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ORIGINAL PAPER

Impacts of land use and climate variability on algal communities since ~1850 CE in an oligotrophic estuary in northeastern New Brunswick, Canada

Frantz Dorcel Ady · Alain Patoine

Abstract We used sedimentary pigments to evaluate algal abundance since 1868 in a relatively unperturbed, oligotrophic northeastern New Brunswick (Canada) estuary and to understand how variations relate to past land transformation or climate factors. Environmental variables included sedimentary pigments (β-carotene, chlorophyll *a*, diatoxanthin, fucoxanthin, alloxanthin, canthaxanthin, echinenone, lutein–zeaxanthin, and chlorophyll *b*), climate variability (precipitation, temperature during the months of April, May, June, July, August) and land-based activities (relative land surface area occupied by hay, oats, wheat, barley, peat extraction). A sediment core was taken downstream of the Pokemouche Estuary in 2010 and sectioned into 2-cm slices whose ages spanned the interval 1868–2010, determined by ^{210}Pb dating. Most pigments showed a marked peak in the 1920s, around the time of most widespread agricultural activities, and declined thereafter at the same time that peat extraction increased. Relative land surface area occupied by oat crops was a statistically significant environmental variable that accounted for 40 % of algal community variability ($p = 0.009$ by redundancy analysis). Correlation analysis suggests that expansion of non-industrial agriculture was associated with increased abundance of algal photoautotrophs in the 1920s, possibly via soil nutrient leaching. In contrast, expansion of mechanized peat extraction since the 1940s was associated with declining abundance of photoautotrophs, possibly a consequence of turbidity or color-induced light limitation, and increasing abundance of groups known to include mixotrophic algae. Overall, long-term changes in algal abundance were better correlated with land transformation variables than with climate variables. Even though resource extraction activities (agriculture, peat mining) historically involved relatively small areas of this coastal catchment (<10 %), algal abundance seems to have fluctuated in response to changes in flux of land-derived matter.

Keywords Agriculture · Algal biomass · Coastal zones · Organic carbon · Peat · Perturbations · Precipitation · Temperature · Water quality · Watersheds · Wetland

Introduction

Estuaries cover <1 % of the global marine area, but represent 20 % of its value in terms of ecosystem goods and services (Costanza et al. 2014), underscoring their importance to human welfare. However, throughout the twentieth century, estuaries worldwide have experienced increasing environmental pressure from a variety of human activities (Barbier et al. 2011)

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and now support about 20 % of the world's human population (Small and Nicholls 2003), a proportion that is expected to increase throughout the twenty-first century (Nicholls et al. 2007). There are clear indications that this increased human occupation of coastal zones has been accompanied by increased nutrient inputs to estuaries and by more frequent or intense algal blooms (Carstensen et al. 2007; Rabalais et al. 2009), at least in heavily perturbed coastal watersheds.

To date, paleoecological studies of estuaries have often been conducted on densely populated catchments that have been heavily impacted by decades of intense land transformation. Indeed, these include estuaries where human occupation varied between 65 and 1600 inhabitants km^{-2} (Zimmerman and Canuel 2000; Turner et al. 2006; Chen et al. 2001; Savage et al. 2010; Li et al. 2011) or where land clearance for agricultural, pasture, or waste disposal purposes varied between 25 and 75 % of watershed area (Chmura et al. 2004; Savage et al. 2010; Chen et al. 2001; Turner et al. 2006). These studies attribute increased algal abundance throughout the twentieth century (or parts of it) to land transformations, most often agriculture expansion. Agriculture has also been the subject of numerous environmental monitoring studies for its impacts on coastal and estuarine eutrophication in heavily impacted watersheds (Meeuwig 1999; Beman et al. 2005). Together, these paleo- and monitoring-based studies show that the concentrations of nutrients or algae in water bodies tend to increase with increasing agricultural activities, most likely through the washout of inorganic nutrients from land to water. However, other land-based activities can be suspected to influence water quality, but have not been examined so far through a paleoecological approach. For example, peat-harvesting operations generally increase organic carbon (Surette et al. 2002) or suspended sediment concentrations (Clément et al. 2009) in Atlantic Canadian streams, and Finlandic rivers (Kenttämies 1980). Because suspended-sediment-derived turbidity or water color derived from organic carbon can decrease light penetration in the water column of estuaries (Cloern 1987) and lakes (Houser 2006; Wetzel 2001), one can expect peat-extraction activities to change the composition of algal communities. On the one hand, decreased light levels caused by excess organic carbon may have a negative impact on photoautotrophic organisms (most algal species) by

limiting photosynthetic activity. Alternatively, it could favor the dominance by mixotrophic algal groups that rely on energy sources other than light. Indeed, aquatic systems with highly colored waters or high dissolved organic carbon concentrations often show a dominance of mixotrophic algal groups such as cryptophytes (Planas et al. 2000; Klug 2002).

In addition to land transformations that alter nutrient flux to estuaries, algal populations may also be influenced by climate variability over decadal or centennial time scales. For example, in the Neuse Estuary, drought periods can be characterized by decreased nutrient concentrations (Burkholder et al. 2006), whereas upstream rain events tend to be associated with increased downstream primary productivity (Mallin et al. 1993). Similarly, subtropical systems tend to support higher algal biomass during the wet than the dry season (Phlips et al. 2012).

The role of temperature on phytoplankton growth and biomass has been well documented in laboratory and field studies. Whereas growth rates increase exponentially with temperature in the range of 0–35 °C in laboratory conditions for a wide variety of species (Rose and Caron 2007), the influence of temperature under field conditions can be species-specific or depend on catchment-scale characteristics. For instance, in Florida's Indian River Estuary, temperature was a positive predictor of total phytoplankton and dinoflagellates, although the relationship reversed in the case of cyanobacteria (Phlips et al. 2010).

This is the first study that compares multiple resource extraction activities (agriculture, peat extraction) and climate variability as factors that influenced long-term variability of estuarine algal abundance in a low-population-density and relatively undeveloped coastal catchment. The first objective of the study was to evaluate the patterns of temporal variability of algal abundance in an unperturbed estuary from the mid-nineteenth century, before mechanized, large-scale resource extraction activities, to the present. Our first hypothesis pertained strictly to temporal variations in algal abundance: in the near absence of major, intense, long-term catchment-scale transformations, algae should not show a recent (post-1950) increase in abundance, as commonly observed in studies conducted in heavily perturbed environments (Zimmerman and Canuel 2000; Chen et al. 2001; Turner et al. 2006; Savage et al. 2010; Li et al. 2011).

The second objective was to evaluate the relative importance of manageable factors (land transformation) and non-manageable factors (climate variability) on the long-term variability of algal abundance. Land transformation activities considered in this study include agriculture and peat extraction, whereas climate variability includes air temperature and precipitation. We predict that correlations between abundance of photoautotrophic groups of algae and land-use factors—if any—should be positive for agricultural indicators (hypothesis 2) and negative for peat-extraction activities (hypothesis 3). With respect to the influence of climate, we predict that algal abundance should correlate positively with both precipitation (hypothesis 4) and temperature (hypothesis 5), in accordance with the studies cited above. According to our sixth and last hypothesis, the long-term fluctuations in algal abundance correlate more strongly with factors related to climate (precipitation and air temperature) than to factors related to land use (agriculture and peat extraction), in watersheds that present relatively low degrees of land perturbation.

Materials and methods

Study site

The Pokemouche Estuary is situated in the northeastern Acadian Peninsula of New Brunswick Province, on Canada's east coast (Fig. 1). The name "Pokemouche" in Mi'kmaq may mean "salt water extending inward" (Canada 2010). The system can be said to be a "bar-built estuary" (Mann 2000), characterized by shallow waters and by the presence of spits or barrier islands that slow hydrological exchanges with the ocean. Its watershed covers 476 km^2, 79 % of which is still forested (Destravil 2013). Human population density is <30 inhabitants km^{-2} (CGERP 2003). The Pokemouche River flows eastwards into Inkerman Lake before discharging into Pokemouche Bay and then into the Southern St. Lawrence Gulf. Lake Inkerman has an average depth of ∼1 m and a surface area of ∼2 km^2. Conductivity values double from the surface (∼18 mS cm^{-1}) to the bottom (∼34 mS cm^{-1}) of the water column, a situation common in estuarine lakes under the influence of tides (Wetzel 2001). The lake surface is covered by ice about 4 months of the year. Together, these conditions limit oxygen diffusion from air or surface waters to sediments. May–August average water quality values for years 2010, 2011 suggest the lake is oligotrophic, following the criteria of Bricker et al. (2003) for coastal systems: 1.5 µg L^{-1} chl-a; <100 µg L^{-1} TN; 20 µg L^{-1} TP (Destravil 2013). The climate of the region is maritime and the annual precipitation averages 1000 mm. The bedrock of the region is composed of sandstone, shale and conglomerates from Carboniferous and Permian rocks (Zelazny et al. 2007).

Sedimentary pigments

A 60-cm sediment core was collected from the center of Lake Inkerman (47.68296°N, 64.83681°W) on 8 August 2010 using a polycarbonate cylinder suction corer. The lake bottom was flat and devoid of aquatic plants. The sediment core was wrapped in aluminium foil to protect pigments from direct sunlight. Within 6 h, the core was extruded and sectioned in 2-cm-thick slices in the lab under dark conditions. Samples were stored at −80 °C until further analyses. Each slice was split in three parts. One part was for pigment extraction. Another was for density and organic content, determined by weight loss on ignition (LOI) at 550 °C during 1 h (Leavitt and Findlay 1994). The third part was for ^{210}Pb activity measurements. Sediments for pigment analyses were first freeze-dried at −50 °C under a nitrogen atmosphere for 48 h at 0.1 mBar, in a Labconco Freezone freeze dryer.

Pigments were extracted with an acetone–methanol–water solution, filtered on 0.45-µm membranes and quantified by HPLC using a Varian Prostar 240 with a Phenomenex Kinetex C18 100 × 4.60 mm column (2.6-µm particle size) following the method described in Leavitt and Hodgson (2001). As lutein (chlorophytes) and zeaxanthin (cyanobacteria) eluted at the same time, we report them as "lutein–zeaxanthin." Ten pigments were detected and quantified: β-carotene, chlorophyll a (chl-a) as markers of total algae; diatoxanthin and fucoxanthin as markers of diatoms, dinoflagellates and chrysophytes; alloxanthin (cryptophytes); canthaxanthin, echinenone and lutein–zeaxanthin (cyanobacteria); chlorophyll b (chl-b, chlorophytes); pheophytin a (degradation product of chl-a). Pigment-algal group associations followed those established by Leavitt and Hodgson (2001) and Paerl et al. (2003). Pigment concentrations were
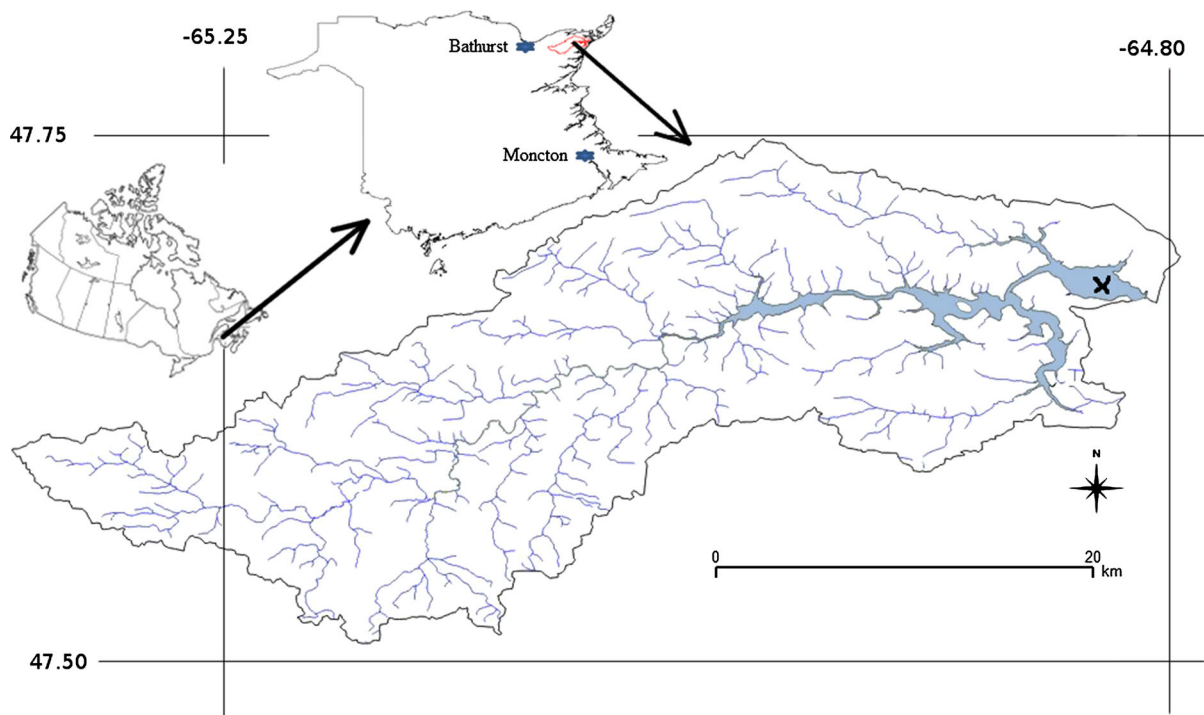
Fig. 1 Map of Canada showing New Brunswick province, the location of the Bathurst and Moncton climate stations within the province, and the Pokemouche River catchment. *Cross* indicates location of sediment coring in Lake Inkerman

expressed as nmol pigment per g organic content (nmol g^{-1} OC). We computed the ratio of chlorophyll *a* over pheophytin *a* as a way to assess the preservation of chlorophyll *a* in sediments (Reuss et al. 2005). Pigment concentrations have proven more valuable than pigment flux (nmol cm^{-2} $year^{-1}$) to express past algal abundance, both in lacustrine (Leavitt 1993) and estuarine (Reuss et al. 2005) environments. Variability associated with freeze-drying, extraction, filtration and chromatography amounted to about 20 % (coefficient of variation on final pigment concentration values).

Lead-210 activity measurement and sediment age estimation

Lead-210 (half life $t_{1/2} = 22.6$ years) activities were measured at GEOTOP laboratories (Université du Québec à Montréal). Measurements were made by alpha counting of the activity of ^{210}Po ($t_{1/2} = 138.4$ days, alpha = 5.30 MeV), which is a daughter isotope of ^{210}Pb. This approach assumes secular equilibrium between ^{210}Po and ^{210}Pb (Not et al. 2008). Counting

was performed in a silicon surface barrier alpha spectrometer (EGG and ORTEC type 576A). Chemical extraction, counting efficiencies and estimation of uncertainties followed Not et al. (2008). Supported ^{210}Pb was estimated as the bottom three determinations of ^{210}Pb activity (Binford 1990). The Constant Rate of Supply (CRS) model, which can account for variable rates of sedimentation (Ghaleb 2009), was chosen to estimate sediment age.

Land transformations

Agricultural data between 1868 and 2005 for Gloucester County (4675 km^2, encompassing the Pokemouche catchment) were taken from the Census of Statistics Canada. Data were available for each decade (1871–1951) or each five-year period (1956–2011). Agricultural indicators of land transformation examined in this study included areas occupied by hay, oat, wheat and barley, expressed as ha km^{-2}, equivalent to percent. Industrial, fully mechanized peat harvesting data (1950–2000) specific to the Pokemouche watershed were obtained from Jacques Thibault, Energy and

Mines New Brunswick (Bathurst Office), and are expressed as percent catchment area drained for peat extraction. Mechanized peat harvesting was virtually non-existent prior to the 1950s.

Climate variability

Daily climate data were downloaded from the Government of Canada Climate Web site (http://climate.weather.gc.ca/). Climate variables included air temperature and precipitation. Only two climate stations in New Brunswick recorded daily data throughout most of the twentieth century: Bathurst (station no 8100500), situated approximately 60 km west of Lake Inkerman, and Moncton (station no 8103100), situated approximately 185 km south of Lake Inkerman.

Mean monthly values for precipitation and temperature were computed for the months of April, May, June, July and August, but only for years that showed no missing values for those months (i.e. means were based on 30 daily values for the months of April and June, 31 daily values for the months of May, July and August). Climate conditions during these spring and summer months are more likely than other months of the year to influence ice-out dates, the length of growing seasons and algal dynamics (Patoine and Leavitt 2006). The Bathurst data series extended back to 1872 or 1873 (depending on month) for the precipitation variables, 1884–1891 for the temperature variables. The Moncton data series started somewhat later: 1898 for precipitation (25 or 26 years later than Bathurst), 1898 or 1899 for temperature (8–14 years later), notwithstanding rare single earlier values. Thereafter, the Moncton data series exhibited few missing values through 2009 (two missing years at most). In contrast, the Bathurst data series showed long data gaps (>15 years). Hence, the Moncton data series was the longest and most consistent climate data series to which pigment concentration data could be compared.

To extend the Moncton data series from 1898 back to 1872 (for precipitation) or 1884 (for temperature), we attempted to estimate monthly precipitation and temperature values from those of Bathurst through linear regression analyses (see "Results" section). The resulting "composite" precipitation data series (observed at Moncton or estimated from Bathurst) spanned from 1872 or 1873 to 2008 or 2009,

equivalent to between 135 and 137 years. Monthly averages based on 30 or 31 daily values were available for each year with no interruptions for 122–133 years, corresponding to a rejection rate <10 %. The composite temperature data series spanned 1884 or 1886–2008 or 2009, depending on month considered, equivalent to 122–128 years. Monthly averages based on 30 or 31 daily values could be computed for each year with no interruptions over a period of 103–109 years, with a rejection rate <15 %, except for August (20 %).

Although two climate stations were situated closer to Lake Inkerman than Moncton and Bathurst, they were active only for a few years after the 1950s and thus could not be used to assess the relative influence of climate for the full twentieth century. The stations were Tracadie, 19 km south of Lake Inkerman, and Bas-Caraquet, 13 km north of Lake Inkerman. We verified that climate conditions observed at the Moncton station were representative of those closer to Lake Inkerman by computing Pearson correlation coefficients between conditions at Moncton and the two local climate stations, based on yearly values of precipitation and temperature during the months of April–August.

Statistical analyses

Data series showed different degrees of temporal resolution: mostly annual for climate data, decadal to quinquennial for land use, and decadal for pigment data. We therefore needed to aggregate all data series to the lowest common resolution, i.e. that for pigment data. Based on the estimated ages of the sediment layers, pigment data expressed average concentrations centered on the following years: 1868, 1893, 1920, 1954, 1975, 1993 and 2004 (Table 1). We therefore computed average land use and climate data for the following periods: P1 (1856–1890), P2 (1891–1907), P3 (1908–1937), P4 (1938–1965), P5 (1966–1984), P6 (1985–1999, pigment sample lost, no pigment data), and P7 (2000–2010). Period-specific averages were computed from one to four values for land variables, and from eight to 32 values for climate variables, depending on the period considered (Table 1). Post-1908 climate data were based on Moncton measurements, with few exceptions. About half of the climate values included in Period 2 (1891–1907) were estimated from the Bathurst station, a proportion that

Table 1 Periods covered by the sedimentary pigment data set and corresponding data sample sizes (number of years) used to aggregate land-use and climate data sets over common time periods (P1–P7)

Sediment slice, top and bottom depths (cm)	Mid-depth (cm)	Estimated year CE, based on CRS model	Lower year limit for data aggregation	Upper limit	Time period	Sample size for agricultural variables	Peat extraction data sample size	Precipitation data sample size and (number of values estimated from the Bathurst station)	Air temp data sample size and (number of values estimated from the Bathurst station)
0–2	1	2004	2000	2010	P7	2	2	8–10 (0)	8–10 (0)
2–4	3	1993	1985	1999	P6	4	2	15 (0)	15 (0)
4–6	5	1975	1966	1984	P5	3	1	18–19 (0–1)	17–19 (0–1)
6–8	7	1954	1938	1965	P4	4	1	28 (0)	27–28 (0)
8–10	9	1920	1908	1937	P3	3	1	30–32 (1–3)	27–29 (0)
10–12	11	1893	1891	1907	P2	2	1	15–16 (6–7)	11–15 (3–7)
12–14	13	1868	Undefined	1890[a]	P1	2	1	15–19 (15–18)	1–5 (0–5)

The estimated year of each sediment slice is based on the ^{210}Pb activity of sediment particles deposited over 2 cm; the estimated year associated with the middle depth thus represents particles deposited before and after that estimated year. Seven time periods (P1–P7) were created such that the time difference between two estimated years (e.g. $1975 - 1954 = 21$ years between P4 and P5) was equally split (10.5 years) between the upper limit of the older period ($1954 + 10.5 = 1965$ for the upper limit of P4) and the lower limit of the newer period ($1975 - 10.5 = 1965$ for the lower limit of P5). The land use data and climate data were aggregated over these same time periods such that average land use and climate conditions could be associated with each value of pigment concentration and estimated sediment age

[a] The upper limit of P1 should be 1881 ($=1868 + (25/2)$), but because of data scarcity before 1880, it was stretched to 1890, such that average air temperature values for P1 could be estimated from 2 to 5 values in most cases, except April where only one value was available

increased to nearly 100 % for Period 1 (Table 1). Because April air temperature data for Period 1 (pre-1868–1890) came from a single value that seemed aberrant (0.0 °C), we repeated the statistical analyses after replacing it with the average temperature value of subsequent periods for that month (3.8 °C). This change had no influence on the results.

To test our first hypothesis, that there should be no increase in algal abundance after 1950, we simply examined a series of plots showing pigment concentration over six periods (P1-P5 and P7). To test our hypotheses regarding the potential influence of land use and climate variability on algal abundance (hypotheses 2–6), we turned to redundancy analyses, a multivariate statistical technique in which a "species" matrix (pigments in columns, periods in rows) is constrained to be a linear combination of an environmental matrix made up of a series of environmental variables (columns) for the same periods (rows). The environmental data matrix was comprised of five land-use variables (relative surface area occupied by hay, oats, wheat, barley, peat extraction) and ten climate variables (precipitation, air temperature for 5 months). Because the number of environmental variables (15)

was greater than the number of periods (6), it was not possible to conduct at once a global test of significance of all environmental factors. The selection of environmental variables followed the method described in Blanchet et al. (2008) to prevent overestimation of the explained variance. Here, the forward selection procedure stops if one or the other of two criteria are met: the probability value of the test variable is >0.05, or the adjusted coefficient of multiple determination (R^2) stops increasing.

As a complementary approach to the alpha-based hypothesis-testing framework presented above, we adopted an exploratory approach that consisted of computing Spearman correlation coefficients (ρ) between the series of pigments data and the series of environmental variables. Because the critical Spearman correlation value for multiple unilateral tests at the 0.05 level and n = 6 would be ρ ∼ 1.0 (following the Bonferroni correction), we explored correlations to identify possible relationships. Spearman rank correlations have been used in paleoecological studies to detect monotonic associations between algal abundance and environmental factors, whether linear or not (Reuss et al. 2005). Environmental variables were the

same as those used in the redundancy analysis. In addition to interpreting the positive or negative signs of correlation coefficients, we wanted to compare the strength of different environmental correlates, irrespective of sign. We thus computed, for each environmental variable, an average correlation coefficient based on the absolute values of pigment-specific correlation coefficients. Functions "rda," "forward.sel" and "cor" in R version 3.1.1 were used to perform redundancy analyses, selection of variables and correlation analyses, respectively (R Core Team 2014).

Results

Core characteristics and chronology

Sediment organic matter averaged 12 % LOI, with a range from 6 to 17 %. Whereas the sediment core measured 60 cm in length, only the topmost 15 cm were datable using ^{210}Pb activity. The uppermost 4 cm exhibited constant ^{210}Pb activity (Fig. 2), suggesting a recent increase in sedimentation or sediment mixing throughout, as is often observed in coastal-zone settings where physical or biological post-depositional redistribution of particles is common (Chen et al. 2001). Lead-
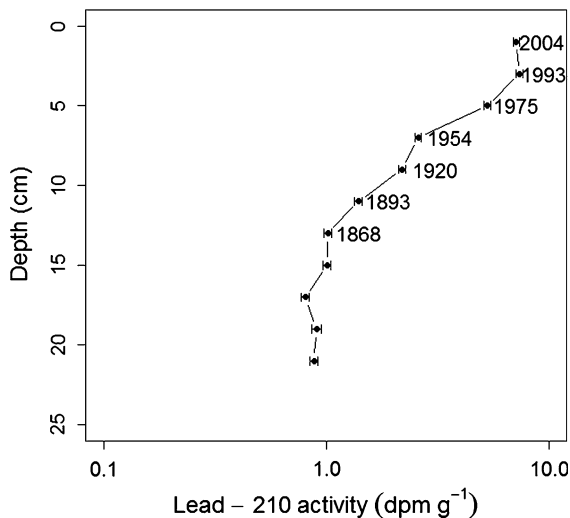

Fig. 2 Lead-210 activity (disintegrations per minute per gram of dry mass) in sediments collected from the coring site in Lake Inkerman, Pokemouche River catchment. The analytical errors for excess ^{210}Pb values are represented by *horizontal bars* and ranged from 3.3 to 4.6 %

210 activity decreased exponentially between 4 and 16 cm and reached a plateau thereafter. The plateau value (0.81 dpm g^{-1}) was taken as the supported ^{210}Pb activity for the entire sediment core (Binford 1990). Excess ^{210}Pb activity (as ln) was modelled as a function of depth through the first 15 cm ($r^2 = 0.95$). Using the CRS model, ages at the middle of each sediment interval were estimated to be 2004, 1993 (no pigment analyses performed), 1975, 1954, 1920, 1893 and 1868. Sedimentation rate averaged 0.05 g cm^{-2} year^{-1} (equivalent to 0.13 cm a^{-1}), reaching a peak (0.07 g cm^{-2} year^{-1} or 0.18 cm a^{-1}) in the 1950s and a trough (0.03 g cm^{-2} year^{-1} or 0.09 cm a^{-1}) in the 2000s.

Pigment profiles

Most pigments showed a marked peak in the 1920s–1950s, followed by a decrease to levels below those that prevailed in the 1860s (Fig. 3). Only chl-*a*, fucoxanthin, and alloxanthin showed increasing trends over the entire period. As indicators of total algal abundance, β-carotene and chl-*a* showed different patterns. β-carotene showed a marked peak in the 1920s. The 1920 peak was followed by a decrease to levels lower than what prevailed in the 1860s (Fig. 3a). In contrast, chl-*a* showed a sharp increase at the beginning of the twentieth century, and continued increasing thereafter (Fig. 3b). Diatoxanthin and fucoxanthin, indicators of diatoms, also showed different patterns of fluctuation throughout the twentieth century. Diatoxanthin showed a peak in the 1920s (Fig. 3c), whereas fucoxanthin increased continually up-core to the near-surface sediments (Fig. 3d). Alloxanthin is an indicator of cryptophytes and showed a marked peak in the 1920s (Fig. 3e). After a period of decreased concentration during the 1950s–1960s, alloxanthin increased to present-day levels. Cyanobacterial pigments (canthaxanthin, echinenone, zeaxanthin) showed similar peak concentrations of pigments in the 1920s, followed by a decrease to levels lower than what prevailed in the 1860s (Fig. 3f–h). Chlorophyll *b*, an indicator of chlorophytes, is the only pigment that showed sustained levels throughout the 1930s, 1940s, 1950s before declining to levels lower than those of the 1860s (Fig. 3i). The ratio of chlorophyll *a* to pheophytin *a* was generally stable, varying between 1.1 and 1.5, except in the 1890s when it decreased to 0.5 (Fig. 3j).

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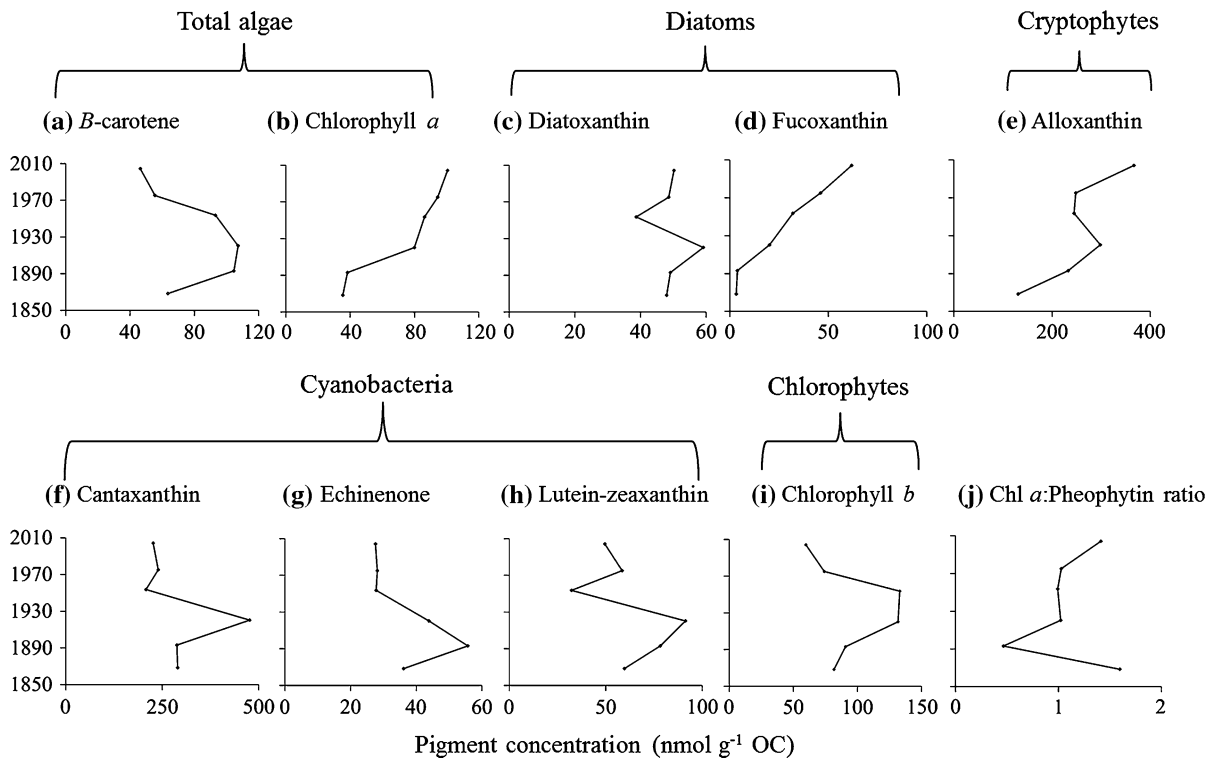
Fig. 3 *a–i* Concentration profiles of sedimentary pigments in Lake Inkerman, 1860–2010, expressed as nmol pigment per gram organic content; *j* chlorophyll *a* to pheophytin *a* ratio (unitless)

Land transformations

Indicators of agricultural activities in the Pokemouche watershed showed marked peaks in the 1920s–1950s, with hay occupying up to ∼2.5 % of the landscape (Fig. 4). Hay was the most important crop in terms of surface area occupied, followed by oats, wheat, and barley. Indicators of agricultural activity declined to levels below 1 % of catchment surface area after the 1960s. While agricultural activities were declining, industrial, mechanized peat extraction activities in the Pokemouche watershed began, and tripled between periods 4 (0.3 % land occupancy) and 7 (1.6 %).

Climate variability

Spatial variability between climate stations

Coefficients of determination between Bathurst and Moncton air temperature values were generally high and statistically significant for the months of April through August ($r^2 = 0.60$; 0.77; 0.70; 0.66; 0.73,
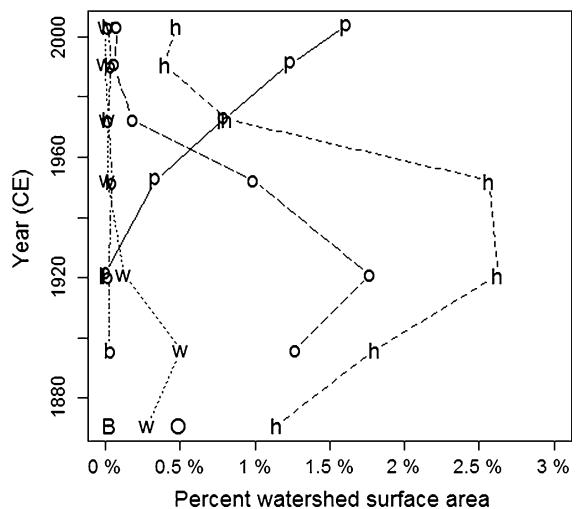
Fig. 4 Historical records of agricultural and peat harvesting activities. Agricultural indicators are for Gloucester County. Peat extraction data are specific to the Pokemouche watershed (*h* hay, *o* oats, *w* wheat, *b* barley, *p* peat extraction)

respectively for n = 12 to 17, $p < 0.002$). Those for precipitation were also statistically significant, but only for the months of April, May and August

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$(r^2 = 0.24; 0.44; 0.14$, respectively for n = 53 to 56, $p < 0.004$). June and July precipitation series were poorly correlated between the two stations ($r^2 \leq 0.03$, $p \geq 0.17$).

Pearson correlation coefficients between precipitation data recorded at the Moncton climate station and those recorded at the Tracadie station (19 km south of Lake Inkerman) and the Bas-Caraquet station (13 km north of Lake Inkerman) were highest for the month of June ($r = +0.70$ and $+0.69$, respectively, $p < 0.005$). Series from other months exhibited high correlation values either for the Tracadie station ($r = +0.56$; $+0.46$; $+0.42$ for April, July, August, respectively, $p = 0.03–0.12$) or the Bas-Caraquet station ($r = +0.56$ for May, $p = 0.038$). For air temperature data, correlation coefficients were strong for all 5 months at one or the other station examined ($r > +0.6$, $p < 0001$).

20th century climate trends at the Moncton station

Precipitation at the Moncton station generally increased throughout the twentieth century for the months of April, May and June by about 1 mm day^{-1} (Fig. 5). The months of June and July were characterized by recent declines in precipitation. Temporal variations were sawtoothed for the months of July and August. Air temperature declined between P1 (1856–1890) and P3 (1908–1937) for the months of April, May and June, before showing a gradual increase thereafter (periods 4–7). Temperatures for the months of July and August tended to show a gradual increase throughout the entire time span considered, despite a noticeable trough during period 3.

Climate and land-use as factors influencing temporal variability of the algal community

Redundancy analyses were performed on a subset of eight pigments, after eliminating fucoxanthin and chl-a on the basis that their patterns of variation reflected more chemical decay processes than variations in algal abundance. The double-criteria, forward selection procedure (Blanchet et al. 2008) used in the redundancy analysis of stable pigments, as a function of 15 environmental variables, resulted in one single environmental variable being selected: relative surface area occupied by oat crops, which accounted for 40 % of pigment community variability ($p = 0.009$). In
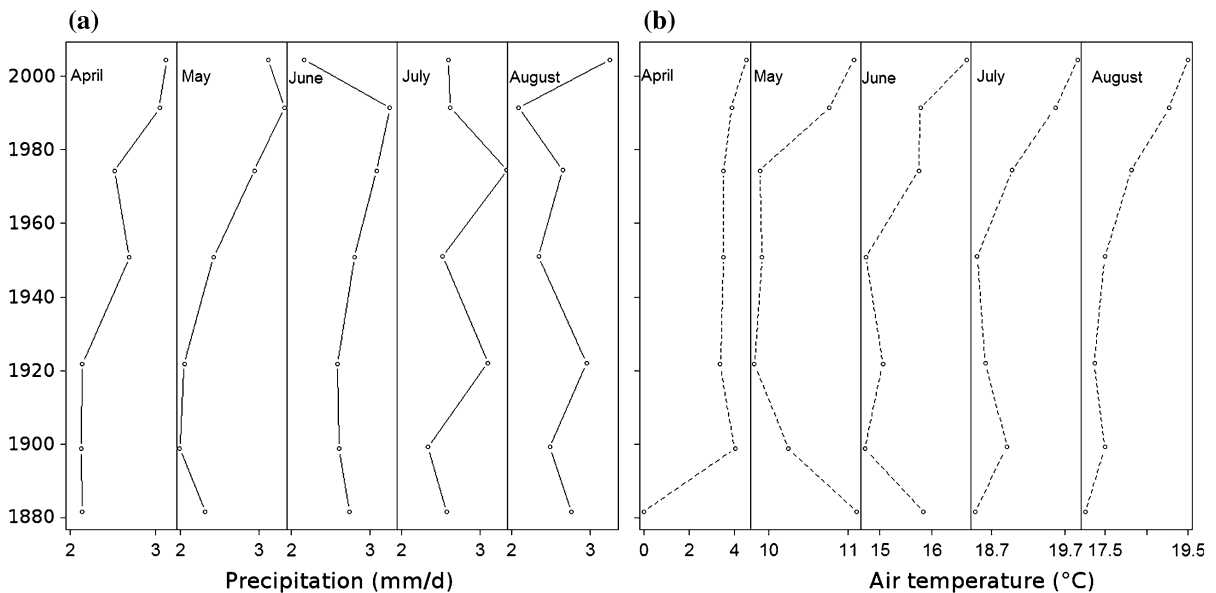
Fig. 5 Century-long variations of **a** precipitation (mm day^{-1}) and **b** air temperature (°C) for seven periods corresponding to the fossil pigment data series and for the months of April–August. Data are averages of annual values observed at the Moncton station (1898 and later) or estimated from the Bathurst station (before 1898). April air temperature for period 1 is based on one single observation and was replaced by a value of 3.8 in analyses (see "Materials and methods" section)

Table 2 Spearman correlation matrix of environmental variables (rows) and concentrations of chemically stable pigments (columns) based on period-specific average values (n = 6 periods)

	β-carotene	Diatoxanthin	Alloxanthin	Canthaxanthin	Echinenone	Lutein–zeaxanthin	Chl-b	Pheophytin	Average of absolute values
Hay	0.94	0.03	−0.20	0.37	0.54	0.43	0.94	0.14	0.45
Oats	1.00	0.20	−0.26	0.54	0.77	0.66	0.83	0.09	0.54
Wheat	0.71	−0.09	−0.77	0.60	0.89	0.66	0.49	−0.20	0.55
Barley	0.41	−0.52	−0.58	−0.26	0.14	−0.20	0.67	−0.09	0.36
Peat extraction	−0.82	−0.03	0.64	−0.76	−0.88	−0.76	−0.58	0.27	0.59
Apr precip.	−0.60	−0.03	0.71	−0.71	−0.94	−0.77	−0.26	0.14	0.52
May precip.	−0.89	−0.14	0.54	−0.66	−0.94	−0.77	−0.60	0.09	0.58
June precip.	−0.09	−0.77	−0.49	−0.26	−0.03	−0.31	0.20	0.66	0.35
July precip.	−0.31	0.37	0.60	0.20	−0.26	0.09	−0.43	0.14	0.30
Aug precip.	−0.31	0.71	0.60	0.37	−0.20	0.26	−0.60	−0.66	0.46
Apr temp.	−0.43	0.31	0.49	−0.54	−0.31	−0.31	−0.49	0.26	0.39
May temp.	−0.49	−0.31	−0.43	−0.14	−0.20	−0.26	−0.43	−0.66	0.36
June temp.	−0.77	0.14	0.37	−0.03	−0.60	−0.26	−0.77	−0.54	0.44
July temp.	−0.49	0.54	0.71	−0.31	−0.31	−0.14	−0.66	0.26	0.43
Aug temp.	−0.66	0.09	0.66	−0.77	−0.71	−0.66	−0.49	0.43	0.56

Values in the last column represent the average of absolute values for each environmental variable

another redundancy analysis, forward selection was performed with the set of 10 climate variables alone, but none of them was selected at the 5 % level.

In general, pigment concentrations were positively correlated with the four indicators of agricultural activity, and negatively correlated with the indicator of peat extraction activity (Table 2). Only alloxanthin (cryptophytes) showed an inverse pattern, being negatively correlated with agricultural indicators, and positively correlated with peat extraction activity. The strongest correlation was observed between β-carotene concentration and relative surface area of oat crops ($\rho = +1.0$). The peat extraction variable generally showed negative correlations with pigments, except for the cryptophyte biomarker alloxanthin, which was strongly positive (+0.64), the degraded chl-a bioindicator pheophytin, which was weakly positive (+0.27) and the diatom biomarker diatoxanthin, which was near zero (−0.03). Peat extraction appeared as the strongest correlate among the 15 environmental variables considered, when taking the average of absolute correlation values across pigments (+0.59). On average, land-use factors tended to be stronger correlates of pigment concentration (+0.50, mean of five average correlation coefficients) than climate factors (+0.44, mean of 10 average correlation coefficients).

Precipitation variables were generally inversely correlated with pigment concentrations, especially during the months of April, May and June (Table 2). Alloxanthin (cryptophytes) and pheophytin (degraded chl-a) were the only pigments that correlated positively with precipitation, except during June. Air temperature variables were inversely associated with pigment concentrations for most pigments (Table 2), except diatoxanthin (diatoms), alloxanthin (cryptophytes) and pheophytin a (degraded chl-a).

Discussion

Because light, heat, oxygen and zooplankton grazing can cause algal pigments to be lost before or after having been deposited in the bottom sediments

(Leavitt 1993), the vertical profile of pigment concentration may not necessarily reflect past temporal fluctuations of algal abundance. It is thus important to evaluate whether the conditions at the coring site were favourable to pigment preservation. First, highly organic sediments can indicate an environment with low dissolved oxygen (Calvert 1987), favourable to pigment preservation. Organic content of the Inkerman core was relatively high, ranging from 6 to 17 % LOI, equivalent to 2.4–6.8 % organic carbon content assuming carbon is 40 % of LOI content. These organic content values are comparable to or higher than those reported in other pigment-based paleoecological studies of estuaries: <10 % LOI for a Florida estuary (Turner et al. 2006); <1 % carbon content for the Changjiang Estuary (Li et al. 2011); <4 % carbon content in Chesapeake Bay (Zimmerman and Canuel 2000). In fact, among the four northern European estuaries examined by Reuss et al. (2005), the Mariager Fjord was the one with the greatest sediment organic matter content ($\sim$15 % LOI), comparable to Lake Inkerman (6–17 % LOI). Furthermore, Mariager Fjord was also the estuary that exhibited the best pigment preservation among the four examined by Reuss et al. (2005), with several carotenoid pigments averaging $\sim$250 nmol g^{-1} OC, values comparable to those reported in this study (20–400 nmol g^{-1} OC, Fig. 3). Similar organic content (possibly indicative of an anoxic environment), and similar pigment concentration values between the Mariager Fjord and Lake Inkerman, suggest that Lake Inkerman sediments were conducive to pigment preservation. Second, the coring site was devoid of aquatic plants, so it is unlikely that there was an important photosynthetically derived oxygen source that could contribute to oxidative pigment degradation. Third, Lake Inkerman is covered with ice 4 months or more per year, thereby limiting oxygen diffusion in the water column. Fourth, Lake Inkerman is flat-bottomed, which should limit sediment and pigment focusing (Hilton 1985), a process that can hinder interpretation of pigment profiles in lacustrine settings. Last, the chl-*a* to pheophytin *a* ratio was relatively constant throughout the core (1.1–1.5), suggesting that pigment preservation conditions remained relatively constant through time (Fig. 3j). Only for the period ca. 1893 did the ratio decrease to 0.5, suggesting an increased rate of transformation of chl-*a* to pheophytin for that time period. If this 1893 decline in the chl-*a* to pheophytin ratio reflected poor

pigment preservation conditions, one would expect to observe a corresponding 1893 low in the other pigment profiles. Such is not the case, however. Pigment concentrations generally increased from 1868 to 1893 or remained stable (Fig. 3), so there is little indication that the pigment profiles were generated solely by degradation processes.

β-carotene is generally considered to be more resistant to chemical degradation (by light, heat, oxygen) than chlorophyll *a* (Leavitt and Hodgson 2001). The β-carotene profile is thus probably more representative of past algal abundance than the chl-*a* profile. Similarly, diatoxanthin is known to be more resistant to degradation than fucoxanthin, once deposited in estuarine or lake sediments (Bianchi et al. 2002; Patoine and Leavitt 2006) and is likely a better indicator of past fluctuations in diatom abundance. Hence, chl-*a* and fucoxanthin were eliminated from further analyses, and their respective diagnostic algal groups, total algae and diatoms, were monitored with the more stable pigments β-carotene and diatoxanthin, respectively.

Although the climate data recorded at the Moncton station was comprised of nearly annual values for the period 1898–2010, it is presented with two caveats: (1) earliest climate data (1898) date to 30 years after the earliest sediment age estimate (1868); (2) climate data were collected far from our study station, 185 km to the south. Regarding the first caveat, the reliability of pre-1898 data, estimated from Bathurst, cannot be less than the respective averages of non-missing values, which is an alternative approach to dealing with missing data (Legendre and Legendre 1998). Considering the worst-case scenario (pre-1898 values estimated from Bathurst for June and July precipitation, $r^2 \leq 0.03$), the estimated values would approximate the variable mean. Therefore, whereas the estimated pre-1898 June and July precipitation data are likely not as reliable as observed data (which do not exist) might have been, their use is preferable to eliminating the earliest sedimentary record from further analyses, especially considering the small sample size of the data set (n = 6 for redundancy and Spearman correlation analyses). To address the second issue, regarding how well Moncton climate data represent conditions that prevailed at the Lake Inkerman study site, we showed that linear correlation coefficients were all positive, as can be expected from assuming representativeness, and generally strong (r > +0.5) at

one or the other local station, except for July and August precipitation. Overall, climate conditions observed at Moncton can be considered as acceptable surrogates for conditions that prevailed near Lake Inkerman, especially in the absence of other alternatives.

In agreement with our first hypothesis, results generally do not point to a post-1950 increase in algal abundance in the Pokemouche Estuary. Unexpectedly though, we observed a 1920s algal peak that coincided with peak values of land area occupied by agricultural activities. Hence, simply in terms of long-term variations in algal abundance, the Pokemouche pigment profile seems unique. It further suggests that the Pokemouche watershed has not experienced the same kind of intense, large-scale land transformations that are elsewhere reported to have contributed to post-1950 algal biomass increases. Indeed, paleoecological studies of estuaries are generally characterized by post-1950 increases in algal abundance and by highly perturbed catchments. For example, human population densities are reported to reach 65 km^{-2} (Turner et al. 2006), 222 km^{-2} (Li et al. 2011) and 474 km^{-2} (Savage et al. 2010). Relative catchment surface area occupied by agricultural activities reach 21 % (Savage et al. 2010), 58 % (Rabalais et al. 2009) and 75 % (Turner et al. 2006). Linear sedimentation rates display values of 0.12 cm $year^{-1}$ (Chen et al. 2001), 0.17–0.25 cm $year^{-1}$ (Turner et al. 2006), 0.19–0.31 cm $year^{-1}$ (Li et al. 2011), 0.7 cm $year^{-1}$ (Reuss et al. 2005 for Laajalahti) and 1.7 cm $year^{-1}$ (Zimmerman and Canuel 2000). In comparison, Lake Inkerman's catchment is much less densely populated (<30 km^{-2}), resource extraction activities occupy less than 10 % of the surface area (Fig. 4), and sedimentation rates range from 0.09 to 0.18 cm $year^{-1}$. However, despite these indications of relatively low-impact land occupation, algal community composition and abundance changed coincidently with increases of agricultural activities in the 1920s ($p = 0.009$ from the redundancy analysis and Table 2), in agreement with our second hypothesis. This suggests that land clearance or application of manure fertilizer in the 1920s on the Pokemouche watershed could have increased soil nutrient runoff to water bodies and stimulated algal abundance, especially that of photoautotrophic groups such as diatoms (diatoxanthin), cyanobacteria (canthaxanthin, echinenone) and green algae (chl-b).

As expected from our third hypothesis, peat extraction activity generally correlates negatively with biomarkers of photoautotrophic algal groups, whereas it correlates positively with alloxanthin (Table 2), a biomarker of the cryptophyte algal group known to include mixotrophic organisms (Klug 2002). We suggest that the recent, post-1950 increase in peat extraction may have had a negative impact on algal abundance of photoautotrophs by increasing the washout of substances that limit light penetration in the water column, i.e. suspended particles or organic carbon. Indeed, it is known that peat harvesting can lead to increases in suspended sediments (Kenttämies 1980; Clément et al. 2009) or organic carbon (Surette et al. 2002) in rivers. Suspended sediments, in turn, contribute to turbidity and can decrease light penetration (Wetzel 2001) and estuarine primary productivity (Cloern 1987). Similarly, dissolved organic carbon can hinder light penetration in the water column of lakes and decrease algal biomass of photoautotrophs (Klug 2002). In contrast, mixotrophic groups of algae (represented in part by alloxanthin) would have had a competitive advantage over photoautotrophs under these reduced-light conditions, as they obtain their energy from reduced organic substrates rather than light (Wetzel 2001). This last idea is supported by the positive correlation between the peat extraction variable and alloxanthin. Dominance of cryptophycean flagellate algae in estuaries, where land-derived substances contribute to light-limitation, has previously been reported (Gameiro et al. 2011), although not specifically in relation to resource extraction activities. The combined effects of reduced nutrient runoff from decreasing agricultural activities after the 1960s, and increased amounts of light-absorbing substances from peat extraction, could explain why photoautotrophic algal biomass appears lower today than in the 1860s, before the advent of large-scale, industrial resource extraction activities (Fig. 3).

We thus interpret Lake Inkerman's pigment profile as a century-long succession of land-based activities, some that stimulate algal growth (agriculture over the period 1850–1950), others that inhibit it (peat extraction post-1950), even though they occupy relatively small catchment surface areas (Fig. 4). In comparison, New Bedford Harbor, on the U.S. east coast, also experienced early primary production peaks associated with non-industrial agricultural activities (Chmura et al. 2004), albeit at a much earlier period

(1700s). Interestingly, Lake Inkerman's average sedimentation rate for the twentieth century (0.13 cm year^{-1}) is closer to Bedford Harbor's pre-1750 sedimentation rate (0.07–0.09 cm year^{-1}) estimated by Chmura et al. (2004) than its post-1800 rate (0.33–0.39 cm year^{-1}), again suggesting that the Pokemouche Estuary has experienced less intense land transformations than what is commonly reported in similar paleoecological studies of coastal systems. In both studies, but at very different times (1700s vs. 1920s), pre-industrial agricultural activities that occupied <10 % of the coastal catchment surface area were seemingly enough to lead to decade-long increases in algal production.

Most pigments were negatively associated with precipitation (Table 2). This is contrary to hypothesis 4, which posited that pigment indicators of total algae would show a strong positive correlation with precipitation because of increased nutrient washout from the land. However, heavy precipitation may have led to short water residence times, thereby hindering the accumulation and sedimentation of phytoplankton biomass. Such negative association between precipitation and water residence time has been reported in previous studies. For example, McGowan et al. (2012) reported a decrease of diatom-derived pigments (fucoxanthin, diatoxanthin) that coincided with wetter winter weather conditions (January–March) in the 1900s in the smaller south basin of Windermere Lake, England. The authors suggest that wetter winter conditions may have caused dilution and washout effects, thereby limiting the sedimentation of phytoplankton pigments. In estuarine environments, Phlips et al. (2012) found evidence suggesting that high flushing rates, combined with increased salinity variability, could be detrimental to phytoplankton populations. In our study, periods of higher precipitation could have also entailed a dilution effect, leading to decreased algal biomass, and decreased pigment accumulation.

In the present study, all pigments were negatively correlated with temperature, with the exception of fucoxanthin. This runs contrary to our fifth hypothesis. Whereas the influence of temperature on algal growth is well understood in the 0–40 °C range (Rose and Caron 2007), other temperature-dependent processes may counteract it. For example, increased temperature can lead to enhanced soil denitrification (bacteria-mediated conversion of soluble nitrate into gaseous

forms), thereby decreasing the amount of nitrogen exported from land to estuaries (Schaefer and Alber 2007). Hence, in our study, it is possible that warm periods, for example 1970–2004 (Fig. 5b) resulted in decreased nitrogen transfers from land to water because of higher bacterial soil denitrification. Because nitrogen often limits algal growth in estuaries (Elser et al. 2007), periods of increased denitrification could have led to decreased algal biomass.

Overall, correlations were generally stronger with the land-based attributes than with the climate variables (redundancy analyses and Table 2). We propose that land use might have had a slightly stronger influence on the algal abundance of Lake Inkerman throughout the twentieth century than climate variability, contrary to our sixth hypothesis. Hence, even though land transformations affected relatively small proportions of the landscape surface area at any given time since 1868 (<10 %), they might have induced long-term changes in algal abundance in Lake Inkerman. The dominance of land use change over climate variability as a driver of long-term changes in algal abundance has been demonstrated in previous studies (McGowan et al. 2012; Savage et al. 2010), albeit for catchments that experienced more severe land transformations than the one presently under study.

Because core sectioning was done at 2-cm intervals, pigment concentrations were averaged over several decades. Thinner slices, e.g. ≤1 cm, could have increased the number of periods analysed sufficiently, to ≥16, enabling us to perform a global test of significance of the 15 environmental factors examined, as recommended in Blanchet et al. (2008) as a way to minimize the risk of Type I error. On the other hand, thinner slices can entail losing representativeness of past algal abundance. Indeed, correlations between estuarine pigment concentrations and phytoplankton biomass values obtained by taxonomic analyses of water samples are stronger when values are averaged over multiple years (5 years) than when expressed at an annual scale, at least for diatoxanthin (Bianchi et al. 2002). At any rate, more evidence is needed to test the role of peat extraction, agriculture and climate variability on the long-term variation of algal community composition and abundance in low-perturbation settings. To that effect, sediment cores from upstream Pokemouche Estuary and adjacent coastal catchments are presently being analysed and will, we hope, yield a more complete picture as to the

unique roles of land transformation and climate in relatively pristine catchments. In the meantime, results from this study suggest that the relatively low degree of human land use in northeast New Brunswick is not an excuse to disregard integrated land management. The Pokemouche Estuary and its catchment have not yet achieved the same degree of land transformation and water quality degradation commonly reported in past studies (Rabalais et al. 2009, and others), but could very well follow the same path if basic principles of coastal zone integrated management are not followed (Ricketts and Hildebrand 2011), and result in water quality degradation through changes in algal abundance and community composition.

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