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Résumé de l'article

La composition des communautés de diatomées benthiques a été étudiée dans les zones supérieures et inférieures de deux marais côtiers de l'estuaire maritime du Saint-Laurent (Québec, Canada), l'un possédant un estran sableux (marais de Pointe-aux-Épinette; PE) et l'autre possédant un estran vaseux (marais de Pointe-au-Père; PP). En nous penchant sur l'abondance et la diversité des diatomées benthiques ainsi que sur les caractéristiques biogéochimiques du sédiment (abondance bactérienne totale, granulométrie, composition élémentaire, concentration de pigments, de polysaccharides), nous avons observé que la zone supérieure du marais PP constituait un milieu singulier. Une plus grande diversité de diatomées a été observée dans cette zone avec une dominance des formes épipéliques alors qu'aux autres sites, nous avons observé une prédominance des formes épipsammiques. Nos analyses statistiques ont montré que l'abondance totale de diatomées est corrélée à la disponibilité des nutriments, alors que l'abondance relative de cellules de types épipélique et épisammique est corrélée à la taille des particules de sédiment. Selon nos estimations, la biomasse associée aux diatomées variait de 11 à 71 g C•m-2 dans le marais PE et de 24 à 486 g C•m-2 dans le marais PP. Cette étude décrit pour la première fois la composition détaillée des communautés de diatomées établies dans les sédiments des marais côtiers nordiques en saison estivale et constitue un premier pas vers la détermination de l'indice biologique diatomique de ces environnements nordiques.

RSE

BENTHIC DIATOM COMMUNITIES FROM TWO SALT MARSHES OF THE ST. LAWRENCE ESTUARY (CANADA)

Communautés de diatomées benthiques de deux marais côtiers de l'estuaire du Saint-Laurent (Canada)

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ABSTRACT

Microphytobenthic diatom communities were investigated in the high and low sections of two salt marshes of the Lower St. Lawrence Estuary (eastern Canada): one featuring a sandy low marsh zone (Pointe-aux-Épinettes; PE) and one with a muddy low marsh area (Pointe-au-Père; PP). Based on diatom composition and diversity, bacterial abundance, chlorophyll-*a*, phaeopigments and geochemical analyses (C_{org}, N_{tot}, granulometry, extracellular polymeric substances), the PP high marsh area appeared to be singular compared to the other sampling sites. Estimated surface biomass ranged from 11 to 71 g C•m^{-2} in the PE marsh and from 24 to 486 g C•m^{-2} in the PP marsh. A higher diversity of diatom species was observed in the PP high marsh area with a dominance of epipelic forms, in opposition to the dominant epipsammic forms at the other sites. Statistical analyses showed that diatom density was mainly affected by nutrient availability while the relative abundance of epipelic and epipsammic species was related to sediment grain size. This study provides original data on the composition of benthic diatoms in surface sediments in St. Lawrence saltmarshes during summer time that represent the first step to the determination of the DBI (Diatom biological index) of these northern environments.

Key words: benthic diatons, bacteria, distribution, salt marshes, biodiversity, St. Lawrence Estuary

RÉSUMÉ

La composition des communautés de diatomées benthiques a été étudiée dans les zones supérieures et inférieures de deux marais côtiers de l'estuaire maritime du Saint-Laurent (Québec, Canada), l'un possédant un estran sableux (marais de Pointe-aux-Épinette; PE) et l'autre possédant un estran vaseux (marais de Pointe-au-Père; PP). En nous penchant sur l'abondance et la diversité des diatomées benthiques ainsi que sur les caractéristiques biogéochimiques du sédiment (abondance bactérienne totale, granulométrie, composition élémentaire, concentration de pigments, de polysaccharides), nous avons observé que la zone supérieure du marais PP constituait un milieu singulier. Une plus grande diversité de

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diatomées a été observée dans cette zone avec une dominance des formes épipéliques alors qu'aux autres sites, nous avons observé une prédominance des formes épipsammiques. Nos analyses statistiques ont montré que l'abondance totale de diatomées est corrélée à la disponibilité des nutriments, alors que l'abondance relative de cellules de types épipélique et épisammique est corrélée à la taille des particules de sédiment. Selon nos estimations, la biomasse associée aux diatomées variait de 11 à 71 g C•m^{-2} dans le marais PE et de 24 à 486 g C•m^{-2} dans le marais PP. Cette étude décrit pour la première fois la composition détaillée des communautés de diatomées établies dans les sédiments des marais côtiers nordiques en saison estivale et constitue un premier pas vers la détermination de l'indice biologique diatomique de ces environnements nordiques.

Mots clés : diatomées benthiques, bactéries, distribution, marais côtiers, biodiversité, Estuaire du Saint-Laurent

1. INTRODUCTION

Estuaries and coastal wetlands are critical transition zones linking terrestrial and marine habitats. Salt marshes are highly dynamic environments and are among the most productive ecosystems in the world (WOODWARD and WUI, 2001). They are characterized by high primary production rates and by intense remineralization processes within the surface sediment (BILLEN and LANCELOT, 1988; POULIN *et al.*, 2007). In addition, they act as natural filters of allochtonous pollutants and actively transform nutrient loads received from the watershed before their introduction into the coastal environment (BALDWIN and MITCHELL, 2000). The environmental significance of these particular ecosystems is now widely recognized and protection efforts have been deployed to reduce impacts of human activities (CLOERN, 2001).

Sediment-dwelling microalgae and phototrophic bacteria (collectively named microphytobenthos hereafter, MPB) play a central role in the functioning of coastal salt marshes through their contribution to stabilize newly deposed sediment (CONSALVEY, 2002) and to support wetland consumers such as benthic macrofauna, meiofauna, fish and birds (GUARINI *et al.*, 2002). Although cyanobacteria are often abundant, diatoms are considered as the most important primary producers in these systems (SULLIVAN and CURRIN, 2000). These diatoms can be divided in two distinct groups: the epipsammic forms attached to particles, and the epipelic free-living forms (ROUND, 1971, 1979). Epipelic diatoms are generally the most important component of the autotrophic biomass (FORSTER *et al.*, 2006) found in these areas. They are affected by water movements and can migrate within the first top centimeters of the sediment (SABUROVA and POLIKARPOV, 2003) allowing the establishment and maintenance of epipelic forms within sedimentary environments (CONSALVEY *et al.*, 2004).

There is a lack of knowledge concerning the density and diversity of microphytobenthic diatoms in northern coastal areas, which limits our understanding of the resilience of these communities exposed to environmental perturbations induced by climate changes and anthropogenic insults. This paper provides initial results on the density and diversity of diatom communities inhabiting two salt marshes located along the south shore of the St. Lawrence Estuary (Eastern Canada) during summer time. The structure of the diatom communities was examined in relation to pigment concentrations, total bacteria abundance, extracellular polymeric substance concentration, sediment grain size distribution and elementary organic matter composition in an attempt to determine the main environmental factors affecting MPB species distribution in such cold environments.

2. MATERIAL AND METHODS

2.1 *Study sites*

Two marshes from the south shore of the Lower St. Lawrence Estuary (Quebec, Canada) were selected for this study: the Pointe-aux-Épinettes (PE) and the Pointe-au-Père (PP) salt marshes (Figure 1). Both located in the same geographical area (Rimouski, Qc), these marshes are affected by similar large-scale physical forcing such as tides, winds, and waves. Lower St. Lawrence Estuary marshes are exposed to important seasonal variations affecting surface water temperature (typically ranging from 0 to 25°C), salinity (from 10 to 30 psu) and nutrient concentrations ([NO_3^-] from 1 to 25 µM) (POULIN, 2008). At both studied sites, low and high marshes areas are included between -1 and 0 m and 1 and 2 m, respectively (related to the mean sea level).

The PE salt marsh is located in the Bic Provincial Park, a protected area created in 1984. The marsh is located at the far end of a protected bay (Anse à l'Orignal) and is protected by small islands, between two steep hills composed of Cambrian claystone/sandstone. The erosion of these geologic formations has promoted the deposition of a large sandy low marsh area. The marsh is dominated by an homogenous emergent macrophyte community (*Spartina alterniflora*, *Spartina pattens* and other halophytes in its upper part) surrounded by a creek network free of vegetation. The PE marsh watershed is part of a forested area without agricultural activity and is entirely protected from anthropogenic stressors.

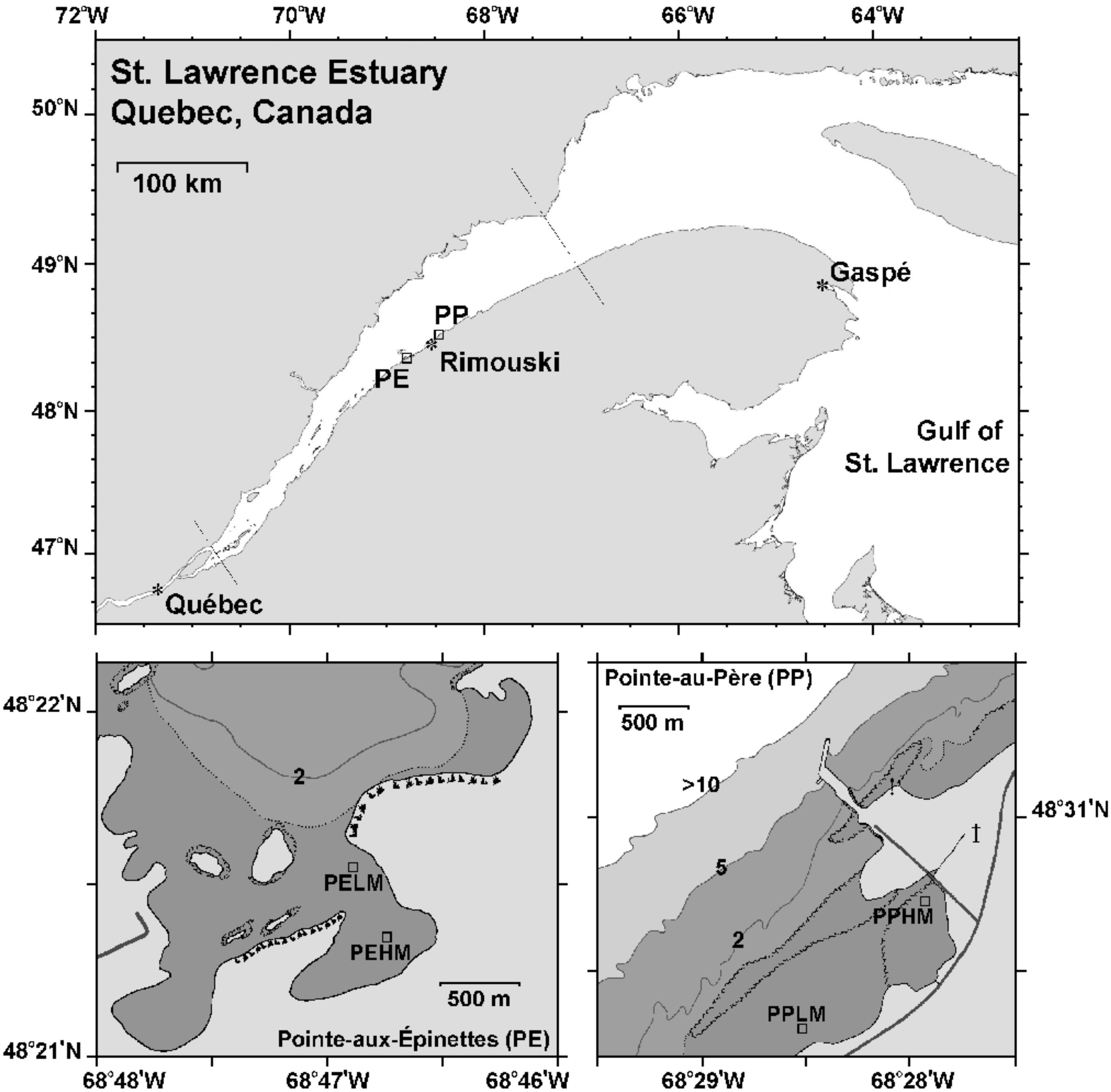

Figure 1. Map of the St. Lawrence Estuary showing the location of the Pointe-aux-Épinettes (PE) and the Pointe-au-Père (PP) salt marshes. The sampling stations were located in the low marsh zone (PELM, PPLM) and high marsh zone (PEHM, PPHM) of each site.
Carte de l'estuaire du Saint-Laurent présentant la localisation des marais de Pointe-aux-Épinette (PE) et de Pointe-au-Père (PP). Les différentes stations d'échantillonnage sont localisées dans le marais inférieur (PELM, PPLM) et le marais supérieur (PEHM, PPHM) de chacun des sites.

The PP salt marsh is part of the Pointe-au-Père National Wildlife area, a protected area since 2002. The marsh is confined in a shallow elongated basin parallel to the main St. Lawrence Estuary axis and sheltered from wave actions by a low, partially submerged ridge made of Palaeozoic claystone. The lower marsh is dominated by a *Spartina alterniflora* community growing between numerous boulders buried in muddy sediment. The upper marsh is nearly a flat platform which terminates seaward with a steep slope or a micro-cliff of 0.5 m. Unlike PE, the PP marsh has been subjected for decades to various anthropogenic pressures (urban sewage and agricultural runoff, landfills and road construction) and is still receiving dissolved nutrient inputs from small tributaries (POULIN, 2008). Erosion structures (such as micro-cliff, micro-ravine, high marsh collapse) occur along drainage channel edges. A preliminary survey conducted in May and July 2004 indicated that surface sediment of the PP salt marsh was not heavily impacted with organic pollutants such as chlorinated compounds but aliphatic hydrocarbons and some light polycyclic aromatic hydrocarbons (PAHs) were detected and their presence was attributed to nearby road traffic (PELETIER, E. unpublished results).

2.2 Sampling and analyses

Sediments were sampled in summer 2005 (7-11 July) from the Pointe-aux-Epinettes (48º 21.3'N; 68º 46.5'W) low marsh zone (PELM) and high marsh zone (PEHM), and from the Pointe-au-Père (48º 30.3'N; 68º 28.0'W) low marsh zone (PPLM) and high marsh zone (PPHM) as illustrated in Figure 1. Six cores were randomly collected (according to the benchmark sampling technique) using truncated 10 cm^3 sterile syringes in a predetermined square of 10 m^2 (benchmark site) and the first two top centimeters were kept for analysis.

Surface sediment samples were processed for diatom analysis following a modification of the Schrader method (1974). A 0.5 g sub-sample of dried sediment was treated with hydrogen peroxide and hydrochloric acid. The samples were washed with distilled water and centrifuged until no acid remained in the samples. An aliquot of 0.5 mL was placed on a cover slip and air dried. Permanent slides were prepared using Hyrax as the mounting medium. A Leitz Wetzlar Orthoplan® microscope, equipped with phase contrast and magnification up to x1000 was used for diatom identification. A minimum of 400 cells were counted in random transects for each sample. Diatom abundance was expressed as number of $cells \bullet g^{-1}$. The Shannon index H' (MAGURRAN, 1988) was used for diversity measures. For statistical analysis, tychoplanktonic, periphytic, epiphytic and epilithic cells were included in the epipsammic group whereas planktonic species were included in the epipelic group. Total bacteria abundances (TB) were determined on formaldehyde fixed samples by epifluorescence microscopy using a 4',6-diamidino-2-phenylindole (DAPI) staining procedure adapted from KUWAE and HOSOKAWA (1999).

Chlorophyll-*a* (Chl-*a*) and phaeopigments (Pheo) were first extracted from sediment using 90% acetone solution and analyzed by fluorescence detection (STRICKLAND and PARSONS, 1972). Extracellular polymeric substances (EPS) concentrations were determined by a phenol-sulphuric acid dosage technique (UNDERWOOD *et al.*, 1995) which measures total carbohydrate concentrations. Surface sediment elementary analysis for carbon (C_{org}) and nitrogen (N_{tot}) was performed with a ECS 4010 Costech® instrument equipped with a zero blank auto-sampler, using a certified sediment sample (n = 10) NIST-1941b as a reference, whereas grain size analyses were done using a Coulter® counter model LS13320C.

2.3 Statistical analyses

Spearman's rank correlations were firstly used to test the correlation between diatom community characteristics (*i.e.* epipelic cells abundance, epipsammic cells abundance, total cells abundance), total bacteria abundances and environmental variables (*i.e*. Chl-*a*, Pheo, EPS, C_{org}, N_{tot}, Clay, Silt Fine Sand, Medium Sand and Coarse Sand). Thereafter, multiple linear regression analyses were used to link these environmental parameters to the variations of diatom community characteristics considering correlation significance at a $p < 0.05$ level. Normality and homoscedasticity were confirmed by the examination of the residuals. Analysis of variance (One Way ANOVA on Ranks) was performed to test for significant differences in diatom density, epipelic and epipsammic species as well as for other environmental variables among different sampling sites (PELM, PEHM, PPLM and PPHM). Prior to ANOVA, normality and homoscedasticity were confirmed by the examination of the residuals. To isolate groups that differed from the others, Holm-Sidak and Tukey post-hoc multiple comparison procedures were performed. Differences between groups were considered significant at the $p < 0.05$ level. Comparisons of means were performed with Sigma Stat® Software Inc.

3. RESULTS

3.1 Environmental variables

Mean (AV ± SD) variable values are presented in Tables 1a and 1b. According to the ANOVAs, sampling sites show significant differences for several variables [C_{org} ($p < 0.001$); N_{tot} ($p = 0.002$); C/N ($p = 0.002$); EPS ($p < 0.001$); Chl-*a* $p = 0.002$); Pheo ($p = 0.017$), and the five sediment types ($p < 0.001$)] while mean Chl-*a*/Pheo ratios did not show any significant inter-site differences ($p = 0.611$). The *a posteriori* test showed that C_{org}, Chl-*a*, Pheo as well as C/N ratios remained statistically higher in PPHM compared to PELM and PEHM with no significant difference between PPLM and other sampling sites (PPHM, PELM and PEHM). The N_{tot} concentration was statistically higher at the PPHM and PPLM sites compared to the PELM site, whereas EPS concentrations remained statistically higher at the PPHM site compared to the other sites, except for PEHM. Sediment grain size distribution showed important spatial variability with a significant higher proportion of clay and silt at the PPHM site, a significant higher proportion of fine sand at PPLM and a significant higher proportion of medium and coarse sand at PELM.

3.2 Diatom composition and bacterial abundance

TB abundances ranged from 1.57 $x10^8$ $cell \bullet g^{-1}$ at PELM to 2.48 $x10^9$ $cell \bullet g^{-1}$ at PPHM. TB remained statistically higher at PPHM compared to PELM and PEHM with no significant

Table 1a. **Mean values (AV) and standard deviations (SD) of sediment characteristics analyzed at stations PELM (Pointe-aux-Épinettes low marsh), PEHM (Pointe-aux-Épinettes high marsh), PPLM (Pointe-au-Père low marsh) and PPHM (Pointe-au-Père high marsh).**

Tableaux 1a. ***Valeurs moyennes (AV) et écarts-types (SD) des caractéristiques géochimiques mesurées aux stations PELM (bas marais de Pointe-aux-Épinettes), PEHM (haut marais de Pointe-aux-Épinettes), PPLM (bas marais de Pointe-au-Père) et PPHM (haut marais de Pointe-au-Père).***

	C_{org} (%)		N_{tot} (%)		C/N		EPS (µg•g^{-1})		Clay (%) (< 2 µm)		Silt (%) (2-63 µm)		Fine sand (%) (64-257 µm)		Medium sand (%) (258-494µm)		Coarse sand (%) (495-2000 µm)	
	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD
PELM	0.32	0.16	0.06	0.01	6	2	2244	728	0.29	0.46	2.47	3.04	33.39	9.07	26.07	4.54	37.98	9.70
PEHM	0.67	0.16	0.08	0.03	12	4	4049	827	1.45	0.39	20.44	7.71	37.33	7.51	11.19	3.86	32.48	8.14
PPLM	0.98	0.37	0.20	0.07	7.3	6.2	2342	479	1.57	0.22	11.27	2.09	48.05	10.86	17.34	3.42	21.99	9.96
PPHM	8.06	3.31	0.35	0.24	35	17	5658	1521	3.15	0.34	61.10	6.89	20.60	2.16	3.91	2.23	11.51	4.62

Table 1b. **Mean values (AV) and standard deviations (SD) of biological variables analyzed at stations PELM (Pointe-aux-Épinettes low marsh), PEHM (Pointe-aux-Épinettes high marsh), PPLM (Pointe-au-Père low marsh) and PPHM (Pointe-au-Père high marsh).**

Tableau 1b. ***Valeurs moyennes (AV) et écarts-types (SD) des caractéristiques biologiques mesurées aux stations PELM (bas marais de Pointe-aux-Épinettes), PEHM (haut marais de Pointe-aux-Épinettes), PPLM (bas marais de Pointe-au-Père) et PPHM (haut marais de Pointe-au-Père).***

	Chl-*a* (µg•g^{-1})		Pheo (µg•g^{-1})		Chl-*a*•Pheo^{-1}		Bacteria (cells•g^{-1})		MPB density (cells•g^{-1})		Epipelic (%)		Epipsammic (%)	
	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD
PELM	62.05	36.18	38.30	23.03	2.86	2.63	1.57E+8	2.81E+7	1.92E+6	1.59E+5	36.77	6.09	63.23	12.93
PEHM	81.00	35.54	77.52	26.93	1.29	0.98	1.77E+8	9.40E+7	1.37E+6	1.02E+5	26.66	4.25	73.61	14.61
PPLM	96.22	27.28	57.17	31.25	2.65	2.24	3.12E+8	1.63E+8	1.58E+6	2.08E+5	12.68	1.62	87.33	18.01
PPHM	570.10	267.49	715.19	319.48	0.79	1.22	2.48E+9	6.72E+8	3.84E+6	6.82E+5	57.86	4.57	41.16	4.91

differences between PPLM and other sampling sites (PPHM, PELM and PEHM).

A total of 53 diatom species were identified during this study (Table 2). Most of them are benthic species with only six planktonic species observed: *Aulacoseira subarctica*, *Coscinodiscus marginatus*, *Cyclostephanos dubius*, *Ondotalla aurita*, *Thalassiosira eccentrica* and *T. proschkinae*. Among the 47 benthic taxa observed, 24 belong to the epipelic group, 12 to the epipsammic group, 4 are tychoplanktonic, 4 are periphytic, 2 are epiphytic and 1 is epilithic. Except for PPHM, a great similarity in species composition and distribution was observed between stations PELM, PEHM and PPLM. The lowest number of species (26 taxa) was observed at PPLM whereas the highest number (31) was observed at PEHM stations. In terms of diatom density, the lowest values (1.22×10^6 cells•g^{-1}) were observed at PEHM whereas the highest one (2.18×10^6 cells•g^{-1}) was observed at PELM. The three dominant species were: *Achnanthes delicatula* (abundance ≥ 50%), *Navicula cryptocephala* (abundance 10-30%) and *Cocconeis disculus* (abundance 5-10%). Diatom density was significantly higher at the PPHM station ($p < 0.001$) with an appreciable difference in the community composition: 44 species were identified and, even though *A. delicatula*, *M. criptocephala* and *C. disculus* remained the most dominant species, each represented less than 30% of total microphytobenthos community. The *a posteriori* test showed that total cell density was statistically higher at the PPHM site compared to the PELM and PEHM areas, with no significant difference between PPLM and other sampling sites.

On the basis of their habitat, diatom species were grouped into epipelic and epipsammic forms. Comparison between sampling sites showed significant differences in total diatom density ($p < 0.001$), epipelic ($p < 0.001$) and epipsammic ($p < 0.001$) species with significantly higher total abundance in PPHM and no statistical difference between other sampling sites. The *a posteriori* test showed the dominance of epipelic forms in PPHM (relative abundance > 57%) compared to PPLM and PEHM whereas epipsammic forms are significantly higher in PPLM compared to all other sites (relative abundance > 87%). Epipelic species are mainly represented by *Diploneis interrupta*, *D. smithii*, *Gyrosigma fasciola*, *G. spenceri*, *Navicula cryptocephala*, *N. peregrina*, *N. radiosa* var. *tenella*, *N. salinarum*, *Nitzschia clausii* and *N. tryblionella* while the epipsammic species are mainly represented by *Achnanthes delicatula* and *Cocconeis disculus*.

Multiple linear regressions showed that among all sampling sites, the variance of the dependent variable diatom density was mainly affected by a linear combination of surface sediment nutrient concentrations (Table 3). About 72% of the variance in diatom cell density is explained by the combination of C_{org} and N_{tot}. Similarly, 81% of the variance of epipelic species abundance could be explained by the combination of C_{org} and N_{tot} whereas the best fit model showed that only 33% of the variance of the epipsammic species could be explained by coarse sand relative concentration variability.

The determination of the Shannon and Weaver diversity measures (H') revealed a higher diversity at the PPHM station (mean H' = 2.58) compared to mean values of 1.46 bits•cells^{-1} at the PELM, PEHM and PPLM stations. MPB biomass was estimated using the calculation model proposed by DE JONGE (1980). The conversion from µg Chl-*a*•g^{-1} dry sediment to mg Chl-*a*•m^{-2} was done by multiplying recorded Chl-*a* concentrations by 12.7, based on an average bulk density of 1.27 g•cm^{-3}, whereas the conversion from Chl-*a* to carbon was obtained using the C/Chl-*a* ratio of 40 (DE JONGE, 1980). The estimated surface biomass at PE marsh ranged from 267 to 1762 mg Chl-*a*•m^{-2} (11 to 71 g C•m^{-2}) while it ranged from 576 to 12170 mg Chl-*a*•m^{-2} at the PP marsh with the highest values observed at the PPHM site. These values correspond to carbon concentrations ranging from 132 to 486 g C•m^{-2} at PPHM and from 24 to 65 g C•m^{-2} at PPLM.

4. DISCUSSION

Our study is the first to describe the summer composition of diatom communities in two northern salt marshes of the Lower St. Lawrence Estuary. Diatom abundance and Chl-*a* concentrations reported here offer some similarities with those reported in the literature in temperate intertidal areas (PELETIER, 1996; SABBE, 1993). However, significant differences were observed among the four sampling stations, with higher diatom cell density and Chl-*a* concentration recorded at the PPHM station compared to both PE sampling sites. Although these differences may be related to spatial heterogeneity, the higher biomass registered at the PPHM station seems to result from favorable environmental conditions for MPB growth. Among important variables involved in diatom growth, nutrient load due to anthropogenic activities is generally suggested as the most probable factor leading to an important increase of MPB in coastal areas (HOWARTH and MARINO, 2006). The particular location of the PP saltmarsh, partly enclosed within an urbanized area, might be expected to contribute to the higher diatom abundance observed at the PPHM station as nutrient deposition may be higher in impacted areas compared to pristine ones. In addition, the higher proportion of clay and silt found at this site might promote nutrient retention compared to more sandy sites which favor nutrient runoff toward estuarine water.

Due to their diversity and abundance in aquatic systems, diatoms have frequently been used as a proxy for aquatic ecosystem perturbations (CHRISTIE and SMOL, 1993; UNDERWOOD and KROMKAMP, 1999). One of the well-

Table 2. **List of microphytobenthic diatom species and their relative abundance (%) at stations PELM (Pointe-aux-Épinettes low marsh), PEHM (Pointe-aux-Épinettes high marsh), PPLM (Pointe-au-Père low marsh) and PPHM (Pointe-au-Père high marsh) in July 2005.**

Tableau 2. ***Liste des espèces de diatomées microphytobenthiques et les abondances relatives (%) dénombrées aux stations PELM (bas marais de Pointe-aux-Épinettes), PEHM (haut marais de Pointe-aux-Épinettes), PPLM (bas marais de Pointe-au-Père) et PPHM (haut marais de Pointe-au-Père).***

	Specific habitat	TAXA	PELM		PEHM		PPLM		PPHM	
			Mean	S.D.	Mean	SD	Mean	S.D.	Mean	SD
1	Epipsammic	*Achnanthes affinis* Grun.	1.03	0.72	2.71	2.36	0.50	0.49	1.36	1.00
2	Epipsammic	*Achnanthes brevipes* var. *intermedia* (Kütz.) Cl.	0.27	0.24	0.43	0.88	0.07	0.16	0.19	0.25
3	Epipsammic	*Achnanthes delicatula (* Kütz.) Grun.	50.63	2.85	60.85	5.91	65.89	5.84	18.51	5.81
4	Epipsammic	*Achnanthes flexella* var. *alpestris* Brun			1.23	1.47	5.31	2.15	1.44	2.06
5	Epipelic	*Amphora coffeaeformis* (Ag.) Kütz.	1.87	1.00	3.58	2.01	4.47	1.44	4.50	3.08
6	Planktonic	*Aulacoseira subarctica* (Müll.) Haworth	0.15	0.36						
7	Epipelic	*Caloneis* sp.							0.35	0.49
8	Epispsammic	*Cocconeis disculus* (Schum.) Cl.	7.01	3.70	4.27	2.23	10.02	2.40	12.18	3.46
9	Epispsammic	*Cocconeis peltoides* Hust.			0.26	0.64	2.94	1.74	0.96	0.52
10	Epispsammic	*Cocconeis pinnata* Greg.	0.47	0.64	1.10	0.85	1.03	0.62	0.88	0.95
11	Epispsammic	*Cocconeis placentula* var. *lineata (*Ehrenb.) Van Heurck	0.78	1.91	0.64	0.80	0.48	0.73	2.27	2.09
12	Planktonic	*Coscinodiscus marginatus* Ehrenb.	0.19	0.15	0.07	0.18	0.05	0.11	0.14	0.24
13	Epipsammic	*Ctenopohra pulchella* (Ralfs & Kütz.) Williams & Round							0.14	0.24
14	Planktonic	*Cyclostephanos dubius* (Fricke) Round	0.47	0.29	0.35	0.51	0.06	0.14		
15	Tychoplanktonic	*Cyclotella meneghiniana* Kütz.	0.76	0.48	0.92	0.56	0.76	0.71	1.24	0.33
16	Epipelic	*Cylindrotheca closterium* (Ehrenb.) Reimann & Lewin			0.07	0.16	0.06	0.14		
17	Epipelic	*Diploneis interrupta* (Kütz.) Cl.							0.69	0.38
18	Epipelic	*Diploneis smithii* (Bréb.) Cl.							0.22	0.20
19	Epipelic	*Fallacia pygmaea* (Kütz.) Stickle & Mann	3.02	4.06	1.92	1.50	0.28	0.33	2.26	1.46
20	Epipsammic	*Fragilaria brevistriata* (Grun.) Van heurck	0.15	0.24						
21	Tychoplanktonic	*Fragilaria capucina* (Desm.)			0.19	0.32				
22	Epipsammic	*Fragilaria pinnata* Ehrenb.	1.62	1.34			0.16	0.25	0.05	0.13
23	Epilithic	*Fragilaria vaucheriae* (Kütz.) Petersen			0.06	0.15			0.05	0.13
24	Periphytic	*Gomphonema* sp.	0.09	0.14	0.06	0.15	0.06	0.14		
25	Epiphytic	*Grammatophora angulosa* Ehrenb.	0.05	0.12	0.15	0.36			0.05	0.13
26	Epipelic	*Gyrosigma acuminatum* (Kütz.) Rabenhorst			0.13	0.21			0.24	0.29
27	Epipelic	*Gyrosigma fasciola* (Ehrenb.) Griffith & Henfrey							0.04	0.09
28	Epipelic	*Gyrosigma spenceri* (Smith) Cl.							1.01	0.53
29	Epiphytic	*Licmophora paradoxa* (Lyng.) Ag.			0.13	0.20	0.06	0.14	0.05	0.13
30	Tychoplanktonic	*Melosira nummuloides* Ag.							0.62	0.89
31	Epipelic	*Navicula cryptocephala* Kütz.	23.43	3.03	15.80	3.52	5.78	4.16	22.93	6.23
32	Epipelic	*Navicula digitoradiata* (Greg.) Ralfs in Pritchard	0.74	0.63	0.43	0.86	0.11	0.18	1.29	0.95
33	Epipelic	*Navicula peregrina* (Ehrenb.) Kütz.							0.60	0.49
34	Epipelic	*Navicula radiosa* var. *tenella* (Bréb.) Grun.	1.04	0.74	1.16	0.67	0.83	0.59	4.03	1.70
35	Epipelic	*Navicula salinarum* (Grun.) Cl. & Grun.							0.19	0.46
36	Epipelic	*Nitzschia acuminata* (Smith) Grun.	0.51	0.72	0.36	0.15	0.17	0.19	1.33	0.97
37	Epipelic	*Nitzschia clausii* Hantz.							3.28	3.22
38	Epipelic	*Nitzschia communis* Rabenhorst	1.98	1.42	0.75	0.72			6.41	1.87
39	Epipelic	*Nitzschia* sp.							1.37	1.02
40	Epipelic	*Nitzschia distans* Greg.			0.07	0.16			1.17	0.64
41	Epipelic	*Nitzschia frustulum* (Kütz.) Cl. & Grun.	1.98	1.35					0.06	0.15
42	Epipelic	*Nitzschia tubicola* (Grun.) Cl. & Grun.	0.13	0.15						
43	Epipelic	*Nitzschia tryblionella (* Hantz.) Rabenhorst					0.06	0.14	1.79	0.60
44	Planctonic	*Odontalla aurita* (Lyngb.) Ag.	0.14	0.23					0.18	0.14
45	Epipsammic	*Opephora olsenii* Møller			0.21	0.36				
46	Epipelic	*Pleurosigma aestuarii* (Bréb. Ex Kütz.) Smith					0.19	0.33	0.79	0.42
47	Periphytic	*Remeria sinuata* (Greg.) Kociolek & Stoermer	0.14	0.23	0.07	0.16				
48	Periphytic	*Rhoicosphenia curvata* (Kütz.) Grun.	0.04	0.10			0.05	0.13	0.96	0.66
49	Epipelic	*Surirella ovata* Hust.			0.47	0.50			1.00	1.23
50	Periphytic	*Tabularia tabulata* (Ag.) Snoeijs	0.10	0.24	0.33	0.47			0.10	0.16
51	Tychplanctonic	*Tabellaria flocculosa* (Roth) Kütz.	0.09	0.22					0.11	0.17
52	Planktonic	*Thalassiosira eccentrica* (Ehrenb.) Cl.	0.86	0.83			0.15	0.24	1.72	0.85
53	Planktonic	*Thallassiosira proschkinae* Makarova	0.26	0.42	1.50	1.41	0.47	0.35	0.27	0.65
		Total number of species	30		31		26		44	

Table 3. **Results of multiple linear regressions testing the effect of environmental variables on diatom density and abundance of epipelic and epipsammic forms at stations PELM (Pointe-aux-Épinettes low marsh), PEHM (Pointe-aux-Épinettes high marsh), PPLM (Pointe-au-Père low marsh) and PPHM (Pointe-au-Père high marsh).**

Tableau 3. ***Résultats des régressions linéaires multiples testant l'effet des variables environnementales sur la densité des diatomées et les abondances des formes épipéliques et épipsammiques aux stations aux stations PELM (bas marais de Pointe-aux-Épinettes), PEHM (haut marais de Pointe-aux-Épinettes), PPLM (bas marais de Pointe-au-Père) et PPHM (haut marais de Pointe-au-Père).***

Dep Variable	Adj Rsqr	Ind Variable	Coefficient	Std Error	P
Density	0.717	Constant	1820772	170145	< 0.001
		N_{tot}	-3380497	1360553	0.021
		C_{org}	373193	63289	< 0.001
Epipelic	0.810	Constant	636320	110487	< 0.001
		N_{tot}	-3495136	883503	< 0.001
		C_{org}	332633	41098	< 0.001
Epipsammic	0.326	Constant	1622117	103803	< 0.001
		Coarse sand	-12500	3588	0.002

documented effects of nutrient inputs on diatom communities is the reduction in number of species along with an increase in the abundance of the remaining ones (COOPER, 1995; DE SÈVE and GOLDSTEIN, 1981). A high dominance of epipsammic species within a relatively low diversified community was observed at the PPLM, PEHM and PELM stations, whereas a slight dominance of epipelic forms within a much more diverse community was found at the PPHM station. The higher diversity observed at the PPHM station is attributable to an increase of epipelic species and the presence of some particular species (such as *Diploneis interrupta* and *Gyrosigma acuminatum*), suggesting the presence of eutrophic conditions at this station. The differences observed in Chl-*a* concentrations among different sites could be partially attributed to the proportion of epipelic *versus* epipsammic diatoms within the community since epipelic forms are generally larger and susceptible to contain more pigments than the epipsammic ones (UNDERWOOD *et al.*, 1995). Although the PP salt marsh can be considered as a human disturbed area, the high MPB diversity recorded at the PPHM station does not reflect the reduction of diatom diversity generally observed in temperate human impacted sites. The absence of toxic industrial wastes and the presence of labile clayey sediment in the PP system might explain the maintenance of high diatom diversity in this marsh.

Organic matter lability, grain size distribution and sediment stability are among marsh sediment characteristics influencing the distribution of microphytobenthic species. In our study, the average C/N ratio ranged from 6.4 to 34.7 among sites, but cannot be used as a relevant proxy to determine the lability of the organic matter due to the high relative carbon content (and low nitrogen) of the *Spartina* rhizosphere (*Spartina* C/N ~ 40 following MEYERS,1994). For example, *Spartina* roots at the PPHM station may account for an important proportion of the observed high C/N ratio, but this value does not necessarily imply a refractory character of the interstitial sediment. Thus, high epipelic cell abundances at the PPHM site could be better explained by the microbial degradation potential within the *Spartina* rhizosphere rather than by the C/N ratio observed in the sediment. Degradation processes estimated through the Chl-*a*/phaeopigments ratio support this finding. A ratio of 10 is generally observed in growing populations but values below 3 usually indicate some cell degradation or important grazing by meiofauna (CARIOU-LEGALL and BLANCHARD, 1995). Elevated pheopigment concentrations, particularly at station PPHM, further suggest active degradation processes of vegetation. In the present study, the lowest mean Chl-*a*/phaeopigments ratio was recorded at the PPHM site with no significant differences among the sampling sites (Table 1b) showing strong pigment degradation.

The composition of diatom communities has been previously reported to be influenced by the size of the sediment particles (ZONG and HORTON, 1998). Previous studies in temperate areas showed that epipsammic taxa were mainly associated with sandy substrates whereas epipelic taxa were mainly found in muddy to clayey substrates (FORSTER *et al.*, 2006). Our results in St. Lawrence marshes are in agreement with these findings since the abundance of epipsammic forms can be roughly predicted from coarse sand concentrations (Table 3). In addition, the muddy character of the sediments at the PPHM station (*i.e.* high clay and silt content; Table 1a) may have contributed to the settling of many epipelic species in this specific area.

The benthic carbon concentrations, derived from Chl-*a* measures at surface sediment in July 2005, ranged from 11 to 71 g C•m^{-2} in the PE marsh, and from 24 to 65 g C•m^{-2} at the PPLM site, with a peak at the PPHM station (>132 g C•m^{-2}). According to these values, the annual potential marsh productivity can be estimated to range from 10 to

$70\ g\ C\bullet m^{-2}\bullet y^{-1}$. This preliminary calculation may underestimate the marsh production since marsh biomass evaluation (using Chl-*a* concentrations) does not take in account bacterial and EPS carbon production which could represent up to 30% of the MPB production (HALL and FISHER, 1985). Diatom productivity observed in both studied salt marshes is of the same order of magnitude as the primary production ($104\ g\ C\bullet m^{-2}\bullet y^{-1}$) recorded in the adjacent biologically rich St. Lawrence Estuary waters (THERRIAULT and LEVASSEUR, 1985).

In conclusion, this work provides the first results on the abundance and diversity of diatom communities inhabiting two northern salt marshes during summer time. Rich organic carbon clayey substrates seem to account for the high diatom counts at the PPHM station along with effluent enrichment, even if no direct links can been established yet. In addition, the relative abundance of epipelic and epipsammic forms is mainly related to the sediment grain size distribution. This study provides reference data from which diatom-based indices (SGRO *et al.*, 2007) could be calculated and used in monitoring salt marsh environmental changes.

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