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Holocene development of maritime ombrotrophic peatlands of the St. Lawrence North Shore in eastern Canada

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ABSTRACT

Macrofossil analyses were used to reconstruct long-term vegetation successions within ombrotrophic peatlands (bogs) from the northern shorelines of the St. Lawrence Estuary (Baie-Comeau) and the Gulf of St. Lawrence (Havre-St-Pierre). Over the Holocene, the timing and the ecological context of peatland inception were similar in both regions and were mainly influenced by fluctuations in relative sea level. Peat accumulation started over deltaic sands after the withdrawal of the Goldthwait Sea from 7500 cal yr BP and above silt–clay deposits left by the Laurentian marine transgression after 4200 cal yr BP. In each region, the early vegetation communities were similar within these two edaphic contexts where poor fens with Cyperaceae and eastern larch (*Larix laricina*) established after land emergence. The rapid transitions to ombrotrophy in the peatlands of Baie-Comeau are associated with particularly high rates of peat accumulation during the early developmental stage. The results suggest that climate was more propitious to *Sphagnum* growth after land emergence in the Baie-Comeau area. Macrofossil data show that treeless *Sphagnum*-dominated bogs have persisted over millennia and that fires had few impacts on the vegetation dynamics. This study provides insight into peatland vegetation responses to climate in a poorly documented region of northeastern America.

Introduction

Peatlands are an important feature of the boreal landscape in the Northern Hemisphere. Although peatland ecosystems cover only 3% of the Earth's land surface, they are one of the largest terrestrial carbon (C) sinks (Yu et al., 2009). Over the Holocene, the initiation and expansion of northern peatlands have played an important role in the global C cycle and feedbacks on climate change (Frolking and Roulet, 2007; Yu, 2011). In Canada, peatlands cover ~12% of the land area (~1.1 million km^2) and contain the equivalent of about half of the organic C stored in soils (Tarnocai et al., 2005). Peatlands are common in the maritime regions of eastern Canada and play an important role in terms of biodiversity, water storage and organic C sequestration (Damman, 1986; Garneau et al., accepted for publication; Glaser, 1992). Ombrotrophic peatlands (bogs) are widespread along the north shore of the St. Lawrence Estuary and Gulf of St. Lawrence in eastern Québec. These ecosystems cover deltaic sands that emerged from the Goldthwait Sea after ~9000 yr and silt–clay deposits left by the mid-Holocene Laurentian marine transgression (Dionne, 2001; Bernatchez, 2003). In spite of their ecological and spatial significance in the coastal plains, little is known about the development of these bogs over the Holocene. It is necessary to understand the factors influencing long-term vegetation dynamics in these peatlands to evaluate how they can be affected by environmental and climate changes.

Over the last decades, only few palaeoecological studies have been conducted in maritime bogs of eastern Canada (Tolonen et al., 1985; Garneau, 1998; Hughes et al., 2006; Robichaud and Bégin, 2009; Payette et al., 2013). Previous peatland paleoecological studies mainly focused on continental boreal regions of the James Bay and Hudson Bay Lowlands (Glaser et al., 2004; Arlen-Pouliot and Bhiry, 2005; Arlen-Pouliot, 2009; Beaulieu-Audy et al., 2009; van Bellen et al., 2011a; Bunbury et al., 2012; Lamarre et al., 2012; Magnan et al., 2012) and within the St. Lawrence Lowlands in southern Québec and eastern Ontario (Lavoie and Richard, 2000; Muller et al., 2003; Elliott et al., 2012; Lavoie et al., 2013). These studies showed that the rates and pathways of vegetation changes in peatlands are driven by a combination of internal processes (e.g., plant competition, peat build-up) and external factors (e.g., climate and fires). The long-term development of boreal and subarctic peatlands typically follows a hydroseral succession from minerotrophic (fen) to ombrotrophic conditions (bog). This isolation of peat-forming vegetation from nutrient-rich groundwater may result primarily from internal factors (Payette, 1988; Yu et al., 2003a) but can also be favoured by changes in the atmospheric moisture balance (Hughes and Barber, 2003).

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At the regional scale, the basin morphology and underlying sediment which control water supplies are important factors influencing the early peatland development (Bauer et al., 2003; Bhiry et al., 2007; van Bellen et al., 2011b; Ireland et al., 2013). The shape of the basin indirectly controls the long-term trends in peat accumulation and surface hydrology (Yu et al., 2003a; Belyea and Baird, 2006). However, the Holocene climate variations have also been an important factor controlling the initiation and expansion of northern peatlands (MacDonald et al., 2006; Korhola et al., 2010). In northern Québec, the active formation of peatlands between 6300 and 4200 yr coincided with the Holocene Thermal Maximum (Payette, 1984). Besides climate variations, the vegetation dynamics of boreal peatlands can also be affected by fire, but this disturbance is much less frequent in these ecosystems than in upland forests (e.g., Kuhry, 1994; Camill et al., 2009; Magnan et al., 2012).

The main objective of this study is to evaluate the factors that influenced the long-term development of the maritime ombrotrophic peatlands along the St. Lawrence Estuary (Baie-Comeau) and the Gulf of St. Lawrence (Havre-Saint-Pierre). More specifically we aim to 1) document the timing of peatland initiation and the early ecological process of peat accumulation within two edaphic contexts and 2) compare the Holocene development of maritime peatlands from two distinct bioclimatic regions. We hypothesise that the ecological mode of peat inception has been similar in both regions but that the peatlands of Baie-Comeau and Havre-St-Pierre have followed different development pathways over the Holocene.

Methods

Study area and sites

Two of the largest ombrotrophic peatland complexes along the north shore of the Estuary and the Gulf of St. Lawrence were investigated on the Manicouagan delta near Baie-Comeau (BC) and on the La Romaine delta near Havre-St-Pierre (HSP) (Fig. 1). We selected sites with relatively flat basins in order to limit the topographic influence on long-term peatland development (sensu Belyea and Baird, 2006). In each region, peatlands were selected within two geomorphic settings below and above the limit reached by the Laurentian marine transgression (i.e., ~14–16 m above present-day sea level; Bernatchez, 2003). Lebel, Plaine and Romaine peatlands developed over well-drained deltaic sands at elevations ranging between 17 and 31 m asl. Baie, Manic

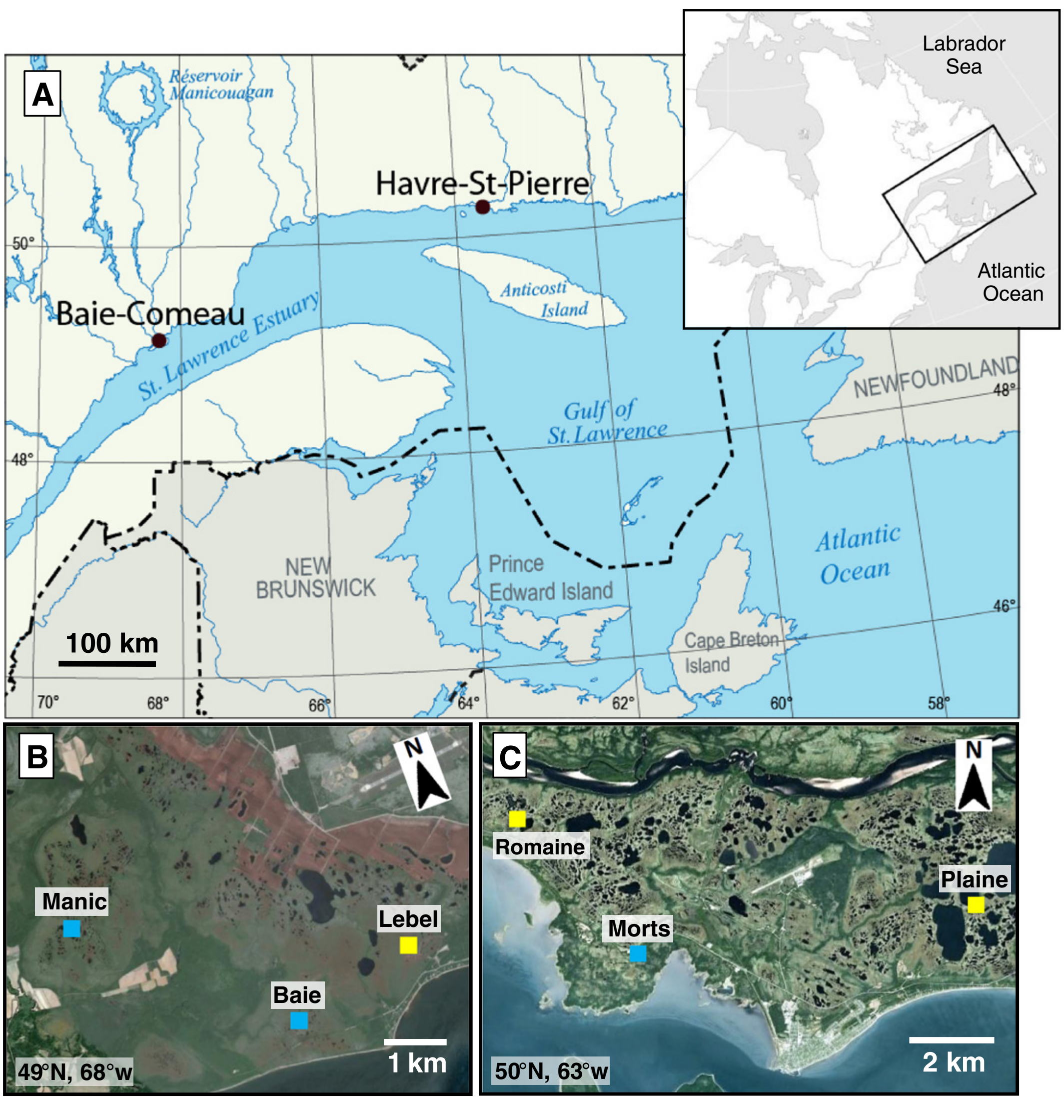

Figure 1. (A) Map showing the two studied regions in eastern Canada and the location of the coring sites in the peatlands investigated on (B) the Manicouagan delta near Baie-Comeau and (C) the La Romaine delta near Havre-St-Pierre. Yellow squares show peatlands on deltaic sands and blue squares represent peatlands above silt–clay deposits.
Satellite images from Google Earth 2013.

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Table 1
Characteristics of the studied peatlands from Baie-Comeau and Havre-St-Pierre.

Study region	Sites	Peatland type	Lat. (N)	Long. (W)	Elevation peat surface (m asl)	Elevation basal sediment (m asl)	Basal sediment type	Peat depth (cm)
Baie-Comeau	Lebel	Raised bog	49° 5.9′	68° 13.3′	22.4	16.7	Deltaic sand	575
	Baie	Raised bog	49° 5.8′	68° 15′	16.8	12.2	Marine silt–clay	461
	Manic	Raised bog	49° 7.08′	68° 18.2′	22.2	16.3	Marine silt–clay	589
Havre-St-Pierre	Plaine	Plateau bog	50° 16.5′	63° 32.3′	34.2	30.6	Deltaic sand	356
	Romaine	Plateau bog	50° 17.7′	63° 42.9′	24.2	22.3	Deltaic sand	187
	Morts	Plateau bog	50° 15.8′	63° 40.1′	14.5	11.7	Marine silt–clay	285

and Morts peatlands are located on a lower terrace at 12–16 m asl and are underlain by poorly-drained marine silt–clay deposits (Table 1).

In the Baie-Comeau area, the dominant peatland types are raised bog dominated by *Sphagnum* spp., ericaceous shrubs (e.g., *Chamaedaphne calyculata*, *Rhododendron groenlandicum*, *Kalmia angustifolia*) and dwarf black spruce (*Picea mariana*) (Fig. 2A). In the Havre-St-Pierre area, the La Romaine delta is covered by extensive plateau bogs which are largely treeless. Their surfaces are typically covered by lichens (*Cladonia stellaris*, *Cladonia mitis* and *Cladonia stygia*) and ericaceous shrubs (*R. groenlandicum*, *Empetrum nigrum*, *K. angustifolia*) interspersed with patches of *Sphagnum* mosses (Fig. 2B). Mean annual precipitation is approximately 1000 mm in both regions and mean annual temperature is 0.62°C in Baie-Comeau and 0.4°C in Havre-St-Pierre (climate data 1971–2003; Hutchinson et al., 2009).

In the Baie-Comeau area, the regional forests are dominated by balsam fir (*Abies balsamea*) and black spruce along with paper birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). The forest cover is increasingly fragmented towards the Gulf of St. Lawrence as the coastal climatic conditions become more subarctic. Havre-St-Pierre is located at the eastern limit of the closed boreal forest within the spruce–moss domain characterised by dense stands of *P. mariana* in protected sites and fragmented open forest stands in more wind-exposed uplands (Payette and Bouchard, 2001).

Field work

At each site, measurements of peat thickness were conducted with a metal probe at 25-m intervals along transects evenly distributed throughout the peatlands to evaluate the morphology of the underlying basin and mineral soil type. Peat cores were collected from the deepest section of the bogs from *Sphagnum*-dominated lawn microforms using a Russian corer (diameter 7.5 cm; Jowsey, 1966). The uppermost 100 cm of the peat sequences was sampled with a Box corer (110 × 8 × 8 cm; Jeglum et al., 1992). The elevation (m asl) of the sampling location was determined using a differential global positioning system (DGPS) (Table 1). In the field, sampled sediments were wrapped with plastic film and placed in PVC tubes. In the laboratory, peat cores were stored in the fridge at 4°C prior to sub-sampling at 1-cm intervals for further analyses.

Chronology

A total of 51 terrestrial plant macrofossil samples (mostly *Sphagnum* remains) were radiocarbon dated by the accelerator mass spectrometry (AMS) technique at the Keck Carbon Cycle Laboratory (University of Irvine, California). Radiocarbon dating was conducted on the main peat stratigraphic transitions. Age–depth models were developed using classical age–depth modelling (CLAM; Blaauw, 2010) by applying linear interpolation between each dated level (1000 iterations). Radiocarbon dates were calibrated using the IntCal09 calibration curve (Reimer et al., 2009). The age of the peat surface was established at −60 cal yr BP (i.e., AD 2010; year of coring). Peat accumulation rates (PAR; mm yr^{-1}) were calculated by dividing every contiguous peat sample (1-cm) by the deposition time (yr cm^{-1}) inferred from the age–depth modelling in CLAM.

Plant macrofossil analyses

Plant macrofossil analyses were used to identify past vegetation assemblages (4-cm intervals; 5-cm^3 peat samples) in two peatlands of Baie-Comeau (Lebel and Baie) and two peatlands of Havre-St-Pierre (Plaine and Morts) (Fig. 1). In each region, the two detailed macrofossil records were compared to the stratigraphy of a peatland located nearby (Manic in BC and Romaine in HSP) to evaluate the synchronicity of the trophic status transitions at the scale of the delta. In these two peat sequences, the main vegetation types were evaluated within 2-cm^3 peat samples at 4-cm intervals. Macrofossil analyses follow the protocol of Mauquoy et al. (2010). Macrofossil remains were separated from the organic matrix by heating the material for about 30 min in a solution of potassium hydroxide (KOH 5%) to dissolve humic and fulvic acids. The material was wet-sieved through a 0.125-mm mesh screen and plant remains were identified and counted in a petri dish using a stereomicroscope at 4 to 40× magnification. The relative abundance (%) of the main vegetation types (*Sphagnum*, other bog mosses, brown mosses, Cyperaceae, wood, roots and leaves) was calculated in a gridded petri dish and corresponds to the area covered by each macrofossil type divided by the total sample area. The other plant macrofossils (e.g., seeds, conifer needles, *Cenococcum* sclerotia) were quantified using a five-point scale of abundance (1 = presence, 2 = occasional,

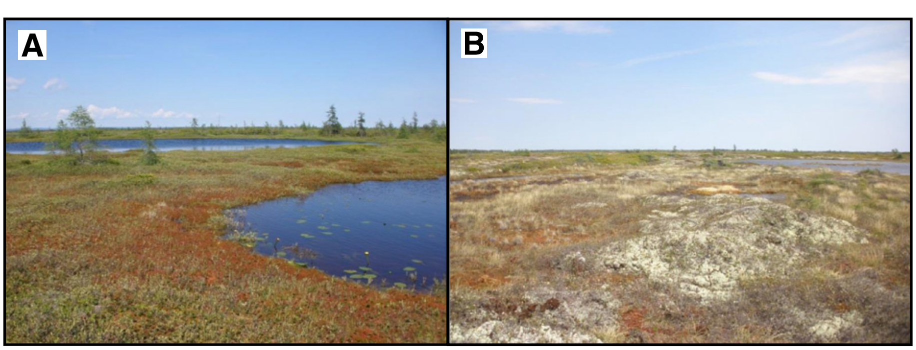

Figure 2. Photographs of (A) Lebel bog on the Manicouagan delta in Baie-Comeau and (B) Plaine bog on the La Romaine delta in Havre-St-Pierre.

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3 = frequent, 4 = very frequent 5 = abundant). References used for plant identification were Ireland (1982), Lévesque et al. (1988), Mauquoy and van Geel (2007) and the macrofossil reference collection from the laboratory of continental paleoecology (Geotop, UQAM, Canada). The plant macrofossil diagrams were plotted using the software package C2 1.7.2 (Juggins, 2011). Hereafter, we refer to bog mosses to describe non-*Sphagnum* bryophytes indicative of ombrotrophic conditions and to brown mosses for minerotrophic taxa. The degree of peat decomposition was evaluated in each macrofossil sample based on the state of preservation of moss leaves from intact (1) to poorly preserved (5). Dry bulk densities were measured on contiguous peat samples (3 cm^{-3}) with oven-drying and ash-free bulk densities and mineral contents were evaluated with loss-on-ignition at 550°C (Heiri et al., 2001). High bulk density usually corresponds with highly decomposed peat whereas low density is associated with well-preserved peat (Yu et al., 2003b). Macrofossil diagram zonation was established using stratigraphically constrained cluster analysis in R version 2.14.0 (R Development Core Team, 2011) with the rioja package (Juggins, 2012). In order to support the palaeoecological interpretations we also present mean water table depth (WTD) values for each macrofossil zone based on testate amoebae analyses conducted on these peat cores and published in Magnan and Garneau (2014).

Charcoal analyses

Macroscopic charcoal analysis was conducted in one peat core from each region that developed over the deltaic sands (Lebel, Plaine). Charcoal sampling was conducted at 1-cm intervals from the fen–bog transition to the top of the cores. Peat samples (1-cm^{-3}) were soaked in a solution of sodium hydroxide (NaOH 10%) for 24 h to dissolve humic acids and bleach charcoal particles to help differentiate charred fragments from dark organic matter. The remaining material was wet sieved through a 0.5-mm mesh screen. The macroscopic charcoal fragments (>0.5 mm) were counted under a Leica stereomicroscope at 16× magnification and recorded in two size-classes (0.5–2 mm and >2 mm). Macroscopic charcoal particles (>0.5 mm) are reliable indicators of local-scale fire events whereas large charcoal pieces (>2 mm) provide strong evidence of in situ fires (Ohlson and Tryterud, 2000).

Results

Chronologies

Peat core chronologies based on radiocarbon dating are presented in Table 2. The age–depth relationships are either close to linear or convex indicating that PAR have been relatively stable or gradually declined over time (Fig. 3). The peatlands of Baie-Comeau show particularly high rates of vertical peat accumulation especially during the early stage. The average PAR range from 0.3 mm yr^{-1} in Romaine bog (HSP) to 1.4 mm yr^{-1} in Manic bog (BC).

Plant macrofossil and charcoal data for the peatlands over deltaic sands

Lebel peatland (BC)

Peat inception on the sandy terrace of the Manicouagan delta at 17 m asl was dated around 5820 cal yr BP. Basal peat consists of decomposed *Sphagnum* mosses with needles of *P. mariana* along with Cyperaceae remnants (zone L1) (Fig. 4; Table 3). *C. calyculata* shrubs rapidly colonised the site and the ectomycorrhizal fungi of *Cenococcum* suggest relatively dry surface conditions during the early peatland stage. The testate amoebae-based WTD reconstruction conducted on this core (Magnan and Garneau, 2014) indicates particularly low water tables during the early stage (mean WTD: 18.5 cm; Table 3). Peat growth above the well-drained sand was very rapid (1.5 mm yr^{-1}; Figs. 3 and 4). Black spruce declined after ~5200 cal yr BP probably overgrown by *Sphagnum* mosses that became dominant along with few bog mosses such as *Pohlia nutans* and *Pleurozium schreberi*. The peatland surface was treeless and dominated by *Sphagnum* between 5210 and 4530 cal yr BP (zone L2). From 4530 to 3070 cal yr BP (zone L3), ericaceous shrubs and Cyperaceae with sparse *Larix laricina* were present locally. Spruce re-established shortly between 3500 and 3100 cal yr BP. The abundance and diversity of ericaceous shrubs decreased between 3070 and 2130 cal yr BP (zone L4) as PAR was low (0.7 mm yr^{-1}). An increase in woody plant remains at the expense of highly decomposed *Sphagnum* mosses around 2400 cal yr BP coincides with two layers containing macroscopic charcoal pieces (Fig. 4). *Sphagnum* and *C. calyculata* dominated the surface over the last 2100 years. *Carex* remains were relatively abundant between 2130 and 330 cal yr BP (zone L5) but were absent from the recent peat layers (zone L6). Spruce briefly recolonised the peatland surface around 2100 cal yr BP. Few macroscopic charcoal particles are found in zone L5 but no significant vegetation changes occurred during that period suggesting that fire has not affected directly the plant cover at the coring location.

Plaine peatland (HSP)

Plaine peatland developed over the La Romaine delta at an elevation of 31 m asl. The early developmental stage (7450–6560 cal yr BP) corresponds to a relatively poor fen colonised by few trees of *L. laricina* with highly decomposed Cyperaceae and brown mosses (e.g., *Calliergon* spp. and *Warnstorfia* spp.) (zone P1; Fig. 5 and Table 3). The fen–bog transition was dated around 6560 cal yr BP with the disappearance of brown mosses and the establishment of *P. mariana* along with *Sphagnum* and *P. nutans* mosses (zone P2; 6560–5430 cal yr BP). *P. mariana* disappeared around 5760 cal yr BP above a peat horizon with abundant charcoal (111 pieces >0.5 mm; 24 pieces >2 mm) (Fig. 5) and *Sphagnum* became dominant between 5430 and 4160 cal yr BP (zone P3). A charcoal layer around 4200 cal yr BP coincides with a marked slowdown in PAR (1 to 0.2 mm yr^{-1}) and increased peat decomposition as *Carex* spp. colonised the site with *L. laricina* (zone P4; 4160–2570 cal yr BP). After 2570 cal yr BP, *Sphagnum* remained dominant along with ericaceous shrubs and black spruce was present locally during a short period *c.* 2000 cal yr BP (zone P5). *Carex* spp. and ericaceous shrubs were abundant on the peatland after ~900 cal yr BP during a period of low PAR (0.3 mm yr^{-1}). Few charcoal particles >0.5 mm were identified in a peat layer dated at ~440 cal yr BP (zone P6; Fig. 5).

Plant macrofossil data for the peatlands above silt–clay deposits

Baie peatland (BC)

Baie peatland was initiated around 4200 cal yr BP above a silt–clay deposit in the lowest section of the Manicouagan delta (12 m asl) following the Laurentian marine transgression. The marine influence at this site was confirmed by the identification of foraminifera tests at the peat/mineral contact (Fig. 6). The absence of plants adapted to brackish or saline conditions in the macrofossil assemblages suggests that the influence of marine waters was short-lived. *Myrica gale* and *L. laricina* rapidly colonised the emerged silt–clay deposit and a successional poor fen with Cyperaceae and brown mosses (mainly *Calliergon* spp.) as described by Garneau (1998) developed between 4210 and 4120 cal yr BP (zone B1). PAR were high within the minerotrophic stage (2.8 mm yr^{-1}) and peat was highly decomposed. Ombrotrophic conditions established from 4120 cal yr BP as suggested by a sharp decline in Cyperaceae and the expansion of ericaceous shrubs (zone B2). The disappearance of *L. laricina* after 3800 cal yr BP suggests that the peatland surface was isolated from mineral-rich groundwaters. The ericaceous shrub cover declined after 3240 cal yr BP but *C. calyculata* persisted from 3240 to 2630 cal yr BP (zone B3). The abundance of woody plants and *Cenococcum* sclerotia increased significantly between 2630 and 1160 cal yr BP (zones B4 and B5) during a period of low PAR (0.5–0.7 mm yr^{-1}) and drier surface conditions inferred from testate amoebae (mean WTD ~10 cm; Table 3). *Dicranum* mosses were relatively abundant around 1200 cal yr BP (zone B5). After 1160 cal yr BP

Table 2
Radiocarbon dates and ages inferred from CLAM (Blaauw, 2010).

Site	Sample depth (cm)	Lab. no. (UCI-AMS)	Material dated[a]	^{14}C age (yr BP)	2σ range (cal yr BP)	Age cal yr BP (CLAM best estimate)
Plaine	16–17	67,838	*Sph.*	Modern	0	0
	24–25	79,504	*Sph.*	150 ± 15	6–281	150
	39–40	73,854	*Sph.*	935 ± 25	793–919	850
	55–56	98,873	*Sph.*	1480 ± 15	1328–1399	1360
	77–78	73,855	*Sph.*	1800 ± 25	1629–1818	1740
	101–102	73,856	*Sph.*	2245 ± 25	2157–2338	2240
	136–137	98,874	*Sph.*	2765 ± 15	2793–2921	2850
	172–173	80,191	*Sph.*	3875 ± 15	4244–4407	4320
	202–203	73,857	*Sph.*, Eric. sds	4100 ± 25	4523–4808	4630
	248–249	79,505	*Sph.*, Eric. sds	4715 ± 15	5327–5577	5430
	300–301	67,839	*Sph.*	5755 ± 15	6495–6632	6560
	356–357	67,840	*Carex* ach.	6540 ± 15	7426–7475	7450
Morts	23–24	98,870	*Sph.*	290 ± 15	300–428	370
	36–37	79,502	*Sph.*	480 ± 15	506–531	520
	48–49	98,871	*Sph.*	955 ± 15	797–926	860
	62–63	73,858	*Sph.*	1145 ± 25	976–1168	1030
	87–88	73,859	*Sph.*	1190 ± 25	1014–1178	1120
	120–121	80,188	*Sph.*, Eric. lvs.	1580 ± 15	1415–1521	1470
	168–169	79,503	*Sph.*, Eric. sds.	2150 ± 15	2066–2299	2150
	191–192	98,872	*Sph.*, Eric. lvs.; *Picea* need.	2250 ± 15	2162–2338	2260
	244–245	67,844	*Sph.*, Eric. lvs.; *Larix* need.	2585 ± 20	2625–2754	2730
	284–286	67,843	*Carex* ach.	3025 ± 15	3166–3327	3240
Romaine	32–33	79,506	*Sph.*	1595 ± 15	1416–1529	1470
	64–65	73,860	*Sph.*	1975 ± 25	1878–1988	1920
	110–111	79,507	*Sph.*	3350 ± 15	3490–3639	3590
	185–187	67,845	*Carex* ach.	6200 ± 15	7016–7168	7080
Lebel	66–67	73,861	*Sph.*	210 ± 25	(−4)–303	180
	79–80	80,190	*Sph.*, Eric. lvs.; *Carex* ach.	430 ± 15	484–514	500
	98–99	79,499	*Sph.*, Eric. lvs./sds.	965 ± 15	798–929	870
	120–121	98,875	*Sph.*	1125 ± 15	979–1061	1020
	143–144	73,862	Eric. lvs.	1475 ± 25	1311–1400	1360
	168–169	73,863	*Sph.*, Eric lvs.	1775 ± 25	1613–1810	1680
	202–204	98,876	*Sph.*	2145 ± 15	2063–2297	2150
	270–271	79,500	*Sph.*; Eric. sds.	2905 ± 15	2966–3139	3040
	331–332	79,501	*Sph.*	3570 ± 15	3832–3910	3870
	400–401	73,864	*Sph.*; Eric lvs.	4090 ± 25	4452–4805	4620
	471–472	98,877	*Sph.*	4465 ± 15	4978–5277	5160
	574–575	67,837	*Sph.*	5090 ± 15	5753–5908	5820
Baie	32–33	98,867	*Sph.*	105 ± 15	28–259	130
	58–59	73,865	*Sph.* Eric. lvs.	300 ± 25	300–455	380
	100–101	98,868	Eric. lvs.	1000 ± 15	840–958	920
	150–151	79,496	*Sph.*	1755 ± 15	1614–1712	1660
	200–202	98,869	*Sph.* Eric. lvs.	2495 ± 15	2491–2715	2590
	250–251	79,497	*Sph.*	2950 ± 15	3065–3209	3130
	304–305	80,196	*Sph.* Eric. sds./lvs.	3060 ± 15	3219–3344	3290
	398–399	73,866	*Sph.*	3670 ± 25	3915–4086	4010
	455–456	79,498	*Sph.*, *Carex* ach.; *Larix* need.	3830 ± 15	4153–4288	4210
Manic	50–51	80,192	*Sph.*	110 ± 15	24–261	130
	220–221	80,193	*Sph.*	1700 ± 15	1548–1691	1610
	365–366	80,194	*Sph.*	3265 ± 15	3447–3556	3490
	588–590	80,195	*Sph.*; *Carex* ach.	3745 ± 15	4000–4153	4100

[a] *Sph.* = *Sphagnum*, Eric. = Ericaceae, lvs. = leaves, ach. = achenes, need. = needles, sds. = seeds.

(zone B6), *Sphagnum* dominated the vegetation assemblages accompanied by few bog mosses (*Polytrichum strictum*, *Pohlia nutans* and *Dicranum* spp.) over the last 280 years.

Morts peatland (HSP)

The influence of marine waters on this lower deltaic terrace (12 m asl) is shown by the foraminifera tests within the basal silt–clay sediment (Fig. 7). The initial conditions with Cyperaceae along with *Scheuchzeria palustris*, *M. gale*, *Menyanthes trifoliata* and sparse *A. balsamea* correspond to the freshwater edge along the coastal topographic sequence (Garneau, 1998). Peat accumulation started within a *Carex*-dominated fen (zone M1; 3240–2930 cal yr BP) where the moss *Campylium stellatum* indicates rich minerotrophic conditions (Vitt and Chee, 1990; Garneau, 1998). *L. laricina* gradually colonised the fen along with brown mosses common to moderate-poor minerotrophic conditions (*Tomenthypnum nitens*, *Calliergon* spp.) and *C. calyculata* (zone M2; 2930–2590 cal yr BP). Ombrotrophic conditions developed from *c.* 2590 cal yr BP with the disappearance of brown mosses and the installation of *Sphagnum* mosses. *L. laricina* and *Carex* spp. persisted between 2590 and 2090 cal yr BP (zone M3) but were replaced by *P. mariana*, *Sphagnum* and bog mosses (mainly *P. strictum* and *Dicranum* spp.) between 2090 and 1750 cal yr BP (zone M4). This period was characterised by dry surface conditions (mean WTD: 19.3 cm), low PAR (0.7 mm yr^{-1}) and higher decomposition. Macrofossil data show a return to a *Sphagnum*-dominated cover after 1750 cal yr BP with abundant *C. calyculata* until 1070 cal yr BP (zone M5). *L. laricina* and *P. mariana* were present locally after 600 cal yr BP but were replaced recently by heath shrubs (e.g., *E. nigrum*, *Vaccinium oxycoccos*) and lichens (zone M6).

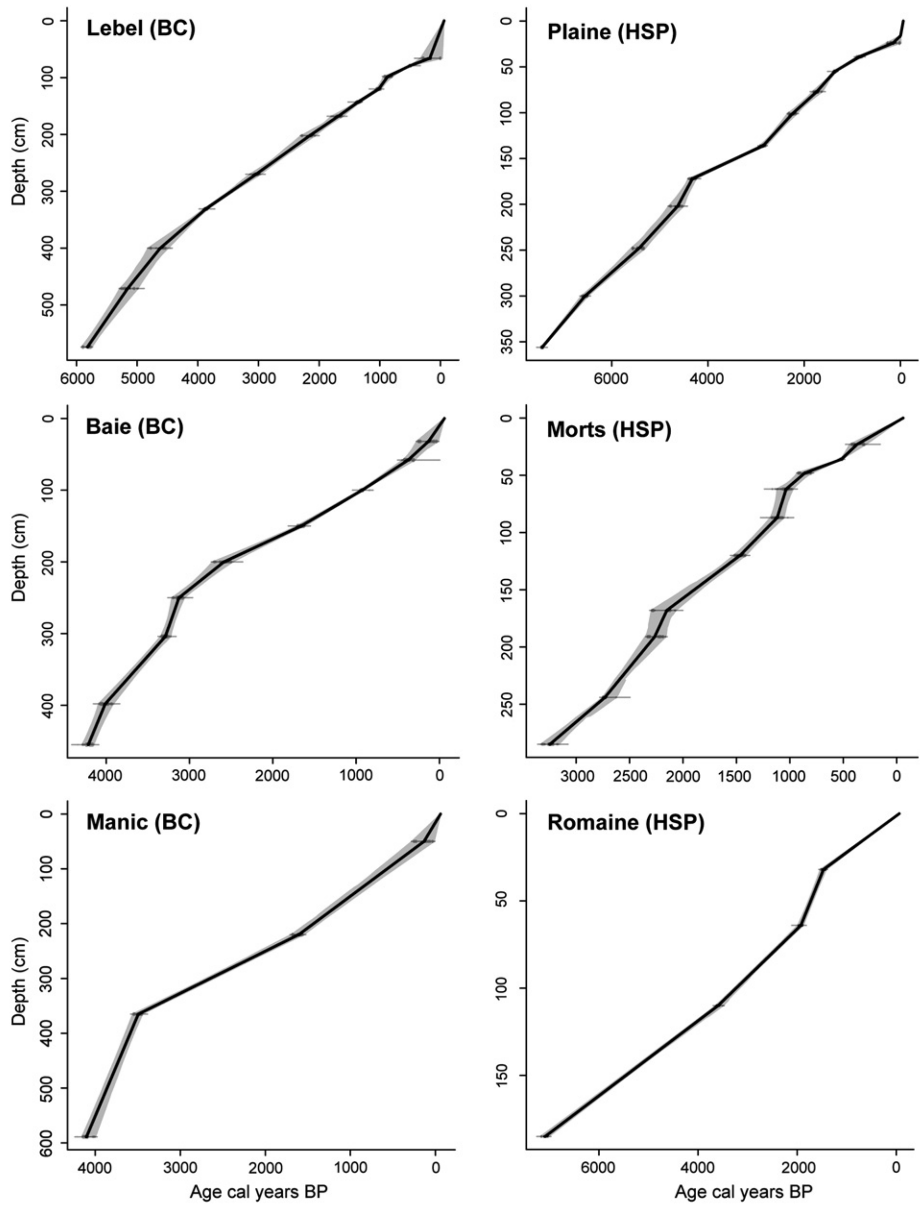

Figure 3. Age versus depth models developed using CLAM for the six studied peatlands. The horizontal bars show the calibrated age ranges at 95% confidence intervals.

Peat stratigraphy synthesis of the six studied peatlands

The regional comparison of the main vegetation changes over time in the studied peatlands including Morts (HSP) and Manic (BC) is shown in Figure 8. In Havre-St-Pierre, peat inception over the deltaic sands of the La Romaine River occurred around the same period in Plaine and Romaine (7450 and 7100 cal yr BP respectively). At Lebel (BC), ombrotrophic *Sphagnum* peat accumulated over the deltaic sands around 5800 cal yr BP. The age of peatland inception was similar in Baie and Manic (~4200–4100 cal yr BP) that both developed over the silt–clay deposits at the upper limit of the Laurentian marine transgression (Table 1; Fig. 8). Peat started to accumulate about 1000 years later in Morts (HSP) than in Baie and Manic around 3240 cal yr BP.

The timing of the fen–bog transition was similar in Plaine and Romaine (HSP) and in Baie and Manic (BC). Overall, the transition to ombrotrophy occurred more rapidly in the peatlands of Baie-Comeau, especially in Lebel where there is no evidence of early minerotrophic conditions. *Sphagnum* mosses were particularly abundant within the ombrotrophic sections of the six peat cores especially in the peatlands of Baie-Comeau.

Discussion

Context of peatland initiation along the St. Lawrence North Shore

In the two studied regions, the ecological context of peat inception was similar and the timing of peatland formation was largely influenced by Holocene sea-level variations. The three oldest peatlands (Plaine, Romaine and Lebel) developed between 7500 and 5800 cal yr BP above sandy deltaic terraces (17–31 m asl) that emerged following the withdrawal of the Goldthwait Sea. In the lower elevations (12–16 m asl.), the peatlands Baie, Manic and Morts developed after 4200 cal yr BP over the silt–clay deposits associated with the Laurentian marine transgression (Fig. 8).

Peat inception in Plaine and Romaine on the deltaic sands of La Romaine River (HSP) occurred during a major period of forest fire activity recorded on the delta between 7360 and 6660 cal yr BP (Payette et al., 2013). At these sites, the particular context of peatland initiation under wet minerotrophic conditions during a fire-prone climate period suggests that peat growth resulted from rising water tables due to massive tree mortality. In Lebel peatland (BC), peat inception through

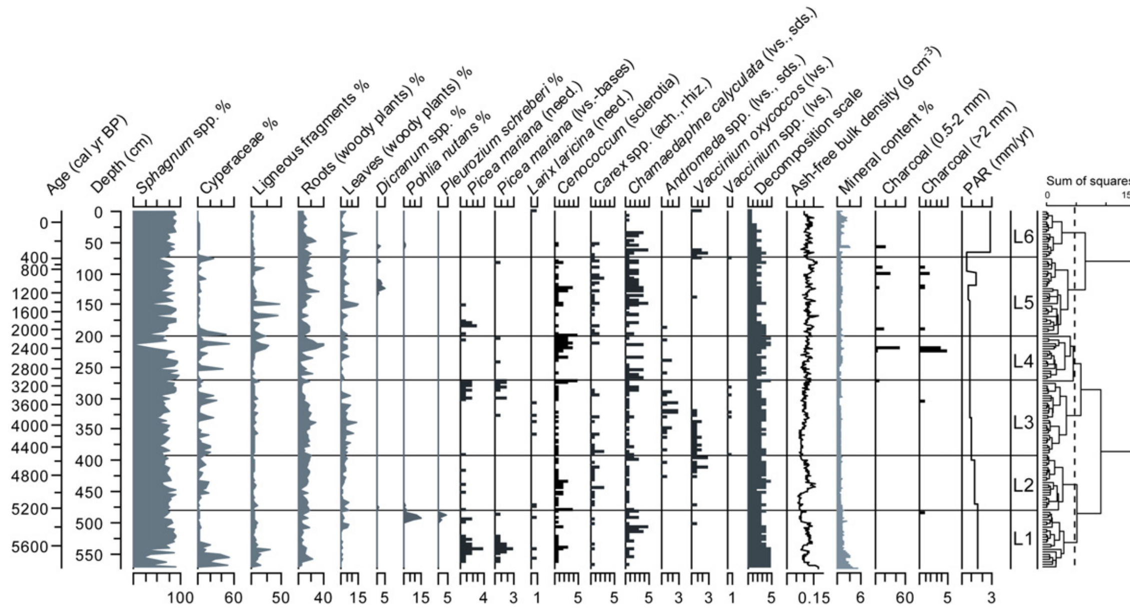

Figure 4. Plant macrofossil diagram of Lebel peatland. Bars represent the scale of abundance (1 = rare, 5 = abundant). need — needles, ach — achenes, rhiz — rhizomes, lvs — leaves, sds — seeds, PAR — peat accumulation rates.

paludification over the well-drained sands around 5800 cal yr BP required a major modification in the local hydrological balance. Payette et al. (2013) showed that the paludification on the La Romaine delta followed the cessation of fire occurrence around 5500 cal yr BP and was attributed to a shift towards wetter climatic conditions in the St. Lawrence North Shore region. In northern Québec and Newfoundland, paludification and extensive forest retreat occurred after 6000 cal yr BP and were attributed to a change towards more oceanic climate conditions (Crawford et al., 2003).

In Baie and Morts peatlands, the early coastal vegetation communities were rapidly isolated from the marine waters by isostatic land uplift and a drop in relative sea level. In the Baie-Comeau region, the synchronicity of peatland initiation in Baie and Manic suggests that peat accumulation started rapidly after marine withdrawal from ~4200 cal yr BP, an indication that the regional climate was propitious to peat growth during that period. Peat inception in Morts may have been delayed by the persistence of marine waters at this site, and hence may reflect a local topographic influence on drainage.

Early vegetation succession and development pathways to ombrotrophy

Our study suggests that the local edaphic conditions have played a role on the early ecological conditions in the studied peatlands. However, the influence of basal sediment on the long-term peatland development pathways seems to have been rather limited. The studied peatlands cover relatively flat basins which has probably favoured a fast drainage of marine waters allowing a rapid peat inception on the emerged sands and silt- clay deposits. Further research at the scale of the basin is needed

Table 3
Description of the macrofossil diagram zones of the four main peat cores.

Site	Zone	Depth (cm)	Age (cal yr BP)	Main features	WTD (cm): mean ± SD[a]
Lebel	L6	72–0	330–Present	*Sphagnum* and Ericaceae	8 (4)
	L5	200–72	2130–330	*Sphagnum* with *Carex* spp.	7.1 (2)
	L4	272–200	3070–2130	*Sphagnum* with *C. calyculata*	10.5 (4)
	L3	392–272	4530–3070	*Sphagnum* with Ericaceae and *P. mariana*	5.6 (2)
	L2	480–392	5210–4530	Treeless *Sphagnum*-dominated bog	6.2 (1)
	L1	574–480	5820–5210	*Sphagnum* with *P. mariana* and bog mosses	18.5 (7)
Baie	B6	116–0	1160–Present	*Sphagnum* with Ericaceae and bog mosses	6.6 (3)
	B5	136–116	1450–1160	*Sphagnum* with *Dicranum* mosses	9.8 (8)
	B4	204–136	2630–1450	*Sphagnum* with *P. mariana*	10.6 (7)
	B3	288–204	3240–2630	*Sphagnum* with *C. calyculata*	8 (3)
	B2	428–288	4120–3240	*Sphagnum* with Ericaceae	6.1 (4)
	B1	456–428	4210–4120	*Carex*-fen with *Calliergon* mosses and *L. laricina*	5.5 (2)
Plaine	P6	52–0	1270–Present	*Sphagnum* with *Carex* spp. and Ericaceae	11.0 (6)
	P5	120–52	2570–1270	Well-preserved *Sphagnum* with *C. calyculata*	17.4 (7)
	P4	168–120	4160–2570	*Sphagnum* with *Carex* spp. and *L. laricina*	5.0 (4)
	P3	248–168	5430–4160	Well-preserved *Sphagnum*	16.1 (8)
	P2	300–248	6560–5430	*Sphagnum* with *P. mariana*	11.0 (8)
	P1	357–300	7450–6560	*Carex*-fen with *L. laricina* and *Calliergon* mosses	−0.9 (4)
Morts	M6	72–0	1070–Present	*Sphagnum* with *P. mariana* and *L. laricina*	14.7 (6)
	M5	140–72	1750–1070	Well-preserved *Sphagnum* with *C. calyculata*	15.1 (9)
	M4	164–140	2090–1750	Bog mosses with *P. mariana*	19.3 (10)
	M3	228–164	2590–2090	*Sphagnum* with *L. laricina* and Ericaceae	15.6 (8)
	M2	260–228	2930–2590	*Carex*-fen with brown mosses and *L. laricina*	—
	M1	284–260	3240–2930	*Carex*-fen with brown mosses and *M. gale*	—

[a] Water table depth value for each macrofossil zone inferred from testate amoebae analyses conducted on these cores and published in Magnan and Garneau (2014).

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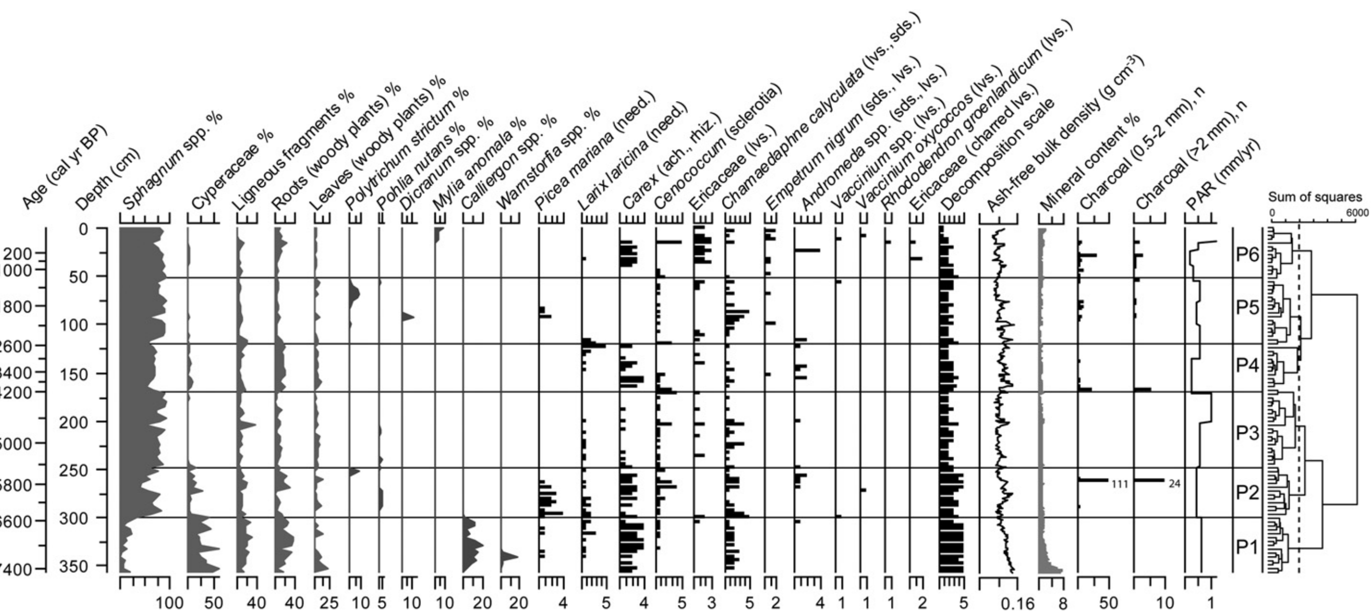

Figure 5. Plant macrofossil diagram of Plaine peatland. The bars represent the scale of abundance (1 = rare, 5 = abundant). need — needles, ach — achenes, rhiz — rhizomes, lvs — leaves, sds — seeds, PAR — peat accumulation rates.

to document the influence of topography and underlying sediment on the development of these peatlands.

Our data showed a difference in the rate of the trophic status transitions between the two study regions (Fig. 8). In the peatlands of Baie-Comeau, the early transitions to ombrotrophy are associated with particularly high rates of peat accumulation. The rapid isolation of peat-forming vegetation from the water table may have resulted from fast peat growth under the wetter climate of the mid-Holocene. In New Brunswick, the ombrotrophication of large portions of a coastal raised bog was attributed to a shift towards wetter/cooler climate after 5500 cal yr BP (Robichaud and Bégin, 2009). In the peatlands of Havre-St-Pierre, the fen–bog transition was likely delayed by a lower primary production (slower PAR) within the fens, an indication that the regional climate was less propitious to *Sphagnum* growth. The study of Magnan and Garneau (in press) showed that the Holocene rates of C sequestration were much lower in the bogs of Havre-St-Pierre than those of Baie-Comeau. The high peat productivity in the Baie-Comeau region likely results from a combination of relatively warm summer conditions and optimal atmospheric moisture balance (Magnan and Garneau, 2014; Garneau et al., in press). The present study provides further evidence regarding the influence of regional climate on long-term development pathways in maritime boreal peatlands.

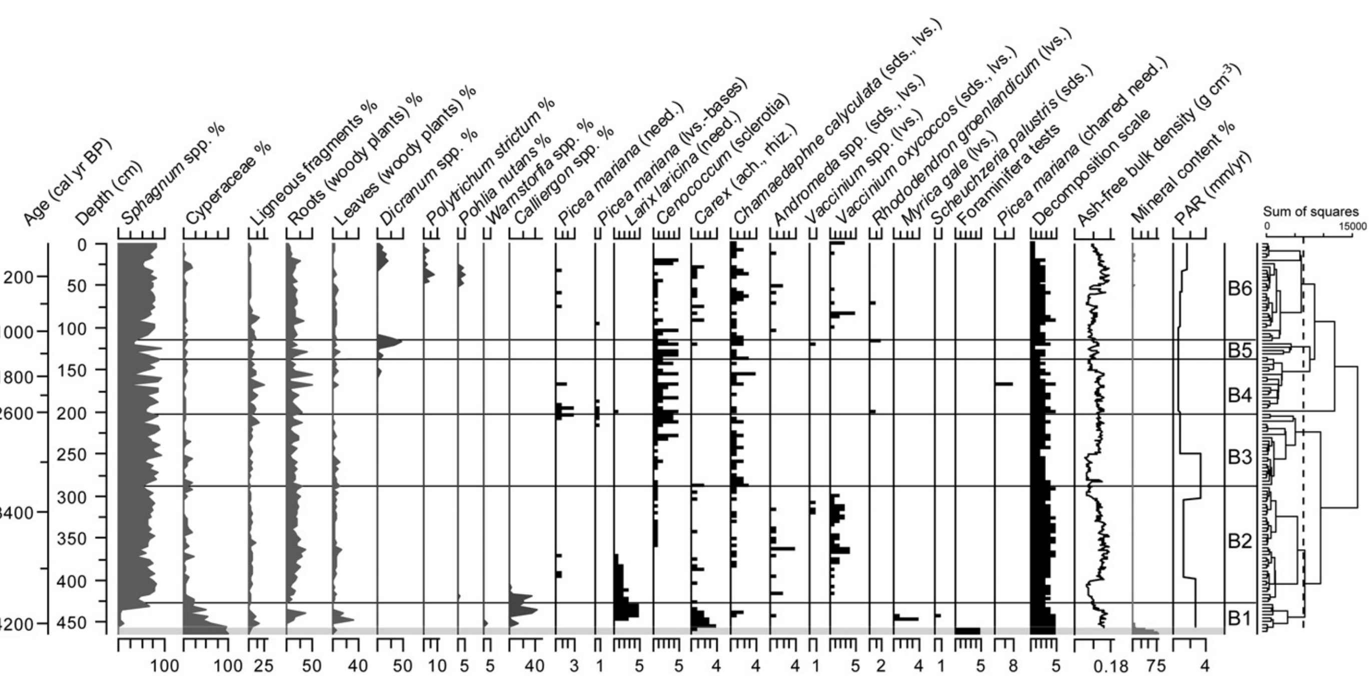

Figure 6. Plant macrofossil diagram of Baie peatland. The bars represent the scale of abundance (1 = rare, 5 = abundant). need — needles, ach — achenes, rhiz — rhizomes, lvs — leaves, sds — seeds, PAR — peat accumulation rates. The grey rectangle shows the lower peat section with high mineral content (>50%).

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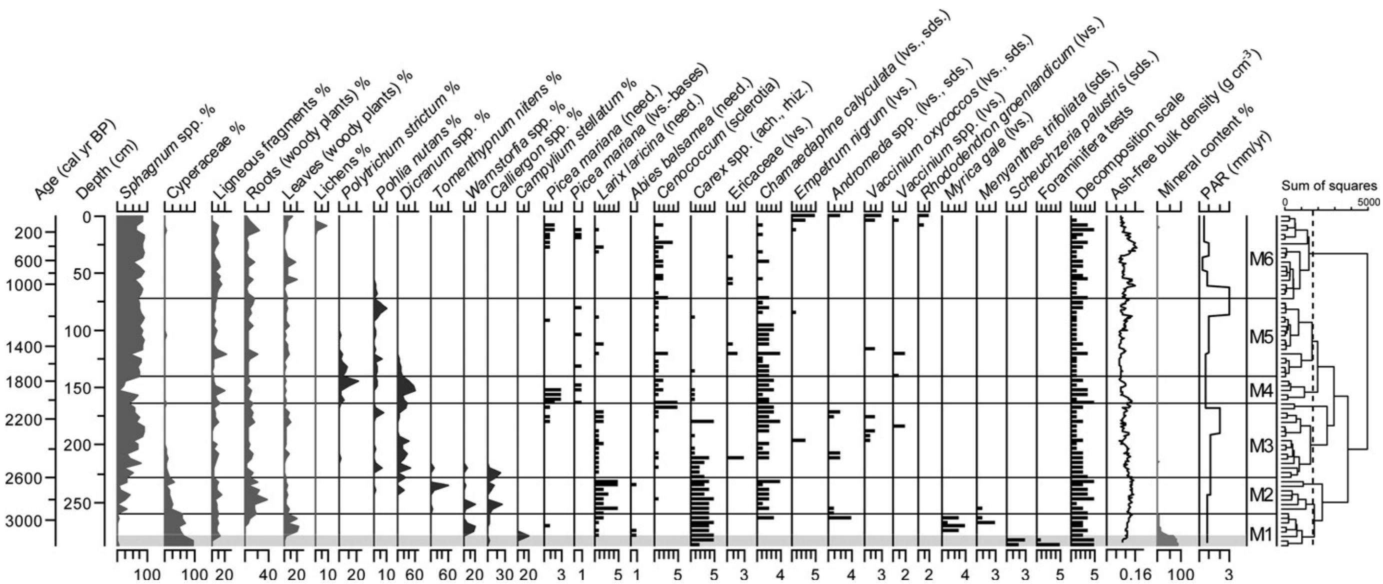

Figure 7. Plant macrofossil diagram of Morts peatland. The bars represent the scale of abundance (1 = rare, 5 = abundant). need — needles, ach — achenes, rhiz — rhizomes, lvs — leaves, sds — seeds, PAR — peat accumulation rates. The grey rectangle shows the lower peat section with high mineral content (>50%).

Vegetation succession within the bogs

The macrofossil data showed a persistence of mostly treeless *Sphagnum*-dominated bogs over millennia in the two studied regions (Figs. 4–7). Our results are in line with previous palaeoecological studies and suggest that fires rarely occur in the maritime bogs of eastern Canada and that their impact on vegetation dynamics is limited (Tolonen et al., 1985; Lavoie et al., 2009; Robichaud and Bégin, 2009). In the maritime region of eastern Canada, the peat sequences are often dominated by ombrotrophic *Sphagnum* mosses alternating with woody layers (Tolonen et al., 1985; Glaser and Janssens, 1986; Robichaud and Bégin, 2009; Payette et al., 2013). The sustained growth of *Sphagnum* in these maritime bogs was probably favoured by high moisture inputs and low evapotranspiration. Such climatic conditions are not propitious to the maintenance of conifers at the bog surface and make these ecosystems less susceptible to fire.

Conclusion

Along the St. Lawrence North Shore, the timing and the ecological context of peat inception over the Holocene were mainly influenced by variations in relative sea-level. The studied peatlands have developed

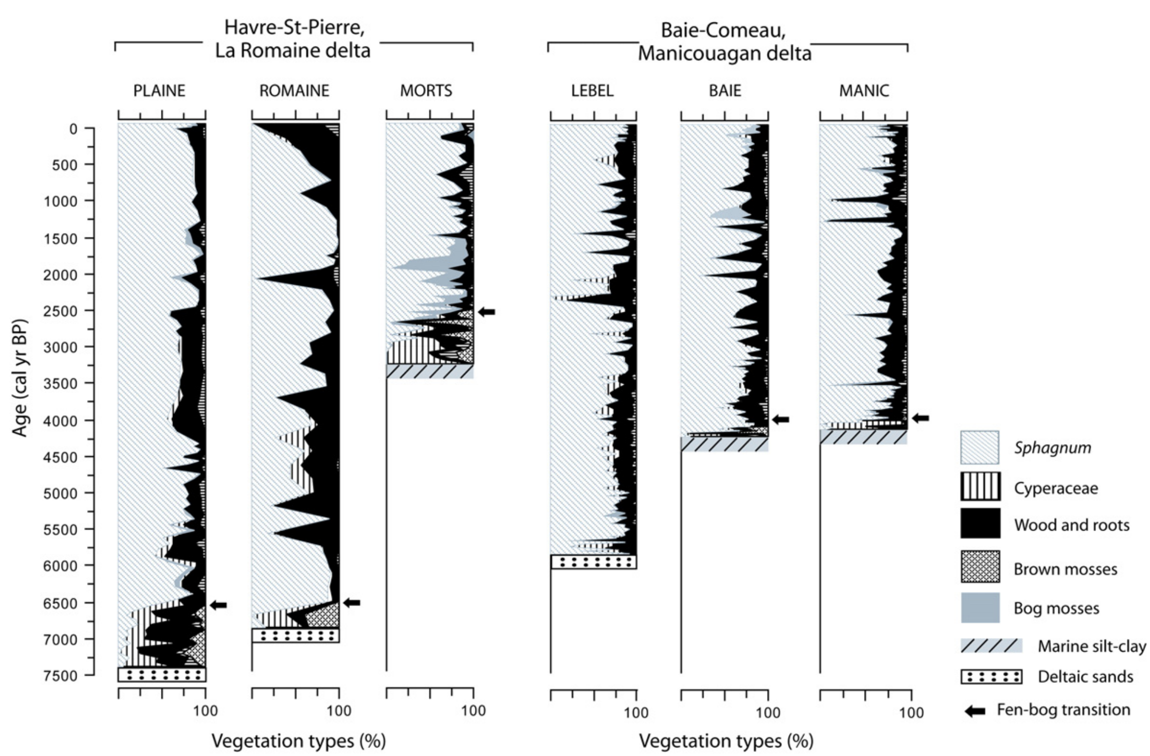

Figure 8. Regional comparison of the peat core stratigraphy showing the main changes in vegetation types (%) over time. The age of the fen–bog transition is indicated.

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over deltaic terraces that emerged following the withdrawal of the Goldthwait Sea after 7500 cal yr BP and above silt–clay deposits after the Laurentian marine transgression from 4200 cal yr BP. Our data suggest that the flat deltaic plains were rapidly drained after land emergence allowing a rapid peatland inception. The influence of the edaphic conditions on the developmental pathways seems to have been relatively limited. Our study shows that the early ecological conditions have been similar in the peatlands of Baie-Comeau and Havre-St-Pierre. However, the peatlands of these two regions have followed different development pathways most likely due to distinct regional climatic influences. The faster transitions to ombrotrophy in the peatlands of Baie-Comeau associated with high PAR suggest that the climate has been more conducive to *Sphagnum* growth. Our macrofossil data showed that treeless *Sphagnum*-dominated bogs persisted over time after the ombrotrophication and that fire had few impacts on the vegetation succession. The evaluation of past vegetation dynamics in the peatlands of the St. Lawrence North Shore provides insights into the response of these maritime ecosystems to climate change.

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