

Diversity and vertical distribution of nematode assemblages: the Saguenay fjord (Quebec, Canada)

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Abstract: Three stations were sampled for a meiofaunal survey in the Saguenay fjord's inner basin (Quebec, Canada). Nematodes were the dominant taxon accounting for 90 % of total individuals. Twenty nematode families and 55 genera were found. Cluster analysis showed two different depth-segregated nematode assemblages, one in the surface layer (0-2 cm) and the other in the subsurface layer (2-10 cm) of the sediment column. A comparison between abundance and biomass vertical distributions showed that smaller individuals were dominant in the surface sediment layer, while larger individuals dominated in subsurface sediment. Selective deposit-feeders were the most abundant feeding group, while epigrowth-feeders were dominant in terms of biomass. Diversity tended to decrease in downstream areas of the fjord. Species composition and size spectra at the three stations suggest the succession of different meiofaunal communities along the fjord. Abundance-biomass comparison (ABC) plots suggested that upstream areas were moderately disturbed. The difference between Shannon's index in terms of abundance and biomass ($H'\delta = H'_{\text{abund}} - H'_{\text{biom}}$) is suggested to be a useful tool in detecting environmental disturbance.

Résumé : *Diversité et distribution verticale des communautés de Nématodes: le fjord du Saguenay (Québec, Canada).* Trois stations ont été échantillonnées afin d'étudier la méiofaune du fjord du Saguenay (Québec, Canada). Vingt familles et 55 genres de Nématodes, le taxon dominant (90 %), ont été trouvés. L'analyse hiérarchique montre deux communautés de Nématodes, l'une en surface (0-2 cm) et l'autre en subsurface (2-10 cm) de la colonne sédimentaire. La comparaison entre les distributions verticales des individus et de la biomasse montre que les organismes de taille plus petite dominent les couches superficielles du sédiment, tandis que les organismes de taille supérieure dominent dans la subsurface. Les dépositivores sélectifs sont le groupe trophique le plus abondant alors que les "suceurs d'épistrates" sont dominants en termes de biomasse. La diversité tend à diminuer d'amont en aval du fjord. La composition spécifique et les spectres de taille dans les trois stations suggèrent la succession de différentes communautés méiofaunistiques le long du fjord. Les graphiques de comparaison abondance-biomasse (ABC) suggèrent que les zones en amont sont soumises à des conditions de perturbation environnementale modérée. La différence entre les indices de Shannon en termes d'abondance et de biomasse ($H'\delta = H'_{\text{abund}} - H'_{\text{biom}}$) semble être un indicateur intéressant pour la détection de ces perturbations environnementales.

Keywords: meiobenthos, nematodes, diversity, vertical distribution, size spectra, Saguenay fjord.

Introduction

Reçu le 1^{er} août 2000; accepté après révision le 5 janvier 2001.
Received 01 August 2000; accepted in revised form 5 January 2001.

The Saguenay is a typical river-fjord system, 170 km long and 1 to 6 km wide opening into the north coast of the Saint

Lawrence estuary (Quebec, Canada). Its macrobenthic communities have been described in the form of species list by Drainville et al. (1978) and Bossé et al. (1996). As for the meiobenthos, only foraminifera communities has been studied (Schafer et al., 1991), while metazoan meiofauna have never been investigated before 1996. In May of that same year a few samples were collected for a preliminary study of the fjord's meiofauna. Almost two months after sampling, between 19-26 July, a unique and catastrophic flood occurred in the Saguenay's land area resulting in the erosion and transportation to the fjord of more than 10 millions tons of sediments (Pelletier et al., 1999). The latter formed a 15 to 40 cm new layer of sediment at the bottom of the upstream zones of the fjord, thereby severely affecting the benthic communities. Part of the results gathered from the study of the meiofaunal samples collected before the flood (i.e. abundance of the major taxa) were used for an impact and recolonization study (Pelletier et al., 1999). The latter showed mortalities between 55 and 98% of meiofauna from downstream to upstream areas, respectively. One year later, meiofauna very slightly recovered their original abundances. In the present study we report more detailed information on the meiofauna existing before this catastrophic event, devoting particular attention to the diversity and the vertical distribution of nematode individuals and biomass in the sediment. The results reported herein represent then the only "picture" of what the local metazoan meiofauna was before the flood, whereby providing a unique reference set of data to be confronted with post flood situation and evolution.

Material and methods

Studied area and sampling

The Saguenay fjord presents at its mouth a shallow 20 m deep sill that limits the intrusion of the St. Lawrence estuary deep waters. A second 80 m deep sill located 18 km upstream from the mouth subdivides the fjord into two main basins, the inner (or upper) and the outer (or lower) basins. The water exchanges between the fjord and the estuary are controlled by a low salinity outward surface current and an inward bottom current of saline water. The bottom current is the Saguenay fjord source of deep water and originates from the St. Lawrence estuary's cold ($\sim 0\text{ }^{\circ}\text{C}$) and saline (~ 32.000) intermediate water layer (Drainville, 1968). The very cold temperatures of the fjord's bottom water (around $1\text{ }^{\circ}\text{C}$ throughout the year) may be responsible for the arctic character of its deeper benthic fauna (Drainville, 1968).

In 1996, between May 26 and 27, three stations were sampled in the Saguenay Fjord's inner basin for the meiofaunal study: PDSAG-13 (215 m depth) ($48^{\circ} 21'$

$98''\text{ N}$; $70^{\circ} 43' 57''\text{ W}$), PDSAG-16 (258 m depth) ($48^{\circ} 21' 93''\text{ N}$; $70^{\circ} 36' 50''\text{ W}$), and PDSAG-20 (267 m depth) ($48^{\circ} 18' 37''\text{ N}$; $70^{\circ} 15' 87''\text{ W}$) (Fig. 1). One box core (USNEL box corer) with a sampled surface of 600 cm^2 ($20 \times 30\text{ cm}$) was collected at each station. Three subsamples were randomly collected from the central, undisturbed part of each box core (at least 3 cm from the box walls) using the "guillotine" hand-held corer (interior section = 7.3 cm^2) described by Tita et al. (2000). Each core sample was sectioned into 1 cm thick slices from 0 to 5 cm depth, and a single 5 cm thick slice was sectioned between 5 and 10 cm depth. All samples were preserved in buffered 4% buffered formalin and stained with Rose bengal.

A sediment sample was collected from the top 10 cm of each box core for granulometric analysis, and determination of water content and total organic matter content. The sediment water content ($f = \text{interstitial water weight} / \text{total sediment weight} \times 100$) was determined by drying the sediment at 50°C until a constant weight was obtained. The same sediment samples were redried at 90°C before organic matter content analysis by ignition at 450°C for 48 hours. Organic matter was estimated by the difference in weight before and after ignition, and is expressed as a percent of sediment dry weight.

Nematode handling and data analysis

Sediment core slices were washed through 1 mm and 63 μm sieves. The sediment retained by the 63- μm -sieve was used for meiofauna extraction by centrifugation using Ludox-TM (Heip et al., 1985). Meiofauna were identified and counted at higher taxonomic levels. Only nematodes were identified at the genus level. When possible, 70 nematodes were randomly collected for genus identification from each sediment slice. When nematode abundance in a given

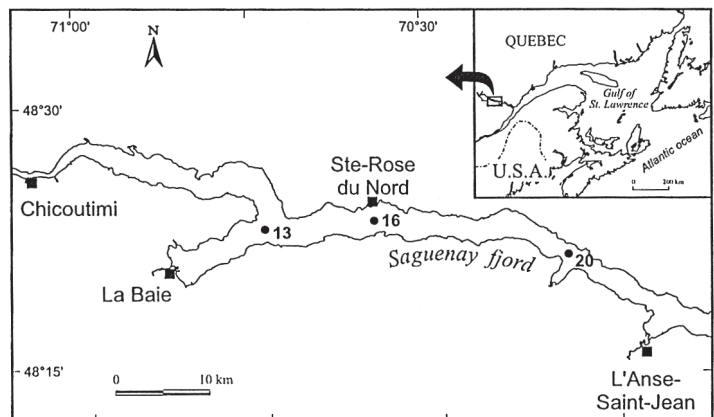


Figure 1. The study area and the three sampled stations (PDSAG-13, PDSAG-16, PDSAG-20).

Figure 1. Zone d'étude et stations échantillonnées (PDSAG-13, PDSAG-16, PDSAG-20).

sediment slice was smaller than 70 individuals, the whole set of organisms found in the same slice were collected. This gave sets of 180 to 210 nematodes per core according to the abundance found in each station. Nematodes were mounted on slides in anhydrous glycerol for identification. Two samples per station were used to estimate the mean individual biomass (m.i.b.) of each genus. Biomass was estimated with the biovolumes method using the equation $V = 530 L W^2$ (Warwick & Price, 1979), where V is the volume (nl), L the total length (μm) and W the maximum width (mm) of a given nematode. The nematode's wet weight ($\mu\text{g w.w.}$) was obtained using a specific gravity of $1.13 \mu\text{g nl}^{-1}$ (Wieser, 1960) and converted into dry weight ($\mu\text{g d.w.}$) assuming a dry/wet weight ratio of 0.25 (Jensen, 1983). Log_2 -classes of body size distributions in terms of $\mu\text{g d.w.}$ (class intervals = $0.5 + \log_2 \text{d.w.}$) were used for species-size distributions. Log_2 -classes were used because they provide better resolution (Schwinghamer, 1981). Diversity was estimated using the following indices: the κ -dominance (Solomon, 1979); Hill's diversity numbers, N_0 , N_1 , N_2 (Hill, 1973); Margalef's species-richness-weighted diversity index, SR (Margalef, 1958); Shannon's index, H' (Margalef, 1958); equitability, J' (Pielou, 1966). H' and J' indices were calculated in terms of both abundance and biomass. In order to have comparable diversity values between the three stations the number of nematodes used for calculating the different indices was standardized to 180 per sediment core, i.e. the minimum number of nematodes sorted for any core. This was done by randomly selecting 180 individuals from those cores where a greater number of nematodes was collected.

A hierarchical analysis was applied in order to identify depth-segregated nematode assemblages in the sediment column. This analysis was carried out taking into account all sediment slices, i.e. six slices per three cores per station, yielding a total of 18 slices per station. The 1-gamma coefficient was used to estimate similarity between species composition in the different slices and a complete linkage method was used to build the cluster graphs.

The nematode assemblages' feeding structure was described using Wieser's feeding groups (Wieser, 1953): 1A (selective deposit-feeders), 1B (non-selective deposit-feeders), 2A (epigrowth-feeders), and 2B (omnivorous-carnivores).

Results

Sediment properties

The sediment was muddy at all three stations, although the percent of the silt-clay fraction ($< 63 \mu\text{m}$) was higher at stations PDSAG-16 (95.3%) and PDSAG-20 (94.5 %) than at station PDSAG-13 (74.3%). The remaining sediment

fraction was mainly composed of very fine sand ($< 125 \mu\text{m}$). Organic matter content of the sediment was of 7.9, 6.7, and 4.8%, and sediment water content of 56, 64 and 67% at stations PDSAG-13, PDSAG-16, and PDSAG-20, respectively.

Meiofaunal composition

Nematodes were the dominant group at the three stations accounting for about 90% of the total meiofauna (Table 1). Copepods were generally the second dominant group followed by polychaetes. Included in the less represented groups were turbellarians, kinorhyncha, ostracods, acari, rotifers, and isopods, together representing less than 1.5% of total meiofauna.

Table 1. Mean relative abundance (%) of the different taxa and abundance (no. individuals 10 cm^{-2}) of total meiofauna (mean \pm SE) in the three stations; Others = turbellarians, kinorhyncha, ostracods, acari, rotifers, isopods.

Tableau 1. Abondance relative moyenne (%) des différents taxa et abondance (nb. d'individus 10 cm^{-2}) de la méiofaune totale (moyenne \pm erreur standard) dans les trois stations ; Others = Turbellariés, Kinorhynques, Ostracodes, Acariens, Rotifères, Isopodes.

Stations	Nematodes	Copepods	Nauplii	Poly- chaetes	Others	Total
PDSAG-13	88.9	5.5	3.6	1.1	0.9	1108 \pm 325
PDSAG-16	90.3	5.3	3.0	0.9	0.5	588 \pm 39
PDSAG-20	90.3	1.7	1.4	5.1	1.5	350 \pm 37

Nematode assemblages composition

Twenty nematode families were found in the studied area. At station PDSAG-13, Linhomoeidae were the dominant family, while Desmoscolecidae dominated at stations PDSAG-16 and PDSAG-20 (Table 2). Fifty-five genera were identified (see annex). Two different species were distinguished but not identified for three genera (*Diplopetloides*, *Sabatieria* and *Terschellingia*), and were indicated with the generic appellation of sp. 1 and sp. 2. The most abundant species were *Terschellingia* sp. 2 at station PDSAG-13, and *Desmoscolex* sp. at stations PDSAG-16, and PDSAG-20 (Table 3). However, *Dorylaimopsis* sp. was always the dominant species in terms of biomass (Table 4).

Vertical zonation

Nematode vertical distributions showed that most of the individuals inhabited the uppermost 2 centimetres of the sediment. However, the biomass peak was found to be almost one cm below the abundance peak, between 1 and 3 cm depth (Fig. 2, left and centre). The discrepancy between these two vertical distributions, individuals and biomass, was due to the mean body size distribution of the organisms (Fig. 2, right). Larger organisms were dominant in the

Table 2. Mean relative abundance (%) of nematode families at the three stations of the Saguenay fjord.

Tableau 2. Abondance relative moyenne (%) des familles de Nématodes aux trois stations du fjord du Saguenay.

	PDSAG-13	PDSAG-16	PDASG-20
Aegialoalaimidae	0.8	1.6	1.4
Anoplostomatidae	0.1		
Axonolaimidae	0.2		
Chromadoridae	6.7	0.6	
Comesomatidae	4.4	5	5.6
Cyatholaimidae	2.7	12.2	13.7
Desmodoridae	0.2	0.2	2.5
Desmoscolecidae	4.7	28.1	25.0
Diplopeltidae	7.0	12.9	6.1
Enchelidiidae	0.6	0.3	0.1
Leptolaimidae	6.2	3.8	4.9
Linhomoeidae	40.8	5.8	3.4
Microlaimidae	0.9		
Monhysteridae	4.1	9.5	5.2
Oncholaimidae			0.3
Oxystominidae	2.4	4.1	3.9
Phanodermatidae	<0.1		
Phanodermatidae			0.1
Sphaerolaimidae	3.8	1.0	0.1
Trefusiidae		2.3	6.4
Xyalidae	14.6	12.6	21.1

subsurface of the sediment, between a 2 and 5 cm depth, while smaller organisms were dominant in the surface layer and below a depth of 5 cm.

A nearly identical distribution pattern for nematode species was found at the three stations with a relatively strong vertical zonation. A hierarchical analysis distinguished a surface assemblage (between a depth of 0 and 2 or 3 cm) and a subsurface assemblage (below a 2 or 3 cm depth) (Fig. 3). At a lower hierarchical distance, two sub-assemblages were found within the sediment's surface layer: (i) an upper sub-assemblage (0-1 cm), and (ii) a lower sub-assemblage (1-2 or 1-3 cm). At station PDSAG-13, the dominant species of the upper surface sub-assemblage (0-1 cm) were *Atrochromadora* sp., *Monhystera* sp., *Leptolaimus* sp., and *Southerniella* sp., while *Elzalia* sp. and *Daptonema* sp. were dominant in the lower surface sub-assemblage (1-2 cm). Dominant species of the subsurface assemblage (2-10 cm) were *Terschellingia* sp. 2, *Dorylaimopsis* sp., *Sphaerolaimus* sp. and *Nannolaimus* sp. At station PDSAG-16, the dominant species of the upper surface sub-assemblage were *Monhystera* sp., and *Southerniella* sp., while *Desmoscolex* sp., *Daptonema* sp. and *Elzalia* sp. were dominant in the lower surface sub-assemblage. Dominant species of the subsurface assemblage were *Terschellingia* sp. 1, *Dorylaimopsis* sp.,

Table 3. Nematode species with mean relative abundance greater than 1 %; Abundance = [(total individuals 10 cm⁻²) ± SE].

Tableau 3. Espèces de Nématodes ayant une abondance relative supérieure à 1 %. Abondance = [(totalité des individus 10 cm⁻²) ± erreur standard].

Stations	Abundance (%)		
	PDSAG-13	PDSAG-16	PDSAG-20
<i>Amphimonhysterella</i> sp.	1.2		
<i>Atrochromadora</i> sp.	4.1		
<i>Camacolaimus</i> sp.	1.1		1.7
<i>Campylaimus</i> sp.	1.6	2.5	4.3
<i>Chromadora</i> sp.	1.6		
<i>Cobbia</i> sp.		4.7	6.3
<i>Cyartonema</i> sp.		1.6	1.4
<i>Daptonema</i> sp.	6.1	5.2	4.1
<i>Desmoscolex</i> sp.	4.7	28.1	25.0
<i>Diplopeltoides</i> sp. 1	1.2	6.1	
<i>Diplopeltoides</i> sp. 2	1.4		
<i>Dorylaimopsis</i> sp.	3.0	4.7	5.3
<i>Elzalia</i> sp.	6.6	1.4	10.1
<i>Halalaimus</i> sp.	2.0	1.2	2.8
<i>Halanonchus</i> sp.			4.9
<i>Halaphanolaimus</i> sp.		1.2	
<i>Leptolaimus</i> sp.	4.8	1.8	2.0
<i>Metalinhomoeus</i> sp.		1.2	1.5
<i>Minolaimus</i> sp.			1.0
<i>Molgolaimus</i> sp.			1.2
<i>Monhystera</i> sp.	3.7	8.9	5.2
<i>Nannolaimus</i> sp.	2.7	10.9	7.4
<i>Oxystomina</i> sp.		2.9	1.1
<i>Paracanthochus</i> sp.			3.9
<i>Paradesmodora</i> sp.			1.3
<i>Paralongicyatholaimus</i> sp.			1.4
<i>Sabatieria</i> sp. 1	1.3		
<i>Southerniella</i> sp.	2.1	3.5	1.9
<i>Sphaerolaimus</i> sp.	2.9		
<i>Terschellingia</i> sp. 1		4.0	1.4
<i>Terschellingia</i> sp. 2	39.3		
<i>Trefusia</i> sp.		2.1	1.5
Others	8.7	8.0	3.2
Abundance	982 ± 312	531 ± 39	316 ± 36

Cobbia sp. and *Nannolaimus* sp. At station PDSAG-20, the upper surface sub-assemblage was dominated by *Desmoscolex* sp. and *Elzalia* sp., and the lower surface sub-assemblage by *Halanonchus* sp. and *Cobbia* sp. The subsurface assemblage was dominated by *Paracanthochus* sp., *Dorylaimopsis* sp., *Cobbia* sp. and *Nannolaimus* sp.

Nematode species-size distribution

The species size distributions at stations PDSAG-16 and PDSAG-20 were very similar (Fig. 4). This similarity was confirmed by a significant correlation between these two distributions ($r = 0.916$; $p < 0.001$). In contrast, no

Table 4. Nematode species with mean relative biomass greater than 1%. Total biomass = [(μg dry weight 10 cm^{-2}) \pm SE].

Tableau 4. Espèces de Nématodes ayant une biomasse relative supérieure à 1 %. Biomasse totale = [(μg poids sec 10 cm^{-2}) \pm erreur standard].

Station	Biomass (%)		
	PDSAG-13	PDSAG-16	PDSAG-20
<i>Chromadorita</i> sp.	2.3		
<i>Cobbia</i> sp.		1.2	1.4
<i>Daptonema</i> sp.	4.0	3.0	2.1
<i>Desmoscolex</i> sp.	1.8	9.7	7.5
<i>Diplolaimella</i> sp.	8.3	11.3	
<i>Diplopeltoides</i> sp. 1		2.1	
<i>Diplopeltula</i> sp.	2.3	3.3	
<i>Dorylaimopsis</i> sp.	26.3	36.6	36.1
<i>Elzalia</i> sp.	9.2	1.8	7.1
<i>Halalaimus</i> sp.	1.4		1.5
<i>Halanonchus</i> sp.			8.1
<i>Minolaimus</i> sp.			1.5
<i>Molgolaimus</i> sp.			1.1
<i>Monhystera</i> sp.		1.2	
<i>Nannolaimus</i> sp.	1.3	4.9	2.9
<i>Oxystomina</i> sp.		1.4	
<i>Paracanthonchus</i> sp.		2.4	16.9
<i>Paralinhomoeus</i> sp.			2.2
<i>Paralongicyatholaimus</i> sp.			2.3
<i>Parasphaerolaimus</i> sp.		3.8	
<i>Phanodermopsis</i> sp.			1.1
<i>Sabatieria</i> sp. 1	3.5		
<i>Southerniella</i> sp.		1.3	
<i>Sphaerolaimus</i> sp.	4.2		
<i>Terschellingia</i> sp. 1	1.7	7.9	2.5
<i>Terschellingia</i> sp. 2	25.9		
<i>Trefusia</i> sp.		1.0	
Others	7.9	6.9	5.7
Total biomass	123 \pm 39	73 \pm 19	50 \pm 12

significant correlation were found between size distributions for stations PDSAG-13 and PDSAG-16 ($r = 0.174$; $p = 0.501$), or between PDSAG-13 and PDSAG-20 ($r = 0.238$; $p = 0.363$). The main difference concerned the modal peaks, which were in the nominal size class of 113 ng d.w. for station PDSAG-13, and 57 ng d.w. for stations PDSAG-16 and PDSAG-20. Species with size classes smaller than 113 ng d.w. were almost exclusively found in the surface assemblages, while larger species were almost exclusively found in the subsurface assemblages.

Nematode feeding structure

At the three stations, selective deposit-feeders (1A) were the most abundant feeding group, followed by non-selective deposit-feeders (1B) (Fig. 5). Nevertheless, in terms of relative biomass, epigrowth-feeders (2A) were the dominant

feeding group at stations PDSAG-16 and PDSAG-20, and the second dominant group after selective deposit-feeders at station PDSAG-13. In surface assemblages, deposit feeders (1A + 1B) dominated with more than 80% of individuals and biomass. In subsurface assemblages, the two deposit-feeding groups together dominated again in abundance accounting for 50 to 70% of individuals. However, epigrowth feeders were the dominant group in terms of biomass accounting for more than 60%. Below a 5 cm depth, at stations PDSAG-13 and PDSAG-16, 1A nematodes represented more than 85% of individuals and 55% of biomass, while at station PDSAG-20 they represented 60% of individuals and 20% of biomass. At the latter station, large epigrowth feeders (mainly *Paracanthonchus* sp.) dominated in terms of biomass (70%) below a 5 cm depth.

Nematode diversity

The κ -dominance curves suggested an increase in diversity from upstream to downstream areas of the fjord's inner basin (Fig. 6). The other indices showed that the increase in diversity was due to a gradually increasing equitability from upstream to downstream areas and not due to an increased number of species (Table 5). The Hill's diversity numbers N_1 and N_2 as well as the Shannon's index (H') and equitability (J') based on abundance were in agreement with the κ -dominance with gradually increasing values from station PDSAG-13 to station PDSAG-20. Margalef's weighted species-richness (SR) also increased from station PDSAG-13 to station PDSAG-20.

The values of H' and J' based on biomass did not show any increasing trend from upstream to downstream areas of the fjord, but were always smaller than corresponding values in terms of abundance. Biomass H' (H'_{biom}) was smaller than abundance H' (H'_{abund}) for 0.28, 0.44, 0.72 bits at stations PDSAG-13, PDSAG-16 and PDSAG-20, respectively. Similarly, J'_{biom} at the three stations had values 5, 8, and 14% smaller than J'_{abund} , respectively.

Discussion

As mentioned in the introduction, the sampling strategy employed for this study was intended to give some preliminary information on the fjord's meiofaunal communities and prepare a more extensive investigation. However, the catastrophic flood that occurred in July 1996, almost two months after our sampling, reformed the original intentions. Therefore, we consider the results here presented as of common interest for their unicity. They indeed represent the only available information on the fjord's meiofauna existing before the flood that caused severe changes in their communities.

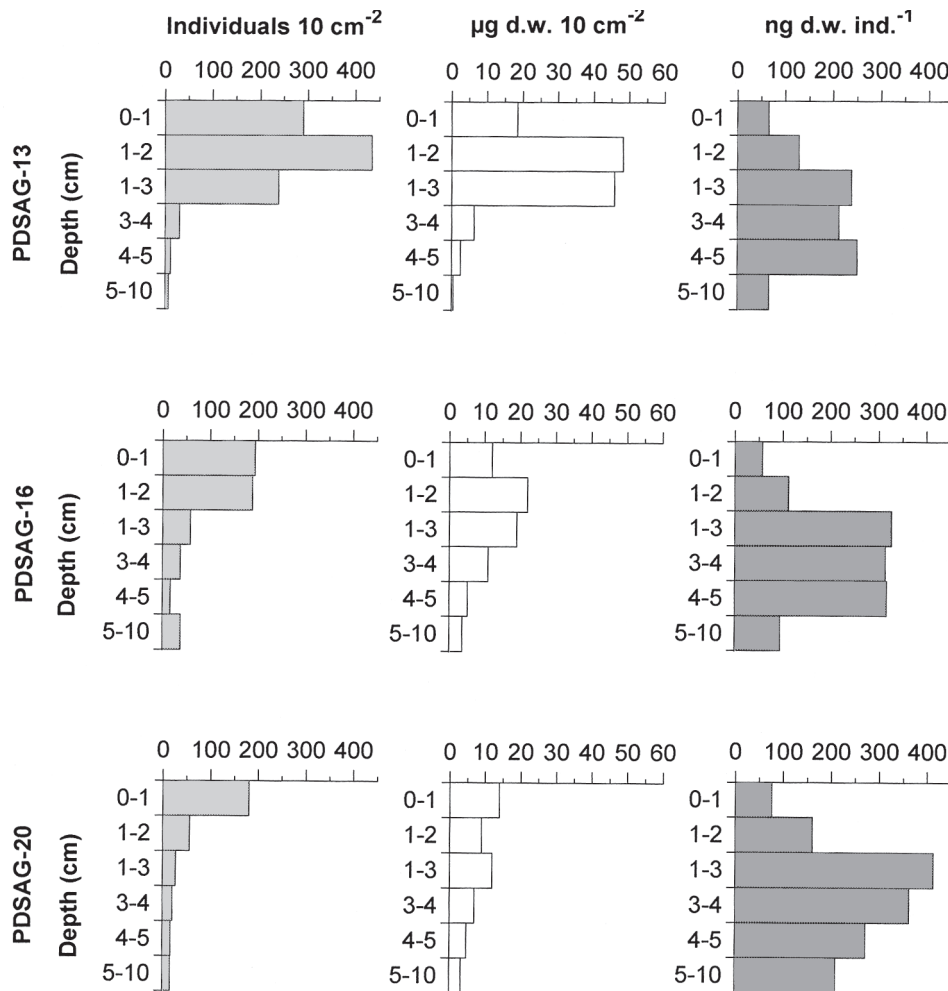


Figure 2. Nematode vertical distributions in terms of number of individuals (left), biomass (centre), total biomass in µg (center), and mean individual biomass in ng (right).

Figure 2. Distributions verticales des Nématodes en terme de nombre d'individus (gauche), biomasse totale en µg (centre) et biomasse individuelle moyenne en ng (droite).

Environmental factors and their influence on nematode assemblages

Sediment organic matter is known to be the basic energy source for the meiofaunal food web. Nevertheless, despite the high concentration of sediment organic matter that was observed in the study area, relatively low nematode abundance and biomass were found. Abundances were comparable to those reported for deep-sea areas (Soetaert & Heip, 1995). This may have been due to the relative proportion of total organic matter which is refractory to biological decomposition and exploitation. Fine vertical-scale measurements showed that between 67 and 83% of the total organic matter in the fjord's inner basin sediments are composed of humic substances (J.-P. Gagné, unpublished). Gagnon et al. (1995) reported vertical profiles of C_{org}/N molar ratios >25 in local sediments, suggesting a refractory

nature of the sediment organic matter. The refractory fraction of this organic matter is mainly composed of important pools of lignin contributing for 5 to 20% of organic carbon compounds (Louchouart et al., 1997).

The vertical zonation of the surface and the subsurface assemblages that was found with the hierarchical analysis was consistent with the vertical profiles of environmental factors reported by other studies carried out in the same area. Sediment porosity is greatest in the top 2 cm of the sediment, below which it rapidly decreases with depth (Perret et al., 1995). Vertical profiles of the redox potential (Eh) derived from a previous study (Gagnon et al., 1995) show a steep gradient from the sediment surface to a 1 cm depth (Fig. 7). The Eh is steady between a 1 and 2 cm depth (≈ -60 mV) and progressively decreases below 2 cm. These changes in the physico-chemical conditions at a depth of 2

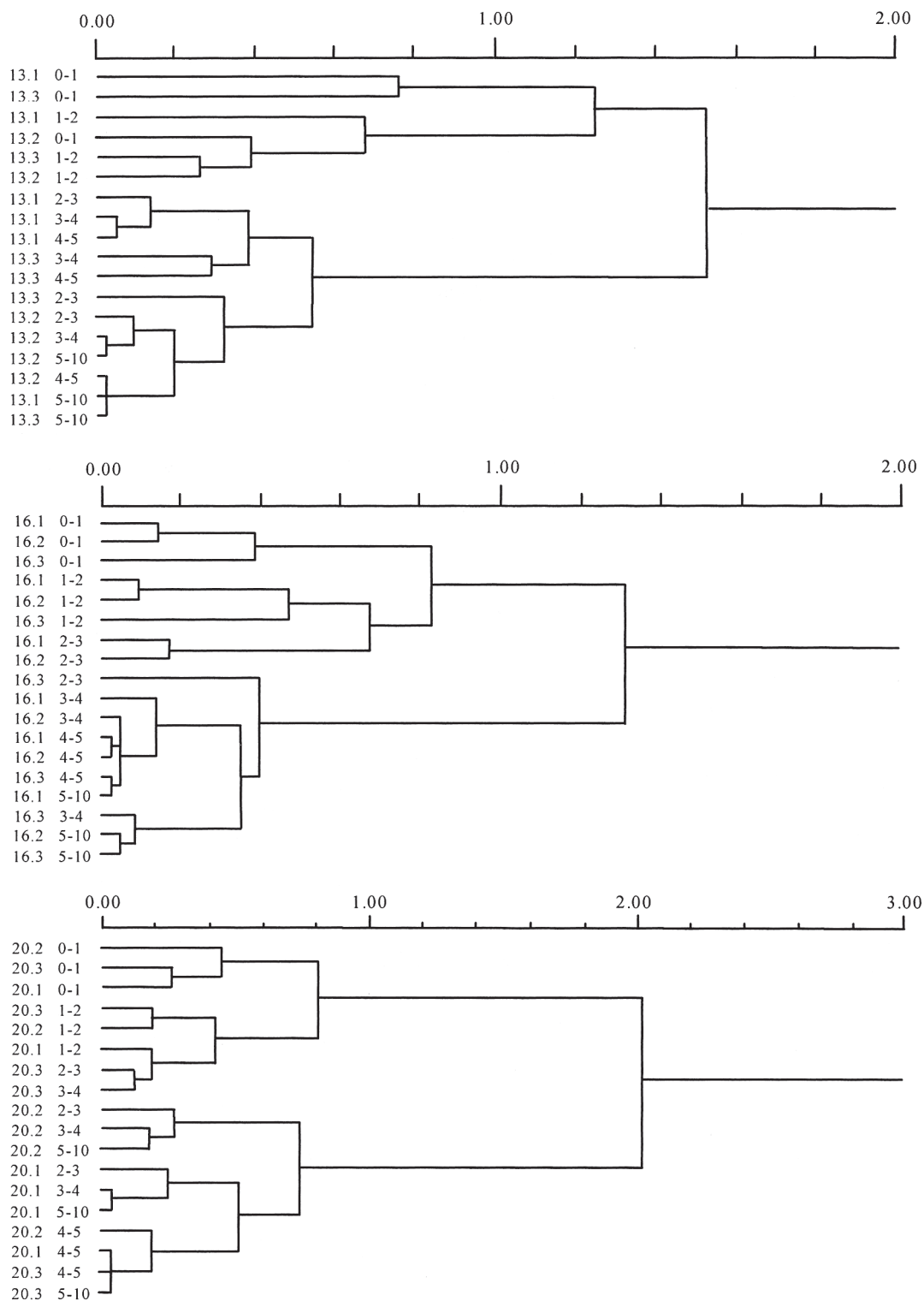


Figure 3. Hierarchical analysis [1-gamma coefficient (Goodman & Kruskal, 1954); complete linkage method] of vertical nematode species distribution at stations PDSAG-13 (up), PDSAG-16 (centre), and PDSAG-20 (low). For each branch, sample and depth (cm) of the sediment slice are indicated.

Figure 3. Analyse hiérarchique [coefficient 1-gamma (Goodman & Kruskal, 1954); méthode de lien complet] sur la distribution verticale des espèces de Nématodes aux stations PDSAG-13 (haut), PDSAG-16 (centre), and PDSAG-20 (bas). Pour chaque branche, l'échantillon et la profondeur (cm) dans le sédiment sont indiqués.

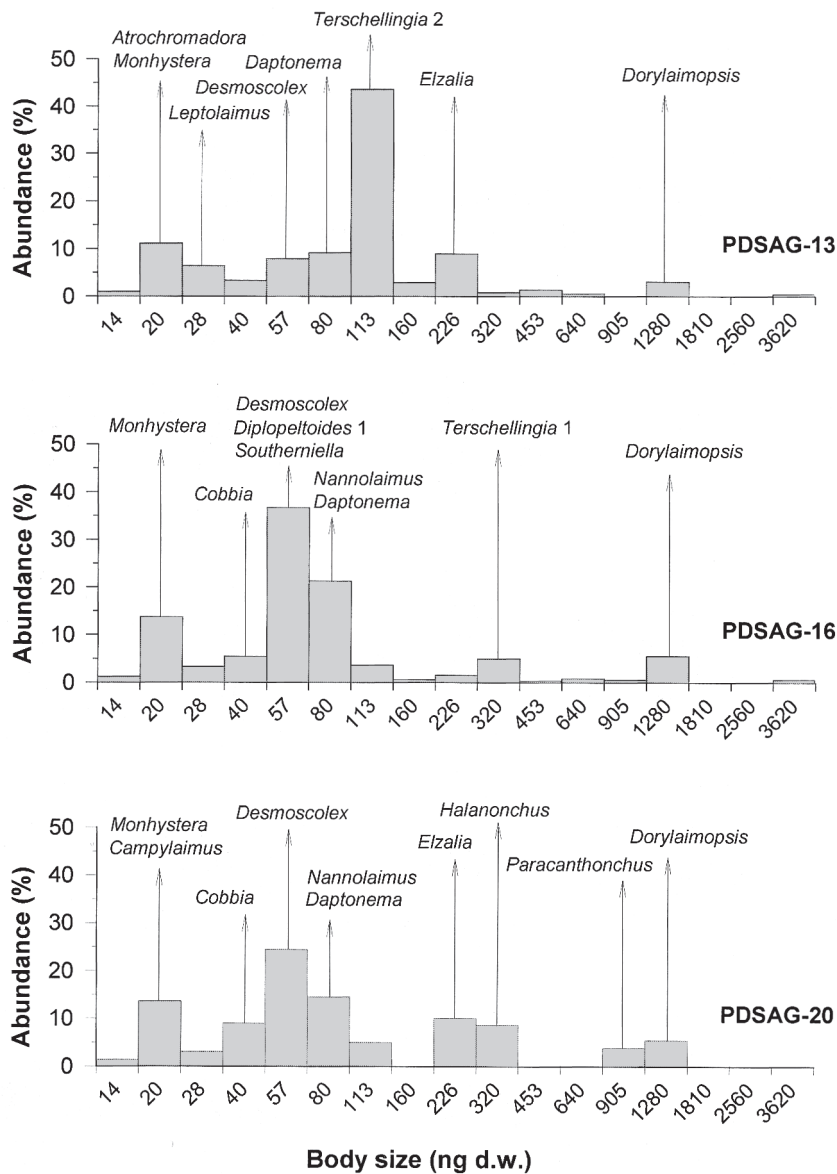


Figure 4. Nematode species size-distributions expressed in ng dry weight. Nominal values of \log_2 intervals represent the upper limit of size classes. Species having a mean contribution $>3\%$ to total abundance are indicated above their corresponding size classes.

Figure 4. Distributions des classes de taille des Nématodes exprimées en mg de poids sec. Les valeurs nominales des intervalles représentent la limite supérieure de chaque classe. Les espèces contribuant à plus de 3 % à l'abondance totale sont indiquées en correspondance de leur classe de taille.

cm are consistent with the depth-segregation of the two nematode assemblages that we found at all three stations.

Size spectra vs. vertical distribution

The importance of species size distribution in functional

studies of benthic communities have been stressed by several studies (Gerlach et al., 1985; Schwinghamer, 1981; Warwick, 1984). However, previous studies took into account integral benthic communities as a whole and only one was more recently carried out specifically on nematofauna (Tita et al., 1999). The latter study showed that species size distributions are influenced by sediment characteristics (e.g. % of silt fraction and trophic resources). Our results suggest that nematode body size classes are also associated with species vertical zonation. At all stations, smaller species dominated the uppermost sediment layer and that below 5 cm, while larger species were dominant in the 2 to 5 cm layer. Very similar findings were reported by Jensen (1983) in a study carried out in a sublittoral soft bottom of the Kattegat where nematodes of larger body size classes dominated in the subsurface sediment. As Schoener (1974) stated, "large individuals, i.e. species, usually eat a greater range of food sizes than smaller ones, probably because their optimal food is relatively rare". Subsurface species may then be adapted to exploit a wider spectrum of food because optimal food particles may be rare and/or of poor nutritional quality. A larger size may also allow such organisms to perform wider movements, thus increasing the foraging area and the probability of intercepting food particles. However, in the present study, below a 5 cm depth, mean body sizes were generally smaller. This can be explained by the decreased relative abundance of the large epigrowth-feeders and the dominance of the selective deposit-feeders which had a smaller mean body size. Selective deposit-feeders mainly feed on bacteria which must still be abundant and productive enough at this depth to sustain a low but yet substantial number of microvore nematodes. Results from recent studies (Vanhove et al., 1998; Steyaert et al., 1999) show that nematode species tend to distribute vertically according more to the vertical distribution of trophic sources rather than to the redox chemistry of the sediment.

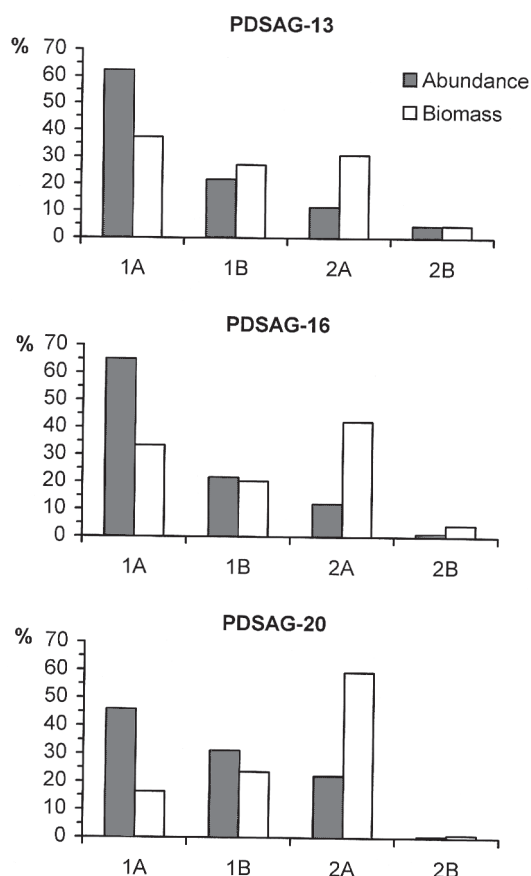


Figure 5. Mean relative abundance and biomass of nematode feeding groups (Wieser, 1953) at the three stations; 1A = selective deposit-feeders, 1B = non-selective deposit-feeders, 2A = epigrowth-feeders, 2B = omnivore-carnivores.

Figure 5. Abondance et biomasse relatives moyennes des groupes trophiques de Nématodes (Wieser 1953) ; 1A = déposivores sélectifs, 1B = déposivores non sélectifs, 2A = suceurs d'épistrates, 2B = omnivores-carnivores.

Composition and diversity

Although the sampling strategy was not appropriate for a statistical comparison of species composition among stations (i.e. only one box core per station and three subsamples per box core were collected), it is worth noting that there was some evidence that station PDSAG-13 had a different nematode family and species composition than stations PDSAG-16 and PDSAG-20. Differences in the sediment silt-clay fraction, which was lower at station PDSAG-13 than at stations PDSAG-16 and PDSAG-20, was probably the main factor responsible for shifts in species composition. Sediment type is known to be an important factor structuring meiofaunal assemblages (Warwick, 1971; Tietjen, 1976).

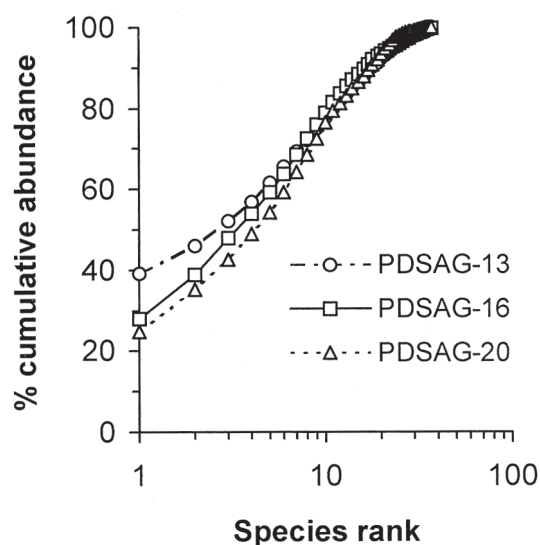


Figure 6. Nematode k-dominance curves for the three stations.
Figure 6. Courbes de dominance k pour les trois stations.

Table 5. Diversity indices for nematode assemblages at the three stations. N_0 , N_1 , N_2 = Hill's numbers; SR = Margalef's index; H' = Shannon's index (out of parenthesis: abundance-based; between parenthesis : biomass-based); J' = equitability (out of parenthesis: abundance-based; between parenthesis : biomass-based).

Tableau 5. Indices de diversité des communautés de Nématodes aux trois stations. N_0 , N_1 , N_2 = numeros de Hill ; SR = indice de Margalef ; H' = indice de Shannon (hors parenthèses : calculé sur l'abondance; entre parenthèses : calculé sur la biomasse) ; J' = equitabilité (hors parenthèses : calculée sur l'abondance ; entre parenthèses : calculée sur la biomasse)

	PDSAG-13	PDSAG-16	PDSAG-20
N_0	37	39	36
N_1	13.1	15.5	16.8
N_2	5.7	8.7	10.1
SR	5.06	5.58	6.08
H'	3.71 (3.43)	3.96 (3.52)	4.07 (3.35)
J'	0.71 (0.66)	0.75 (0.67)	0.79 (0.65)

Species equitability generally decreases with increasing environmental disturbance (Huston, 1979), which may explain the observed tendency of diversity to increase from upstream to downstream areas of the fjord. A comparison between N_0 and J' indices indicated that this increase was due to a gradually increasing evenness and not to an increase in the total number of species. As a general feature, diversity indices had values relatively low if compared with those reported for meiofauna elsewhere in the North

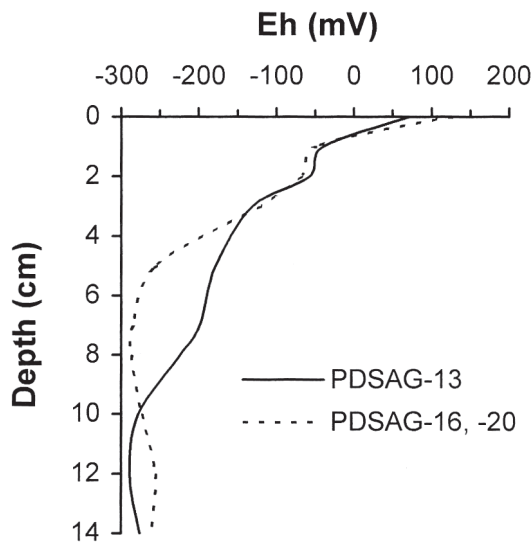


Figure 7. Vertical profiles of the sediment redox potential (Eh) at station PDSAG-13 and at a station located between stations PDSAG-16 and PDSAG-20 (after Gagnon et al., 1995).

Figure 7. Profils verticaux du potentiel redox dans le sédiment (Eh) aux stations PDSAG-13 et dans une station située entre PDSAG-16 and PDSAG-20 (d'après Gagnon et al., 1995).

Atlantic. Margalef's (SR) and Shannon's diversity indices (H') were comparable to those reported for Atlantic deep-sea nematode assemblages (Tietjen, 1976). The relatively low values of equitability (J'), compared to other regions (for a review see Boucher & Lamshead, 1994), suggest that the lower diversity could be the result of a certain environmental instability, especially at station PDSAG-13. A possible cause of disturbance may be a relatively frequent occurrence of sediment slides and turbidites in the area of station PDSAG-13 (Perret et al., 1995). The ABC (abundance/biomass comparison) plots of this station (Fig. 8) show the abundance and biomass curves crossing each other. This trend was very similar to those reported by Warwick et al. (1987) in moderately disturbed areas (physical, biological or pollution disturbance) or in "immature" states of benthic assemblages. The ABC plot for station PDSAG-20 was typical of an undisturbed zone and the plot for station PDSAG-16 was intermediate between that for stations PDSAG-13 and PDSAG-20.

As a consequence of the significant differences among species mean body size, H' and J' indices were calculated both on the basis of abundance and biomass. As Wilhm (1968) stresses, it is generally preferable to use biomass, production or any other energetic measure to describe diversity when individual sizes of a given population are very different. This analysis showed that H'_{biom} and J'_{biom} were always smaller than H'_{abund} and J'_{abund} . The difference

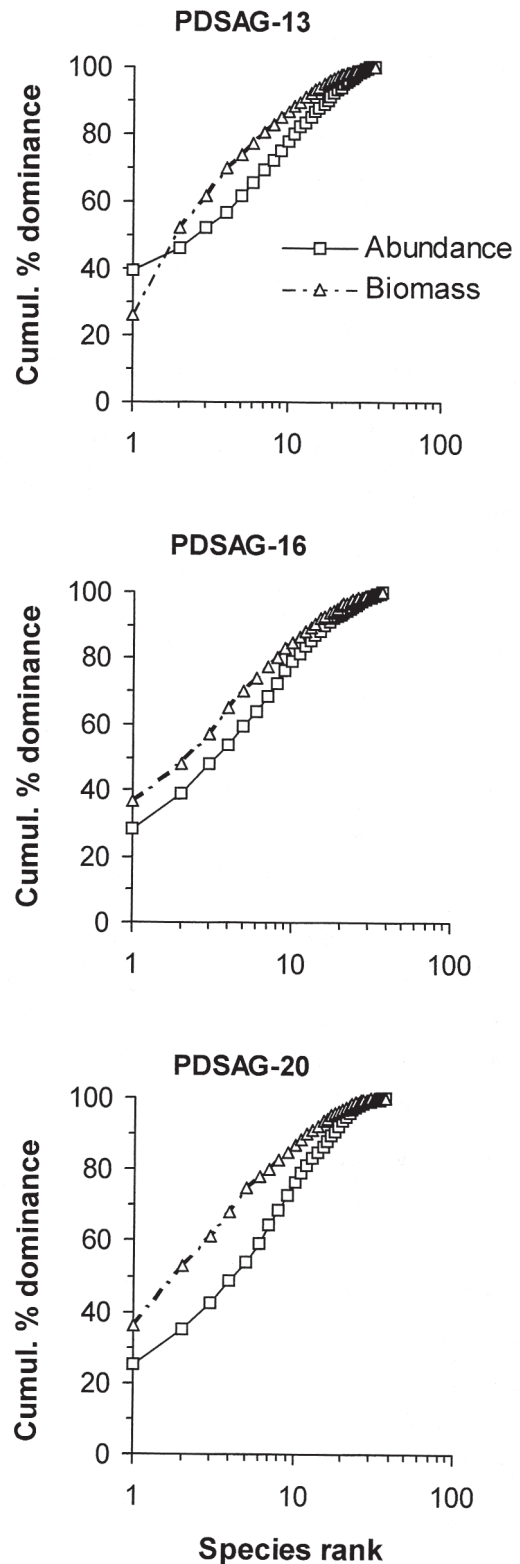


Figure 8. Nematode ABC plots (abundance/biomass comparison) for the three stations.

Figure 8. Graphiques ABC (comparaison abondance/biomasse) pour les trois stations.

between H' and J' values based on abundance and biomass, respectively, increased toward downstream areas of the fjord. This was explained by biomass-based H' and J' that did not show any decreasing gradient from upstream to downstream areas of the fjord. An explanation of this finding can be found by comparing these data with the ABC plots. It is known that when an environmental disturbance or instability occurs, small species with an opportunistic behaviour predominate. As a consequence, in highly disturbed conditions the biomass curve in an ABC plot will be below the abundance curve (Warwick et al., 1987). This means that dominance would be greater for individuals than for biomass distributions within species and since H' depends on evenness, its values will be greater for H'_{biom} than for H'_{abund}. In other words, the difference between Shannon's indices based on abundance and on biomass (H' δ = H'_{abund} - H'_{biom}) is inversely proportional to the environmental disturbance. This was observed in our studied area, with a positive and progressively greater difference from station PDSAG-13 (moderately disturbed) to station PDSAG-20 (undisturbed). Further studies should be carried out in order to validate or not H' δ as a useful tool for disturbance studies.

Appendix: List of nematode species found in the study area with corresponding feeding groups (Wieser, 1953), mean individual body length, body width, and dry weight (D.w.) Stations: PDSAG-13, -16, -20.

Annexe : Liste des espèces de Nématodes trouvées dans la région étudiée avec indications sur les groupes trophiques correspondants (Wieser, 1953) et les valeurs moyennes de longueur, largeur et poids sec. Stations : PDSAG-13, -16, -20.

	F. g.	Length (μ m)	Width (μ m)	D.w. (ng)	Stations		
					13	16	20
<i>Amphimonhystrella</i> sp.	1B	549	19	90	+	+	+
<i>Anoplostoma</i> sp.	1B	424	14	12	+		
<i>Antomicron</i> sp.	1A	544	21	36	+		
<i>Araeolaimus</i> sp.	1A	806	24	92	+		
<i>Artrochromadora</i> sp.	2A	460	17	20	+		
<i>Axonolaimus</i> sp.	1B	771	26	137		+	
<i>Calyptronema</i> sp.	2B	526	17	25	+	+	+
<i>Camacolaimus</i> sp.	2A	874	18	47	+	+	+
<i>Campylaimus</i> sp.	1B	379	17	17	+	+	+
<i>Chromadora</i> sp.	2A	482	21	36	+	+	
<i>Chromadorita</i> sp.	2A	989	34	171	+	+	
<i>Cobbia</i> sp.	2A	791	17	35	+	+	+
<i>Cyartonema</i> sp.	1A	413	13	12	+	+	+
<i>Daptonema</i> sp.	1B	577	26	79	+	+	+
<i>Desmoscolex</i> sp.	1A	223	37	48	+	+	+
<i>Diplolaimella</i> sp.	1B	3835	50	2681	+	+	
<i>Diplopettoides</i> sp. 1	1A	578	23	48	+	+	
<i>Diplopettoides</i> sp. 2	1A	546	19	29	+		
<i>Diplopeltula</i> sp.	1A	989	52	553	+	+	
<i>Doliolaimus</i> sp.	1B	791	28	92	+		
<i>Dorylaimopsis</i> sp.	2A	1325	51	1068	+	+	+

<i>Elzalia</i> sp.	1B	745	31	168	+	+	+
<i>Halalaimus</i> sp.	1A	1182	20	84	+	+	+
<i>Halanonchus</i> sp.	1B	1803	29	262		+	+
<i>Halaphanolaimus</i> sp.	1A	565	17	25		+	+
<i>Hypodontolaimus</i> sp.	2A	520	24	45	+		
<i>Leptolaimoides</i> sp.	1A	457	22	32		+	+
<i>Leptolaimus</i> sp.	1A	436	18	22	+	+	+
<i>Linhystera</i> sp.	1A	449	38	87			+
<i>Metachromadora</i> sp.	2A	820	23	95		+	
<i>Metalinhomoeus</i> sp.	1B	838	35	84	+	+	+
<i>Metasphaerolaimus</i> sp.	2B	747	24	174	+		
<i>Metoncholaimus</i> sp.	2B	396	21	64			+
<i>Microlaimus</i> sp.	2A	1078	33	27	+		
<i>Minolaimus</i> sp.	2A	527	21	245		+	+
<i>Molgolaimus</i> sp.	2A	439	16	37	+		+
<i>Monhystera</i> sp.	1B	813	21	18	+	+	+
<i>Nannolaimus</i> sp.	1A	989	19	62	+	+	+
<i>Oxystomina</i> sp.	1A	1479	42	68	+	+	+
<i>Paracanthochus</i> sp.	2A	1479	42	677		+	+
<i>Paradesmodora</i> sp.	2A	476	21	30			+
<i>Paralinhomoeus</i> sp.	1B	634	32	100			+
<i>Paralongicyatholaimus</i> sp.	2A	1161	32	253		+	+
<i>Paramonohystera</i> sp.	1B	647	24	54		+	+
<i>Parasphaerolaimus</i> sp.	2B	1112	66	1029		+	+
<i>Phanodermopsis</i> sp.	2A	1761	63	1207	+		+
<i>Pierrickia</i> sp.	1A	530	12	12	+		
<i>Sabatieria</i> sp. 1	1B	1142	32	337	+	+	+
<i>Sabatieria</i> sp. 2	1B	715	23	57			+
<i>Southerniella</i> sp.	1A	570	22	52	+	+	+
<i>Sphaerolaimus</i> sp.	2B	778	31	130	+	+	
<i>Stephanolaimus</i> sp.	1A	418	17	27			+
<i>Terschellingia</i> sp. 1	1A	1233	33	268	+	+	+
<i>Terschellingia</i> sp. 2	1A	1049	22	80	+	+	
<i>Trefusia</i> sp.	1A	1047	18	63		+	+
<i>Valvaelaimus</i> sp.	2A	680	23	54			+

Acknowledgements

This study was supported by a research grant (# CG0003540) from the Natural Sciences and Engineering Research Council of Canada (NSERC) to Professor Gaston Desrosiers. Guglielmo Tita acknowledges scholarship assistance from the Groupe de Recherche en Environnement Côtier (GREC) of the Université du Québec à Rimouski.

References

- Bossé L., Saint-Marie B. & Fournier J. 1996.** Les invertébrés des fonds meubles et la biogéographie du fjord du Saguenay. *Rapport technique canadien des sciences halieutiques et aquatiques*, **2132**, 45 pp.
- Boucher G. & Lambshead J.D. 1994.** Ecological biodiversity of marine nematodes in samples from temperate, tropical, and deep-sea regions. *Conservation Biology*, **9** (6): 1594-1604.
- Drainville G. 1968.** Le Fjord du Saguenay: I. Contribution à l'océanographie. *Naturaliste Canadien*, **95**: 809-855.
- Drainville G., Lalancette L.-M. & Brassard L. 1978.** Liste préliminaire d'invertébrés marins du fjord du Saguenay

- recueillis de 1958 à 1970 par le Camp des Jeunes Explorateurs. Ministère de l'Industrie et du Commerce du Québec, Direction Générale des pêches maritimes, *Cahier d'information*, **83**: 27 pp.
- Gagnon C., Mucci A. & Pelletier E. 1995.** Anomalous accumulation of acid-volatile sulphides (AVS) in a coastal marine sediment Saguenay Fjord, Canada. *Geochimica et Cosmochimica Acta*, **59**: 2663-2675.
- Gerlach S.A., Hahn A.E. & Schrage M. 1985.** Size spectra of benthic biomass and metabolism. *Marine Ecology Progress Series*, **26**: 161-173.
- Heip C., Vincx M. & Vranken G. 1985.** The ecology of marine nematodes. *Oceanography and Marine Biology Annual Review*, **23**: 399-489.
- Hill M.O. 1973.** Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54**: 427-432.
- Huston M. 1979.** A general hypothesis of species diversity. *American Naturalist*, **113**: 81-101
- Jensen P. 1983.** Meiofaunal abundance and vertical zonation in a sublittoral soft bottom, with test of the Haps corer. *Marine Biology*, **74**: 319-326.
- Louchouart P., Lucotte M., Canuel R., Gagné J.-P. & Richard L.-F. 1997.** Sources and early diagenesis of lignin and bulk organic matter in the sediment of the Lower St. Lawrence Estuary and the Saguenay Fjord. *Marine Chemistry*, **58**: 3-26.
- Margalef R. 1958.** Information theory in ecology. *General Systems*, **3**: 36-71.
- Pelletier E., Deflandre B., Nozais C., Tita G., Desrosiers G., Gagné J.-P. & Mucci A. 1999.** Crue éclair de juillet 96 au Saguenay - Lac St-Jean : 2. Impacts sur les sédiments et le biote du fjord Saguenay. *Canadian Journal of Fisheries and Aquatic Science*, **56**: 2136-2147.
- Perret D., Locat J. & Leroueil S. 1995.** Force development with burial in fine-grained sediments from the Saguenay Fjord, Quebec. *Canadian Geotechnical Journal*, **32**: 247-262.
- Pielou E.C. 1966.** The measurements of diversity in different types of biological collections. *Journal of Theoretical Biology*, **13**: 131-144.
- Schafer C.T., Collins E.S. & Smith J.N. 1991.** Relationship of foraminifera and thecamoebian distributions to sediments contaminated by pulp mill effluent: Saguenay Fjord, Quebec, Canada. *Marine Micropaleontology*, **17**: 255-283.
- Schoener T.W. 1974.** Resource partitioning in ecological communities. *Science*, **185**: 27-39.
- Schwinghamer P. 1981.** Characteristic size distributions of integral benthic communities. *Canadian Journal of Fisheries and Aquatic Science*, **38**: 1255-1263.
- Soetaert K. & Heip C. 1995.** Nematode assemblages of deep-sea and shelf break sites in the North Atlantic and Mediterranean Sea. *Marine Ecology Progress Series*, **125**: 171-183.
- Solomon D.L. 1979.** A comparative approach to species diversity, in: Ecological Diversity in Theory and Practice. Grassle J.F., Patil G.P., Smith W. and Taillie C. (eds.), pp. 29-36, International Cooperative Publishing House, Fairland, U.S.A..
- Steyaert M., Garner N., van Gansbeke D. & Vincx M. 1999.** Nematode communities from the North Sea: environmental controls on species diversity and vertical distribution within the sediment. *Journal of the Marine Biological Association of the United Kingdom*, **79**: 253-264.
- Tietjen J.H. 1976.** Distribution and species diversity of deep-sea nematodes off North Carolina. *Deep-Sea Research*, **23**: 755-768.
- Tita G., Desrosiers G. & Vincx M. 2000.** New type of hand-held corer for meiofaunal sampling and vertical profile investigation: a comparative study. *Journal of the Marine Biological Association of the United Kingdom*, **80**: 171-172.
- Tita G., Vincx M. & Desrosiers G. 1999.** Size spectra, body width and morphotypes of intertidal nematodes: an ecological interpretation. *Journal of the Marine Biological Association of the United Kingdom*, **79**: 1007-1015.
- Vanhove S., Lee H.J., Beghyn M., Vangansbeke D., Brockington S. & Vincx M. 1998.** The metazoan meiofauna in its biogeochemical environment: The case of an Antarctic coastal sediment. *Journal of the Marine Biological Association of the United Kingdom* **78** (2): 411-434.
- Warwick R.M. 1971.** Nematode associations in the Exe Estuary. *Journal of the Marine Biological Association of the United Kingdom*, **51**: 439-454.
- Warwick R.M. 1984.** Species size distributions in marine benthic communities. *Oecologia*, **61**: 32-41.
- Warwick R.M., Pearson T.H. & Ruswahyuni 1987.** Detection of pollution effects on marine macrobenthos: further evaluation of the species abundance/biomass method. *Marine Biology*, **95**: 193-200.
- Warwick R.M. & Price R. 1979.** Ecological and metabolic studies on free-living nematodes from an estuarine mud-flat. *Estuarine and Coastal Marine Science*, **9**: 257-271.
- Wieser W. 1953.** Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. *Arkiv für Zoologie*, **2**: 439-484.
- Wieser W. 1960.** Benthic studies in Buzzards Bay. II. The meiofauna. *Limnology and Oceanography*, **5**: 121-153.
- Wilhm J.L. 1968.** Use of biomass units in Shannon's formula. *Ecology*, **49**: 153-156.