary ranges between 2° and 13°C according to the time of year (Ingram & El-Sabh, 1990). This area offered three main advantages: an easy accessibility, a well known macrofaunal community (Vincent et al., 1987; Miron & Desrosiers, 1990; Olivier et al., 1993; Caron et al., 1993a,b; Caron, 1995; Caron et al., 1995a,b), and the presence of different sediment-bottom types. The latter was an interesting attribute for studying the different intertidal meiofaunal assemblages of this part of the estuary. Sediment type is a key factor that determines the structure of meiofaunal assemblages (Hicks & Coull, 1983; Heip et al., 1985). The macrofauna is characterized by the Atlantic boreal community of *Macoma balthica* (L.) (Desrosiers et al., 1980; Desrosiers & Brêthes, 1984; Desrosiers et al., 1984). Among the dominant macrofaunal species of this community, there are three molluscs (*Macoma balthica*, *Mya arenaria* and *Hydrobia minuta*) and two polychaetes (*Nereis virens* and *Nephtys caeca*). The polychaete *Nereis virens* has been shown to affect meiofauna either by predation or by sediment disturbance (Olivier et al., 1993; Tita et al., 2000).

The present study had two objectives: (i) describing the composition and density of the metazoan meiofauna in the selected study area; and (ii) describing the spatial distribution and the feeding structure of the nematode assemblages according to the sediment type. This study represents a complement to Tita et al. (1999) that focused attention on the size spectra and the morphological adaptations of the nematode species found in the here described assemblages.

MATERIALS AND METHODS

The study area

The study area was the intertidal zone of the Anse-à-l'Orignal of the Parc du Bic located in the southern shore of the St Lawrence estuary (Figure 1). Forty-eight stations, distributed over the whole area, were sampled between 4 and 7 June 1996. The stations were the same as those that were sampled by Miron & Desrosiers (1990) for a study on *Nereis virens* and *Nephtys caeca* populations. The shore profile of the Anse-à-l'Orignal has a complex configuration with several inlets and islets to which a correspondingly complex distribution of sediment facies is associated. As a general feature, heterogeneous muddy flats occur at the upper-tide level, and relatively homogeneous sandflats at the lower-tide level. The latter is a sandy shore, while the mid-tide level is a gravelly–sandy shore exposed to wave action in its eastern part and relatively sheltered in its western part. As for the upper-tide level, the sediment is more muddy especially in its eastern part where there is a *Spartina* salt-marsh. The whole area's surface is irregular due to the presence of large boulders and rocky substrates, especially in the eastern part, where they cover 20–40% of the bottom.

The environmental factors

At each station, a sediment sample was collected from the top 2 cm of sediment using a punch with an internal diameter of 26 mm. The sediment water content (% of total weight) was estimated by weighing the sediment before and after drying it at 50°C until a constant weight was obtained. The same sediment samples were re-dried at 90°C for total organic matter content analysis by combustion at 500°C for six hours (Luczak et al., 1997). Another sediment sample was collected for granulometric analysis. The Folk's (1974) triangular diagram was used to characterize the sediment present at all stations. Small sediment samples for the analysis of photopigment concentrations (chlorophyll-*a* and phaeopigments) were collected from the top 1 cm using short tubes as corers (internal diameter= 1.2 cm). These samples were kept cool in an ice-box until arrival at the laboratory where they were preserved in a freezer at −80°C until analysis by fluorometry (Parsons et al., 1984). Exposure time (Texp) was estimated by directly timing the exposure period at neap and spring tides, and was expressed as % of tidal cycle period. Reported Texp values represent the mean value from spring and neap tides. The seawater salinity and temperature were sampled with a digital portable meter (YSI, model 3050) at the low water line.

The meiofauna

Meiofauna was sampled using a hand-held corer with an internal section of 7.3 cm^2 (Tita et al., 2000a). A preliminary study (unpublished) on the meiofauna of the sediment's top 10 cm of the same area showed that more

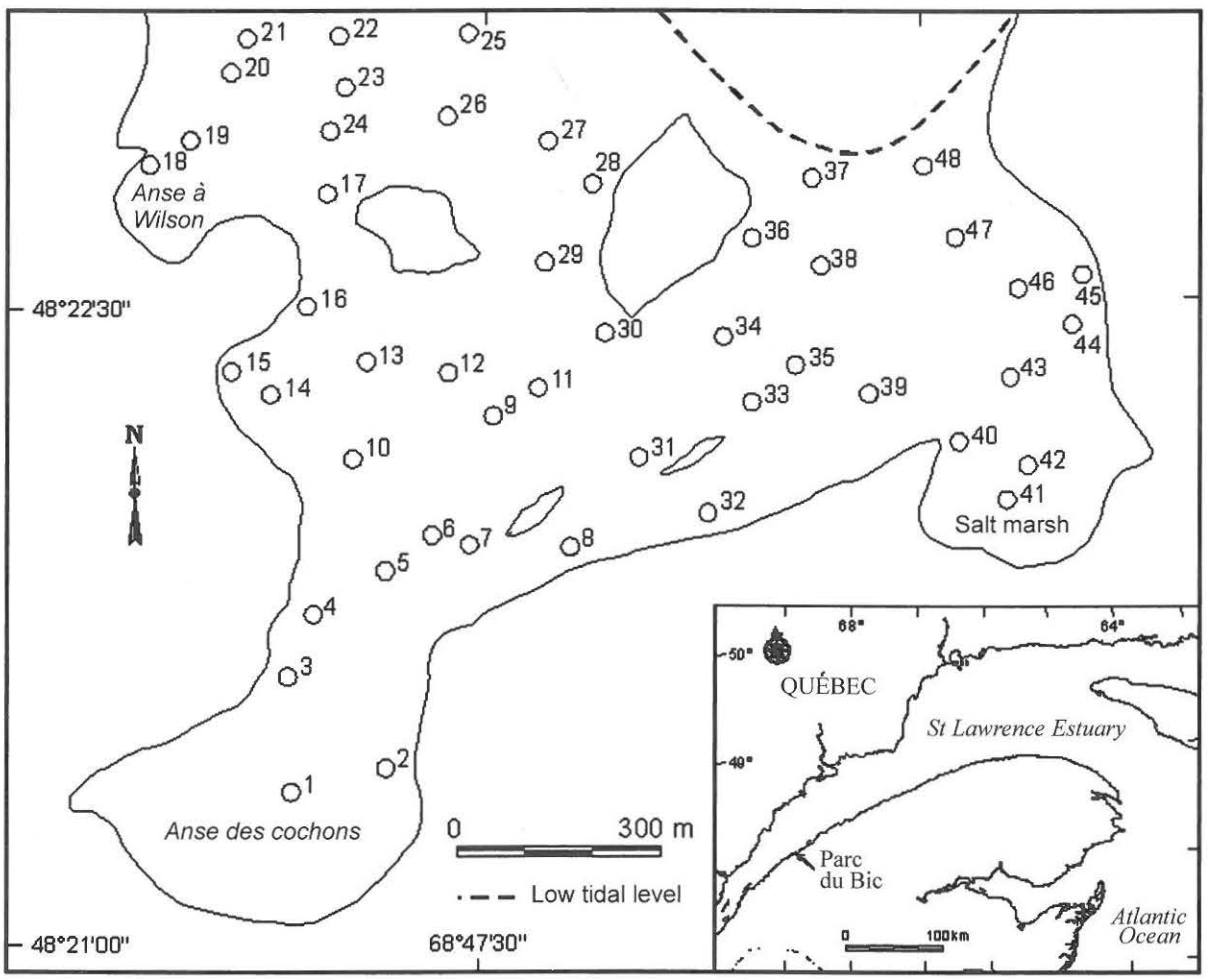

Figure 1. The study area (Anse-à-l'Orignal) and the 48 sampled stations.

Table 1. *Minimum, maximum, average, standard deviation, and coefficient of variation for the different environmental factors in the whole study area (48 stations).*

	%				μg 10 cm^{-2}		μm	%			
	Texp	Wat	OM	P/C	Chl-*a*	Phae	Md	Mean	Fine	V. fine	Silt
Minimum	8.8	17.0	0.9	0.13	53.3	9.4	44	0.9	3.4	1.8	0.9
Maximum	63.9	41.9	7.0	1.06	115.0	57.9	390	47.2	84.8	73.5	79.5
Average	33.9	24.2	1.8	0.38	79.4	27.3	140	9.3	27.9	29.6	19.9
SD	17.5	4.5	1.2	0.25	16.3	13.7	81	10.1	22.1	19.6	21.1
CV	51.7	18.6	65.5	66.9	20.5	50.2	57.7	108.6	79.4	66.2	106.1

Texp, exposure time; Wat, water content of the sediment; OM, organic matter; P/C, Phae/Chl-*a* ratio; Chl-*a*, chlorophyll-*a*; Phae, phaeopigments; Md, granulometric median of total sediment; Mean, Fine and V. fine, mean (250–500 μm), fine (125–250 μm) and very fine (63–125 μm) sand; Silt, grain size <63 μm.

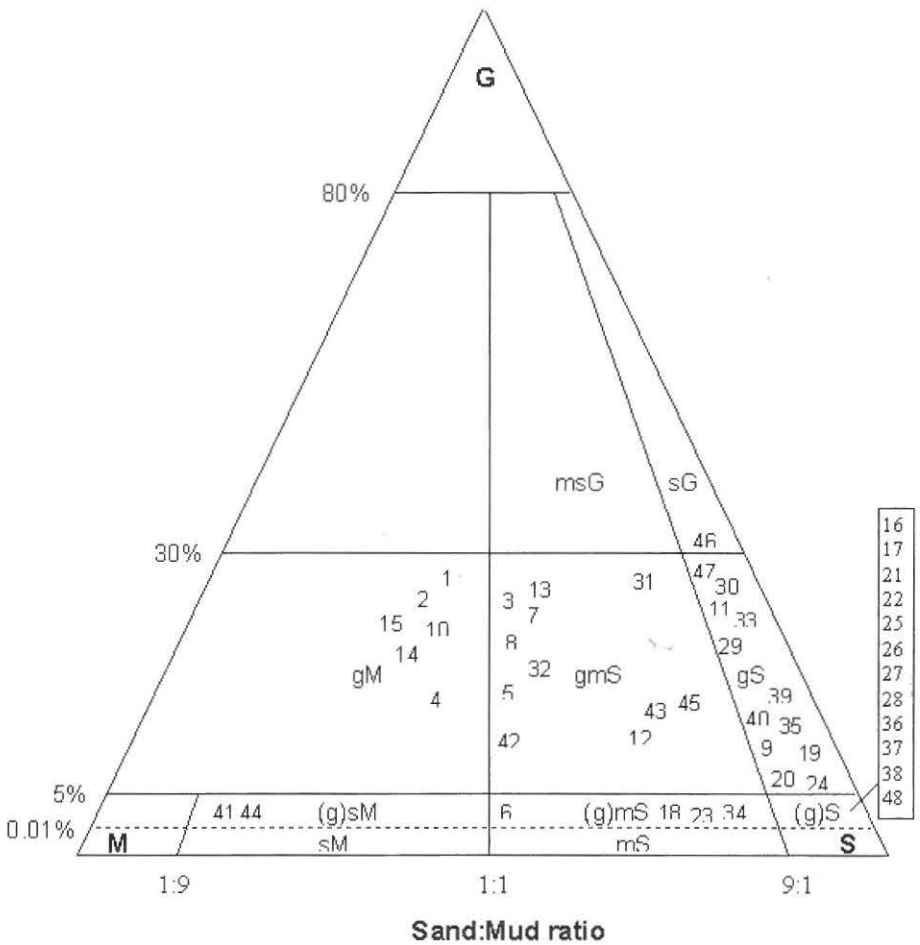

Figure 2. Triangular diagram (Folk, 1974) placing stations according to their sediment granulometric properties. G, gravel (>2 mm); sG, sandy gravel; msG, muddy sandy gravel; S, sand (0.063–2 mm); gS, gravelly sand; (g)S, slightly gravelly sand; gmS, gravelly muddy sand; (g)mS, slightly gravelly muddy sand; mS, muddy sand; M, mud (<0.063 mm). Per cents indicate % of gravel.

Table 2. *Abundance of meiofaunal taxa (individuals 10 cm^{-2}) in the five nematode assemblages.*

	Nematodes	Copepods	Nauplii	Turbellarians	Ostracods	Rotifers	Others	Total
A1	557 ±127	78 ±29	171 ±55	53 ±16	47 ±33	13 ±16	10 ±1	929 ±217
A2	1313 ±266	162 ±51	398 ±129	40 ±9	26 ±8	9 ±4	12 ±4	1960 ±404
A3	507 ±92	40 ±12	62 ±19	51 ±10	11 ±4	7 ±4	3 ±1	680 ±101
A4	1044 ±197	24 ±11	85 ±16	150 ±18	46 ±15		3 ±1	1353 ±213
A5	622 ±104	99 ±20	458 ±105	46 ±11			1 ±1	1228 ±117

than 95% of the nematodes in muddy sediments and 50% in sandy sediments inhabited the top 2 cm. Other meiofaunal taxa were always concentrated in the top 2 cm (>85%). For this reason and for analysis time constraints, only the top 2 cm of the sediments were sampled and considered sufficient to describe the horizontal distribution of the nematode assemblages. Samples were fixed and preserved in 4% formalin, and stained with rose bengal.

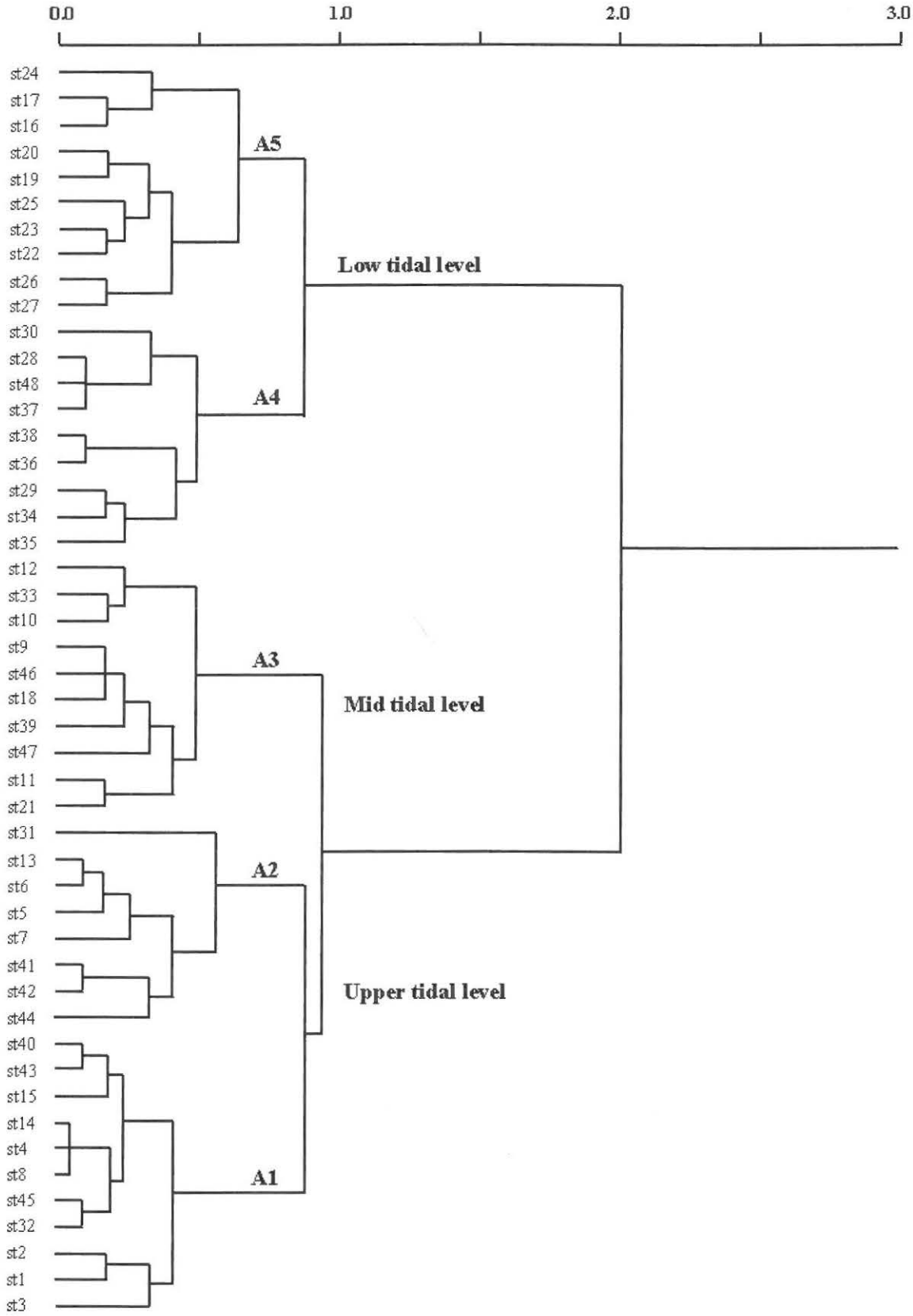

Figure 3. Hierarchical analysis (1-gamma coefficient, complete linkage) based on the nematode specific composition found at the 48 stations. Clusters A1, A2, A3, A4 and A5 represent different assemblages (see text).

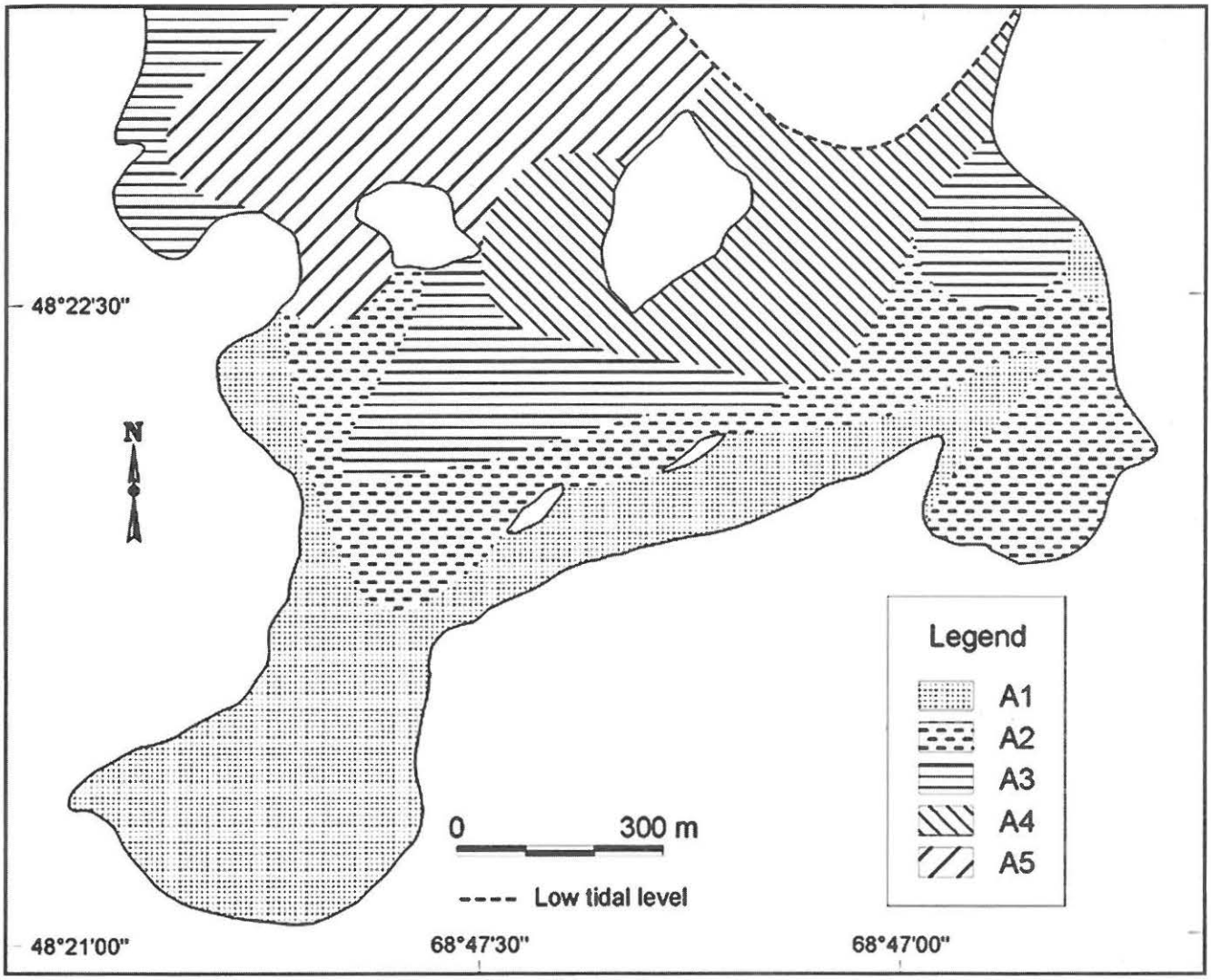

Figure 4. Spatial distribution of the five nematode assemblages (A1, A2, A3, A4, A5).

They were then washed through 1-mm and 63-μm sieves. The sediment retained by the 63-μm sieve was used to extract the meiofauna by centrifugation using Ludox-TM (Heip et al., 1985). Organisms were identified and counted at higher taxonomic levels, except nematodes and copepods that were identified at the species level. One hundred and ten nematodes per sample were randomly collected and mounted on glycerine slides for identification (McIntyre & Warwick, 1984). Thirty additional individuals were collected from samples of stations with the highest densities (Stations 28, 32, 36, 38, 41, 42, 44). Genus and species identifications were based on Platt & Warwick (1983, 1988) and Hopper (1969), while family systematic was based on Lorenzen (1994). Two multivariate techniques were used to describe nematode assemblages: (i) a hierarchical analysis using the l-gamma coefficient (Goodman & Kruskal, 1954) with a complete linkage method for building the cluster graph; and (ii) a discriminant function analysis (DFA). The hierarchical analysis was used to estimate similarity between nematode species compositions in the 48 stations, and to distinguish nematode assemblages. The DFA (forward stepwise model) was used to identify the most responsible environmental factors determining the spatial distribution of nematode assemblages.

In order to investigate the influence of sediment properties in structuring nematode assemblages, the granulometric characteristics were plotted in the DFA using two variables: silt (i.e. % of the sediment fraction with grain size $<63\,\mu$m), and Md63 (i.e. median of the sediment fraction with grain size $>63\,\mu$m). A multivariate analysis of variance (MANOVA) was performed in order to verify significant differences of each environmental factor between nematode assemblages. Twenty individuals per nematode species were randomly sorted and used to estimate the mean individual specific biomass (m.i.b.). For the rarest species (less than 20 individuals found), the total number of recorded individuals was used for the m.i.b. estimation. Biomass was estimated with the biovolumes method (Warwick & Price, 1979). Nematode wet weight (μg WW) was obtained using a specific gravity of 1.13 (Wieser, 1960). Mean total organic carbon (C_{org}) of nematodes was estimated assuming that C_{org} was equal to 12.4% of the wet weight (Jensen, 1984). The feeding structure of nematode assemblages was described using the six feeding groups proposed by Moens & Vincx (1997): microvores (M), ciliate-feeders (CF), deposit-feeders (DF), epigrowth-feeders (EF), facultative-predators (FP), and predators (P). This classification partially derives from the Wieser

Table 3. *Nematode species with a relative abundance greater than 1% at the five assemblages; n, mean abundance (ind 10 cm^{-2}) (mean ±SE); biom, mean biomass (µg C_{org} 10 cm^{-2}) (mean ±SE).*

A1 N=563 ±129 biom=177 ±41		A2 N=1313 ±266 biom=248 ±86		A3 N=507 ±92 biom=85 ±17		A4 N=1044 ±197 biom=155 ±21		A5 N=622 ±104 biom=96 ±14	
Anoplostoma blanchardi	19.1	*Sabatieria punctata*	18.8	*Eleutherolaimus* sp.	11.1	*Metachromadora (M.)* sp.	47.7	*Eleutherolaimus* sp.	26.4
Theristus (D.) procerus	18.8	*Microlaimus* sp. 1	12.2	*Microlaimus* sp. 1	9.0	*Viscosia* sp.	9.1	*Daptonema* sp. 2	8.6
Metachromadora (M.) remanei	11.7	Chromadoridae A	10.9	*Anoplostoma blanchardi*	8.5	*Dichromadora hyalocheile*	6.6	*Odontophora* sp.	7.7
Daptonema tenuispiculum	9.9	*Anoplostoma blanchardi*	7.5	*Paramonohystera* sp. 1	8.3	*Ascolaimus* sp.	5.1	*Daptonema tenuispiculum*	7.2
Chromadoridae A	8.6	*Metachromadora (M.) remanei*	6.2	*Sabatieria punctata*	7.3	*Odontophora* sp.	3.2	*Viscosia* sp.	6.0
Sabatieria punctata	6.2	*Desmolaimus* sp.	5.8	*Odontophora* sp.	5.6	*Pomponema sedecima*	2.9	*Paracanthonchus* sp.	4.4
Paracanthonchus caecus	4.6	*Daptonema tenuispiculum*	5.1	*Daptonema tenuispiculum*	5.5	*Chromadorita* sp.	2.7	Chromadoridae B	4.4
Hypodontolaimus balticus	2.8	*Paramonohystera* sp. 1	4.5	*Viscosia* sp.	5.0	*Dichromadora* sp.	2.5	Tripyloididae	3.3
Monhystera sp. 1	2.1	*Leptolaimus papilliger*	3.6	*Theristus (D.) procerus*	4.4	Chromadoridae B	2.2	*Microlaimus* sp. 1	2.7
Enoplus sp.	1.8	*Theristus (D.) procerus*	3.4	Chromadoridae A	3.0	*Daptonema tenuispiculum*	1.8	*Metachromadora (M.)* sp.	2.3
Leptolaimus papilliger	1.7	*Ptycholaimellus ponticus*	3.3	*Ptycholaimellus ponticus*	2.9	*Paracanthonchus caecus*	1.5	*Richtersia inaequalis*	2.1
Chromadorita sp.	1.6	*Tripyloides* sp. 1	1.9	*Paracanthonchus caecus*	2.4	*Microlaimus* sp. 1	1.4	*Pomponema sedecima*	1.9
Sphaerolaimus sp. 2	1.1	*Chromadorita* sp.	1.5	*Desmolaimus* sp.	2.3	*Axonolaimus* sp. 1	1.2	*Dichromadora* sp.	1.6
Paramonohystera sp. 1	1.0	*Halalaimus* sp. 1	1.4	*Metachromadora (M.)* sp.	2.0	*Gammanema* sp.	1.2	*Paracanthonchus caecus*	1.4
		Neochromadora poecilosoma	1.1	*Chromadorita* sp.	1.8	*Microlaimus* sp. 2	1.0	*Southernia* sp.	1.3
		Monhystera sp. 1	1.0	*Daptonema* sp. 2	1.7			*Microlaimus* sp. 2	1.1
				Sabatieria longispinosa	1.5			*Chromadorita* sp.	1.1
				Microlaimus sp. 2	1.2			*Sabatieria ornata*	1.1
				Ascolaimus sp.	1.1			*Enoplolaimus* sp. 1	1.1
				Dichromadora hyalocheile	1.0			*Sabatieria longispinosa*	1.0
				Pomponema sedecima	1.0				
				Hypodontolaimus balticus	1.0				
Others	9.1	Others	11.5	Others	12.4	Others	10.0	Others	13.3

Table 4. *List of functions included or excluded in the forward stepwise model of the discriminant function analysis (global Wilk's lambda=0.088;* F=*5.60;* P<*0.000). Only functions with* F ⩾ *1.0 were included in the model.*

	Partial lambda	*F*	*P*
In model			
Texp	0.508	9.21	0.000
Chl-*a*	0.727	3.57	0.014
Phae	0.796	2.43	0.064
Wat	0.830	1.95	0.122
P/C	0.834	1.89	0.132
Silt	0.902	1.03	0.402
Not in model			
OM	0.936	0.628	0.646
Md63	0.908	0.940	0.452

(1953) where feeding groups 1A, 1B, 2A, and 2B correspond to M, CF+DF, EF, FP+P, respectively. Moens & Vincx's feeding groups of the species recorded in our study area were established according to their buccal morphology and similarity to the 'types' described by these authors. A complete list of the species with their corresponding attributed feeding group is reported in Appendix 1.

As for copepods, all individuals of each sample were identified to species level. However, because of their absence and very low abundance in several stations, statistical analysis for describing community spatial distribution was inappropriate. Therefore, only species and corresponding relative abundance are reported.

RESULTS

Some environmental factors

During the sampling period, the seawater salinity was 23.4 ±0.2 psu and the temperature 10.2 ±0.5°C. As a general feature, the other environmental factors showed a great heterogeneity within the study area (Table 1). The sediment

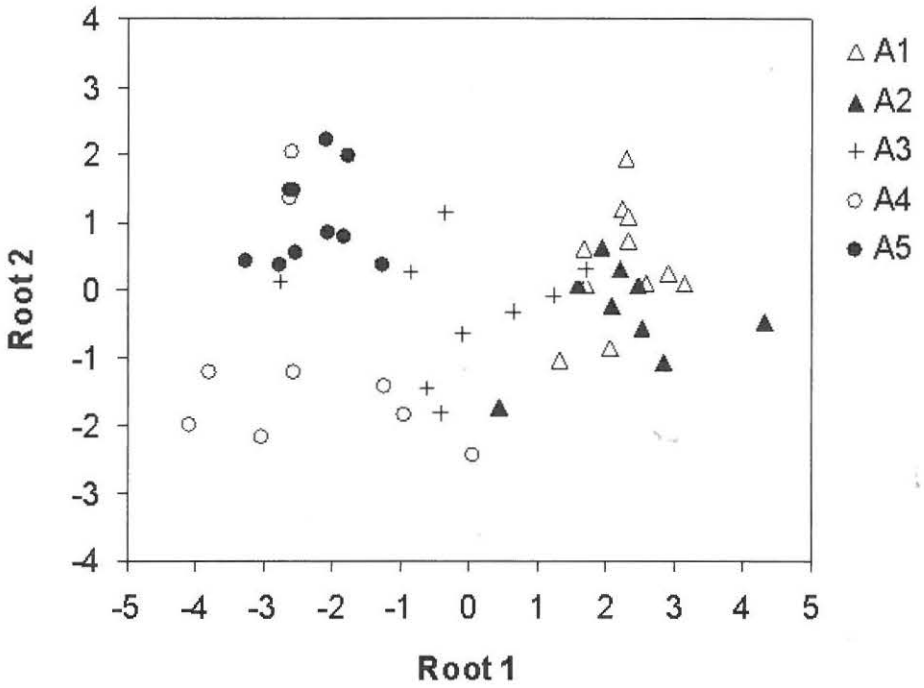

Figure 5. Discriminant function analysis plot applied on the five groups of stations identified with the hierarchical analysis (Wilk's lambda=0.088; *F*=5.60; *P*<0.0000). List of functions are reported in Table 4.

Table 5. *Results from the discriminant function analysis: squared Mahalanobis distances (M) between assemblages with* F *values, and probabilities (*P*).*

	A1			A2			A3			A4		
	M	*F*	*P*	M	*F*	*P*	M	*F*	*P*	M	*F*	*P*
A2	2.25	1.47	0.213									
A3	7.63	5.00	***	7.92	4.67	**						
A4	25.36	16.60	****	24.82	14.62	****	6.38	3.76	**			
A5	23.88	16.66	****	25.49	15.90	****	7.46	4.65	**	4.85	3.03	*

*, *P*<0.05; **, *P*<0.01; ***, *P*<0.001; ****, *P*<0.0001.

Table 6. *Results from the MANOVA applied for investigating functions' differences between the five assemblages (Wilk's lambda=0.077; P<0.0000).*

	F	*P*
Texp	23.21	****
Phae	12.32	****
Silt	12.16	****
P/C	9.36	****
Chl-*a*	7.21	***
Wat	4.21	**
OM	3.14	*
Md63	2.43	0.062

*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$; ****, $P<0.0001$.

granulometric composition was very diverse in the different zones of the Anse-à-l'Orignal (Figure 2). In the low-tide level, the sediment was gravelly to slightly gravelly sand, while, in the upper-tide level, the sediment was gravelly muddy sand to gravelly mud. The sediment granulometric median (Md) was generally greater in the east side of the Anse-à-l'Orignal.

Nematode assemblages and other meiofauna

Nematodes were the dominant taxon in all stations accounting for 50–80% of total meiofauna (Table 2). Twenty-six families, 69 genera and 106 species of nematodes were found in the whole area (see Appendix). The hierarchical analysis clearly separated the three tide levels, i.e. lower (Ltl), mid (Mtl), and upper (Utl) (Figure 3). Utl stations clustered into two main groups (A1 and A2), as

Table 7. *Probabilities (P) resulted from post hoc test (Newman–Keuls method) for the different functions. Average values of functions in the five assemblages are reported in italics (mean ±SD).*

	A1	A2	A3	A4	A5
Texp (%)	*49 ±7.9*	*50 ±9.2*	*32 ±11.9*	*22 ±15.0*	*15 ±5.8*
A2	0.836				
A3	***	**			
A4	****	****	*		
A5	****	****	**	0.134	
Phae (μg 10 cm^{-2})	*37 ±12.7*	*38 ±10.0*	*28 ±12.8*	*18 ±6.0*	*14 ±3.3*
A2	0.828				
A3	*	0.051			
A4	****	****	*		
A5	****	****	*	0.350	
Silt (%)	*35 ±17.9*	*40 ±25.2*	*13 ±13.2*	*3 ±2.5*	*7 ±3.3*
A2	0.495				
A3	**	***			
A4	****	****	0.311		
A5	***	****	0.398	0.536	
P/C	*0.58 ±0.28*	*0.55 ±0.20*	*0.36 ±0.24*	*0.18 ±0.05*	*0.19 ±0.07*
A2	0.806				
A3	0.052	*			
A4	***	***	0.122		
A5	***	***	0.059	0.945	
Chl-a (μg 10 cm^{-2})	*69 ±11.7*	*72.5 ±11.9*	*82 ±13.2*	*99 ±17.3*	*77 ±11.5*
A2	0.566				
A3	0.144	0.254			
A4	****	***	**		
A5	0.379	0.448	0.406	**	
Wat (%)	*25 ±3.6*	*28 ±7.9*	*23 ±2.2*	*23 ±1.2*	*22 ±0.9*
A2	*				
A3	0.420	**			
A4	0.250	**	0.918		
A5	0.498	**	0.886	0.967	
OM (%)	*2.4 ±1.62*	*2.2 ±1.06*	*1.8 ±1.26*	*1.1 ±0.09*	*1.1 ±0.19*
A2	0.577				
A3	0.444	0.510			
A4	*	0.099	0.154		
A5	0.069	0.155	0.310	0.976	
Md63 (μm)	*240 ±149*	*153 ±90*	*189 ±107*	*158 ±23*	*119 ±18*
A2	0.201				
A3	0.243	0.691			
A4	0.152	0.913	0.480		
A5	0.056	0.432	0.380	0.641	

*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$; ****, $P<0.0001$.

Table 8. *Significant correlations (r) between the abundance of the dominant nematode species of the upper and lower tide levels and the environmental factors.*

	OM	Chl-*a*	Phae	P/C	Texp	Wat	Silt
Upper-tide level							
Anoplostoma blanchardi	0.54 ****		0.53 ***	0.47 **	0.74 ****	0.53 ***	0.62 ****
Theristus (D.) procerus	0.40 **	−0.35 *	0.45 **	0.43 **	0.61 ****		0.56 ****
Metachromadora (M.) remanei		−0.30 *	0.43 **	0.43 **	0.45 **	0.60 ****	0.55 ****
Sabatieria punctata	0.29 *				0.40 ***	0.48 ***	0.41 **
Microlaimus sp. 1 Chromadoridae A	0.37 **		0.48 ***	0.45 **	0.59 ****	0.47 ***	0.59 ****
Lower-tide level							
Metachromadora (M.) sp.	−0.42 **	0.62 ****	−0.36 *	−0.40 **		−0.42 **	
Viscosia sp.	−0.33 *	0.56 ****	−0.60 ****	−0.61 ****	−0.64 ****	−0.34 *	−0.61 ****
Dichromadora hyalocheile		0.30 *	−0.44 **	−0.41 **	−0.53 ***		−0.39 **
Eleutherolaimus sp.	−0.36 **	−0.50 ***	−0.30 *		−0.32 *	−0.42 **	
Daptonema sp. 2	−0.32 *		−0.47 ***	−0.40 **	−0.45 **		−0.40 **
Odontophora sp.	−0.37 *	0.38 **	−0.70 ****	−0.66 ****	−0.61 ****	−0.42 **	−0.64 ****

*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$; ****, $P<0.0001$.

well as Ltl stations (A4 and A5). Mtl stations clustered in a single main group (A3). The five clusters A1, A2, A3, A4, and A5 were interpreted as different assemblages, each with its spatial distribution (Figure 4). Nematode assemblages were different in species composition and/or in structure (Table 3). Copepods and turbellarians had similar relative abundance (2–10%), representing alternatively the second and third dominant groups. As for copepods, 21 species were found with *Microarthridion laurenticum* dominating in the upper-tide levels (60–70%), followed by *Platychelipus littoralis* (10–25%), *Stenhelia (D.) palustris* (2–8%), *Halectinosoma curticorne* (1–3%), *Tachidius brevicornis* (0.5–2%), and *Nannopus palustris* (0–2%). In the lower-tide levels, *Rhizothrix minuta* was generally the dominant species (30–70%) followed by *Microarthridion laurenticum* (10–45%), *Thompsonula hyaenae* (0–15%), *Stenhelia (S.) divergens* (5–10%), and *Halectinosoma elongatum* (0–5%). Ostracods represented the fourth group but were not found at assemblage A5. Rotifers were exclusively found in Utl and Mtl assemblages.

Environmental factors vs nematode assemblages

The DFA was performed in order to evaluate the influence of the different environmental factors in determining spatial segregation of nematode assemblages. The forward stepwise procedure was used to determine what factors were relevant ($F \geq 1.0$) and therefore to be included in the model (Table 4). As the DFA plot shows, root 1 separated stations of the Ltl from stations of the Utl, while stations of the Mtl lay in between (Figure 5). Root 2 separated assemblages of same tide levels, especially A4 and A5. Distances between assemblages resulted from the analysis are reported in Table 5. The MANOVA showed significant differences between assemblages for all environmental factors excepted for the granulometric median of the sediment fraction greater than 63 μm (Md63) (Table 6). The Newman–Keuls multiple pairwise comparisons allowed identification of these differences (Table 7). The DFA and MANOVA results were supported by the significant correlations that the abundance of dominant nematode species showed with some environmental factors (Table 8). Species from the Utl (A1 and A2) were generally positively correlated with these factors, while species from the Ltl (A4 and A5) were negatively correlated. No significant correlation was found between species abundance and Md63.

Nematode feeding structure

In terms of relative abundance, DF were generally the dominant feeding group in all assemblages excepted for A3 and A4 where EF dominated (Figure 6). Facultative predators were almost absent in the Utl and were relatively abundant in the Mtl and the Ltl. In terms of relative biomass, the DF group was dominant in A1, A2, A3, and A5, while EF was dominant in A4. In A1, large P made of these feeding group the second dominant one (~30%) in terms of biomass although it represented only 5% in terms of abundance.

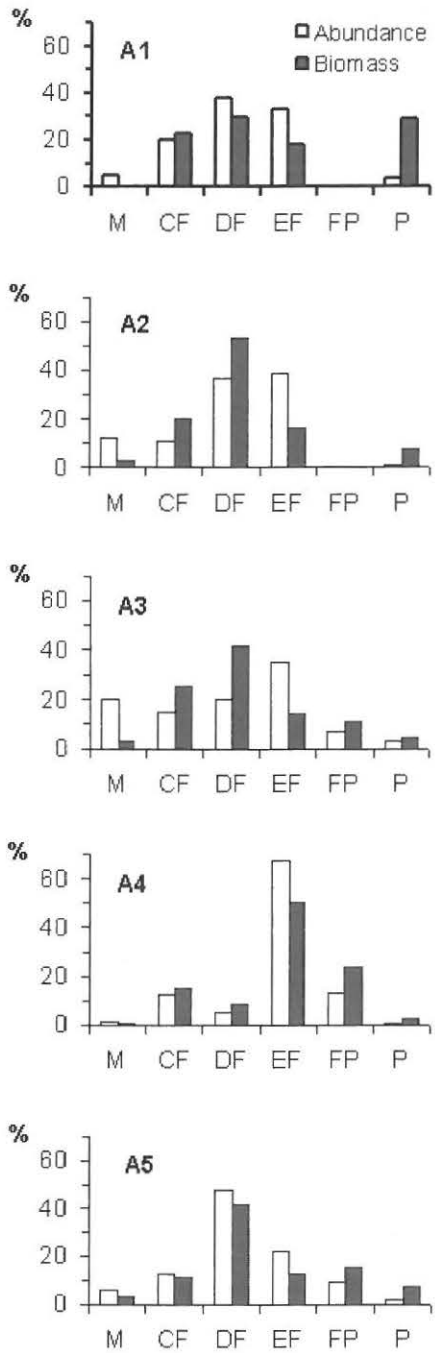

Figure 6. Relative abundance and biomass of the six nematode feeding groups (Moens & Vincx, 1997) in the five assemblages. M, microvores; CF, ciliate-feeders; DF, deposit-feeders; EF, epigrowth-feeders; FP, facultative-predators; P, predators.

DISCUSSION

Comparison with other areas

In our study area we found a meiofauna composition at higher taxonomic levels comparable to that reported for similar latitudes in the intertidal zones of the eastern Atlantic Ocean (between 45°–55° N). Nevertheless, densities were generally lower. Li & Vincx (1993) reported nematode densities between 1740 and 5328 ind 10 cm^{-2} for the polyhaline (salinity=24.3–32.0 psu) sandy sediments of the Westerschelde (Belgium). Much higher densities (annual average=12,400 ind 10 cm^{-2}) were reported by Warwick & Price (1979) for the muddy sediment of the Lynher estuary (UK). However, density values in Li & Vincx refer to the sediment top 10 cm and in Warwick & Price to the top 6 cm. In our study, we sampled the top 2 cm of sediment where the meiofauna represented respectively more than 95% and 60% of the abundance integrated over a sediment depth of 10 cm, for muddy and sandy sediments, respectively. Nonetheless, by estimating densities for equivalent sampled depths we always found lower density values in our study area. Comparable densities to those we found were reported by Warwick & Gee (1984) for the muddy sediment of the Tamar estuary (UK) (nematode densities=500–1015 ind 10 cm^{-2}). It is also worth noting that sampling for the present study was carried out in June, at the end of the spring season. No data are presently available for later months when benthic primary production (i.e. diatom blooms) significantly increases (unpublished data). This may very likely have positive effects on meiofaunal densities.

Nematode assemblages vs environmental factors

Five different nematode assemblages were found in the study area: two at the upper (A1, A2), one at the mid (A3), and two at the lower (A4, A5) tide levels. The discriminant analysis showed that the Texp was the most discriminating function between nematode assemblages (i.e. lowest partial lambda). A greater Texp may be responsible for secondary effects such as wider temperature and salinity variations during low tide. In the Ltl, surface sediment temperature during the ice-cover-free season (May–October) may vary between 5–20°C, and in Utl between 1–38°C. Several authors stressed the importance of temperature as a structuring factor of meiofaunal assemblages with implications on the physiological adaptations required to inhabit specific environments (Hopper et al., 1973; Wieser et al., 1974; Wieser & Schiemer, 1977; Heip et al., 1985; Moens & Vincx, 2000a,b). Great salinity variations caused either by water evaporation (increase in salinity), especially in the warmer months, or freshwater percolation from the soil water table (decrease in salinity) may also demand particular physiological adaptations with consequences on the meiofauna species composition (e.g. Moens & Vincx, 2000a,b).

Chlorophyll-*a* and phaeopigments concentrations were found to be the second and third most important functions, respectively. The former tended to increase from Utl to Ltl, while the latter showed an opposite trend. This resulted in a gradually increasing P/C ratio (phaeopigments/chlorophyll-*a*) from Ltl to Utl. It is worth noting here that the abundance of EF and FP species dominant in the Ltl (*Metachromadora (M.)* sp., *Dichromadora hyalocheile*, and *Viscosia* sp.) were positively correlated with chlorophyll-*a* and negatively correlated with phaeopigments and P/C ratios. In contrast, EF species dominating in the Utl (*Metachromadora (M.) remanei*, *Microlaimus* sp. 1, Chromadoridae A) showed opposite correlation trends. This difference between EF of upper and lower tide levels was probably due to a different type of exploited phytodetritus. In the upper-tide level, old or partially degraded phytodetritus may contribute more to the diet of EF, while in the low-tide level species of this feeding group

may rely more on 'fresher' phytodetritus. Vincx (1989, 1990) also reported significant correlations between the sediment concentration of chlorophyll-*a* and the meiofaunal abundance and community structure in the North Sea.

The sediment water content and silt percentage were the fourth and sixth most discriminant functions between nematode assemblages. Both of these factors give an indication of the sedimentary interstitial environment. More specifically, silt is responsible for the degree of sediment pore space filling, which determines the upper size limits of the interstitial species (Schwinghamer, 1981). In a study complementary to the present one Tita et al. (1999) investigated the nematode size spectra of assemblages A1, A3, and A5 in regard of sediment characteristics. This study showed that silt has a great importance in determining nematode lifestyle, i.e. interstitial vs burrowing, therefore significantly influencing their species composition. Tita et al. (1999) also showed that from A5 to A3 and A1 there was a gradual increase in average nematode body size (372, 424, 814 ng dw ind^{-1}, respectively) and body width (29, 40, 70 μm, respectively). As a result of the larger body size, in assemblage A5 a lower individual respiration rate than in assemblage A3 and A1 was estimated (1.12, 1.25 and 2.26 nl O_2 h^{-1}, respectively). The difference in organisms' body width can be interpreted as the dominance of burrowing lifestyle in the muddy Utl and of interstitial lifestyle in the sandy Ltl. Tita et al. (1999) found that the shift from one lifestyle to the other occurs around a body width of 32 μm. Moreover, consistently with Wieser (1959) and Coull (1988), they suggested that a median sediment grain diameter of 120 μm with a small silt fraction may virtually represent the lower granulometric limit allowing interstitial life.

Final considerations

This study, together with Tita et al. (1999), represents the first set of data available for the meiofaunal communities in the St Lawrence estuary. However, further studies are needed in order to estimate the local meiofaunal production, and to better understand the interactions between meiofauna and macrofauna. Moreover, a more extensive sampling of the intertidal and subtidal zones of the St Lawrence estuary should be carried out. This would provide a better general picture of meiofauna distribution and diversity in this large estuary.

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Appendix 1. *List of nematode species recorded in the studied area with their respective feeding groups after Wieser (1953) (W) and Moens & Vincx (1997) (M&V). 1A, Selective deposit-feeders; 1B, non-selective deposit-feeders; 2A, epigrowth-feeders; 2B, omnivore–carnivores; M, microvores; DF, deposit-feeders; CF, ciliate-feeders; EF, epigrowth-feeders; FP, facultative-predators; P, predators.*

Species	W	M&V	Species	W	M&V
Adoncholaimus fuscus	2B	FP	*Hypodontolaimus schuurmansstekoveni*	2A	EF
Aegialoalaimidae	1A	M	*Innocuonema* sp.	2A	EF
Aegialoalaimus sp.	1A	M	*Karkinochromadora* sp.	2A	EF
Amphimonhystrella sp.	1B	DF	*Leptolaimus elegans*	1A	M
Anoplostoma blanchardi	1B	CF	*Leptolaimus papilliger*	1A	M
Antomicron sp.	1A	M	Linhomoeidae	1A	M
Aponema sp.	2A	EF	*Linhomoeus* sp.	1A	M
Ascolaimus sp.	1B	CF	*Metachromadora (Metachromadoroides) remanei*	2A	EF
Axonolaimus sp. 1	1B	CF	*Metachromadora (Metachromadoroides)* sp.	2A	EF
Axonolaimus sp. 2	1B	CF	*Microlaimus* sp. 1	2A	EF
Bathylaimus sp.	1B	CF	*Microlaimus* sp. 2	2A	EF
Bolbolaimus sp. 1	2B	FP	*Monhystera* sp. 1	1B	DF
Bolbolaimus sp. 2	2B	FP	*Monhystera* sp. 2	1B	DF
Camacolaimus sp. 1	2A	EF	*Monoposthia costata*	2A	EF
Camacolaimus sp. 2	2A	EF	*Nannolaimoides effilatus*	2A	EF
Camacolaimus tardus	2A	EF	*Neochromadora poecilosoma*	2A	EF
Chaetonema sp.	1B	CF	*Neochromadora* sp.	2A	EF
Chromadora macrolaima	2A	EF	*Odontophora* sp.	1B	CF
Chromadora sp. 1	2A	EF	*Oncholaimus* sp.	2B	FP
Chromadoridae A	2A	EF	*Oxystomina* sp.	1A	M
Chromadoridae B	2A	EF	*Paracanthonchus caecus*	2A	EF
Chromadorita sp.	2A	EF	*Paracanthonchus* sp.	2A	EF
Comesomatidae	1B	DF	*Paradesmodora* sp.	2A	EF
Cyartonema sp.	1A	M	*Paralinhomoeus* sp.	1A	M
Daptonema sp. 1	1B	DF	*Paramonohystera* sp. 1	1A	M
Daptonema sp. 2	1B	DF	*Paramonohystera* sp. 2	1A	M
Daptonema sp. 3	1B	DF	*Paramonohystera* sp. 3	1A	M
Daptonema tenuispiculum	1B	DF	*Polygastrophora* sp.	2B	FP
Desmodora sp.	2A	EF	*Pomponema sedecima*	2B	FP
Desmodoridae	2A	EF	*Ptycholaimellus ponticus*	2A	EF
Desmolaimus sp.	1B	DF	*Richtersia inaequalis*	1B	DF
Desmoscolex falcatus	1A	M	*Sabatieria longispinosa*	1B	DF
Dichromadora hyalocheile	2A	EF	*Sabatieria ornata*	1B	DF
Dichromadora sp.	2A	EF	*Sabatieria punctata*	1B	DF
Diplolaimella sp.	1B	DF	*Siphonolaimus* sp.	2B	FP
Diplopeltoides sp.	1A	M	*Southernia* sp.	1A	M
Doliolaimus sp. 1	1B	CF	*Sphaerolaimidae*	1B	CF
Doliolaimus sp. 2	1B	CF	*Sphaerolaimus* sp. 1	2B	P
Eleutherolaimus sp.	1B	DF	*Sphaerolaimus* sp. 2	2B	P
Elzalia sp.	1B	CF	*Spilophorella* sp.	2A	EF
Enchelidiidae	2B	P	*Spirinia* sp.	2A	EF
Enoplolaimus sp. 1	2B	P	*Stephanolaimus* sp.	1A	M
Enoplolaimus sp. 2	2B	P	*Symplocostoma* sp.	2B	FP
Enoplus sp.	2B	P	*Terschellingia* sp.	1A	M
Epacanthion sp.	2B	P	*Theristus (Daptonema) procerus*	1B	DF
Gammanema sp.	2B	FP	*Theristus* sp.	1B	DF
Gnomoxyala sp.	1B	CF	*Trefusia* sp.	1A	M
Halalaimus sp. 1	1A	M	*Tripyloides* sp. 1	1B	CF
Halalaimus sp. 2	1A	M	*Tripyloides* sp. 2	1B	CF
Halanonchus sp.	1B	CF	Tripyloididae	1B	CF
Halichoanolaimus robustus	2B	P	*Viscosia* sp.	2B	FP
Hypodontolaimus balticus	2A	EF	Xyalidae A	1B	DF
Hypodontolaimus inaequalis	2A	EF	Xyalidae B	1B	DF