Environmental factors structuring benthic primary producers at different spatial scales in the St. Lawrence River (Canada)

David Lévesque[a,c,*], Christiane Hudon[b,c,] Patrick M. A. James[a] and Pierre Legendre[a,c]

[a]Département des Sciences Biologiques, Université de Montréal,

C.P. 6128, Succursale Centre Ville, Montreal, QC, Canada, H3C 3J7

[b]Water Science and Technology Directorate, Environment and Climate Change Canada,

105 McGill St., Montreal, QC, Canada, H2Y 2E7

[c]Groupe de recherche interuniversitaire en limnologie et en environnement aquatique (GRIL)

*Corresponding Author: david.levesque@umontreal.ca, Tel: 1 514 343-6792 FAX: 1 514 343- 2293

Abstract

The influence of environmental factors controlling the biomass of submerged aquatic macrophytes, cyanobacterial mats, and epiphyton were examined at three nested spatial scale within the St. Lawrence River: 1) along a 250-km-long upstream-downstream river stretch, 2) among three fluvial lakes located within that river stretch and 3) within each fluvial lake at sites located upstream, at the mouth, and downstream of the St. Lawrence River tributaries. Over its 250-km-long course, large increases of water colour (5-fold), suspended matter (10-fold), dissolved organic carbon (DOC) (2-fold) and dissolved N and P concentrations (2.5-fold) were observed in the St. Lawrence River, showing the cumulative effects of human activities on water quality. In contrast, biomass of submerged vascular macrophytes dropped 10-fold downstream whereas biomass of epiphytes and cyanobacterial mats rose significantly. Biomass of the three benthic primary producers (PP) was explained (59%) by the combined effects of conductivity, TP and spatial structure. Macrophyte biomass was related to changes in conductivity (+), biomass of epiphyton responded to DIN:TDP ratio (+) and light extinction coefficient (+) and cyanobacterial mats coincided with differences in DOC (+) and NH_4^+ (-). Within-lake structure was the most important spatial component for all benthic PP, suggesting that local effects, such as enrichment by the inflow of tributaries, rather than upstream-downstream gradients, determined the biomass of benthic PP. Our study shows that the sum of local tributary inflows exerts major overall pressures on benthic PP in the St. Lawrence River and that conversely, small-scale management of individual watersheds, can markedly improve local ecological condition of the river ecosystems.

Keywords

Submerged aquatic macrophytes, cyanobacterial mats, epiphyton, fluvial ecology, spatial structure, St. Lawrence River

Introduction

Benthic primary producers (PP), such as submerged vascular macrophytes and filamentous algae, occasionally cover important portions of the littoral of large rivers, supporting secondary production in addition to being an important habitat and food source for many fish and invertebrates (Jeppesen et al. 1998). Despite their important role in aquatic ecosystems, our understanding of environmental processes controlling the abundance and composition of communities of benthic PP in large rivers is still limited.

Rivers have been described as a gradient of physical conditions (depth, width, velocity, temperature, and turbidity) affecting community patterns and distribution from upstream to downstream by the river continuum concept (RCC) (Vannote et al. 1980). This view of rivers as a longitudinal continuum has been progressively expanded to encompass the spatial and temporal variations of nutrient cycling through organisms and detritus in the resource spiraling concept (Elwood et al. 1983) and spatial discontinuities induced by dams in the serial discontinuity concept (SDC) (Ward and Stanford 1983; Ward and Stanford 1995). The lateral connectivity and the importance of the annual flood pulse in reconnecting the main channel to its floodplain were elaborated through the flood pulse concept (Junk et al. 1989). Subsequent efforts (Thorp et al. 2006) developed the riverine ecosystem synthesis, in which rivers are conceptualized as a mosaic of large and discrete patches, combining concepts of hierarchical patch dynamics and eco-geomorphology (hydrology, geomorphology, climate and vegetation). Patches represent areas characterized by a series of functional attributes such as geology, climate, vegetation, nutrient and organic matter concentrations, discharge and current speed. The riverine ecosystem synthesis hypothesizes that river processes are driven by the spatial arrangement of patches rather than by the downstream gradient of the river continuum.

Spatial structure is rarely explicitly taken into account when examining the environmental factors controlling biological communities (Cottenie 2005). This is often problematic since environmental factors encompass pure environmental control and environmentally-induced spatial variation and does not account for neutral processes (i.e. dispersion) (Legendre and Legendre 2012). The environmental factors evoked to explain variation in biological communities also depend on the spatial scale of analysis (Forman and Godron 1986). Some environmental variables show large variation at small spatial scales which create high heterogeneity in biological communities in relatively small areas while others show more variation at large spatial scales giving rise to community variations in large study areas (Borcard et al. 2004). Until now, only a few studies have considered multiscale spatial and environmental effects together (Alahuhta and Heino 2013; Capers et al. 2010; Gallego et al. 2014; Mikulyuk et al. 2011; O'Hare et al. 2012) and none of them has yet examined large rivers.

At the landscape scale, watershed characteristics control river morphometry and water residence time, discharge and current velocity, which in turn influence the amount of substrate suitable for the establishment of benthic PP species (Duarte and Kalff 1986; Franklin et al. 2008; Morrice et al. 2004). Geology, land use and soil type influence pH, conductivity, concentrations and forms of nutrients and organic matter in the water (Alahuhta and Heino 2013; Barko and Smart 1986; Capers et al. 2010). At the watershed scale, nutrient concentrations (Carignan and Kalff 1980; Jones et al. 2002) and light availability (Barko et al. 1982; Lacoul and Freedman 2006; Sand Jensen 1989) determine the composition of benthic PP in rivers and lakes. In rivers, the importance of filamentous algae tends to increase with stream order until rising water turbidity and depth induce a shift towards phytoplankton (Hilton et al. 2006). At local scales, point-sources of pollution, tributary inflow and biotic interactions may control the dominance of different groups of benthic primary producers. The influence of grazers (Lacoul and Freedman 2006) and of competition for light and nutrients between submerged macrophytes, loosely attached algae and epiphyton (Franklin et al. 2008; Hilton et al. 2006; Vadeboncoeur and Steinman 2002) are also well documented.

The present study uses three groups of benthic primary producers (submerged aquatic macrophytes, cyanobacterial mats and epiphyton) in the St. Lawrence River to examine the relative importance of environmental factors acting at three naturally-nested spatial scales: 1) at the large scale of a 250-km-long fluvial section, 2) at the intermediate scale of three large fluvial lakes located within this stretch and 3) within each lake, by using sites located upstream, at the mouth and downstream of inflowing tributaries. Over its course, the St. Lawrence River alternately runs through narrow (≈2-4 km-wide) cross-sections and three large (≥10 km-wide) fluvial lakes with numerous incoming tributaries. This large river thus provides us with a longitudinal series of fluvial lakes likely to support a number of distinct patches characterized by different benthic PP assemblages (Thorp et al. 2006). Heterogeneity of water characteristics in this system is generated by the presence of the greater Montreal area as well as by the inflow of numerous tributaries draining farmlands, resulting in a local degradation of water quality, regionally along the littoral area of fluvial lakes, and globally along the downstream axis of the St. Lawrence River (Hudon and Carignan 2008).

We hypothesized that the biomass distribution of benthic PP would 1) respond to water quality degradation (increase in turbidity and nutrients) and 2) be spatially-structured at a local scale, in our case within each individual fluvial lake because of the high heterogeneity in water characteristics generated by tributaries draining different geological formations in the St. Lawrence River watershed. Specifically, we expected a decrease in submerged aquatic macrophytes and an increase in cyanobacterial mats and epiphyton biomasses. To test these hypotheses, we quantified the biomass of benthic PP (submerged aquatic macrophytes, cyanobacterial mats and epiphyton) and coinciding environmental conditions over a 250-km stretch of St. Lawrence River in late summer 2008. Sampling was concentrated in a single season, at the maximum of benthic primary producer biomass (end of August, beginning of September), to remove the effects of seasonal successions and hydrological variation. Our results should allow us to determine whether benthic PP respond to small-scale local patches (Thorp et al. 2006) or to the position along the river continuum, thus improving our understanding of the scale at which management and remedial actions must take place.

Methods

Study area

The study took place across three fluvial lakes of the St. Lawrence River (Lake Saint-François, Lake Saint-Louis and the lower portion of the Ottawa River, and Lake Saint-Pierre) located in a 250-km-long stretch of the fluvial section of the St. Lawrence River between Cornwall (Moses-Saunders hydropower dam) and Trois-Rivières (Fig 1). Lake Saint-François lies ≈175 km downstream of the outlet of Lake Ontario into dammed Lake St. Lawrence. The Moses-Saunders hydropower dam regulates the flow (≈7500 m^3

s^{-1}) of Lake St. Lawrence into Lake Saint-François (235 km^2), which has high water clarity (Secchi depth >5m) (Table 1) and stabilized water levels within ± 10 cm by Beauharnois dam (downstream). The watershed of Lake Saint-François is composed of rural area, moderately populated (100-500 hab. km^{-2}) and receives only small tributaries (< 25 m^3 s^{-1}). Lake Saint-Louis (140 km^2), located downstream of the Beauharnois dam, is set in the densely populated (>500 hab. km^{-2}) Montreal metropolitan area. St. Lawrence River discharge (≈9500 m^3 s^{-1}) and water level (0.5-1.4 m) variations in Lake Saint-Louis are seasonally modulated by the partial inflow of the Ottawa River (discharge ≈1838 m^3 s^{-1}), the largest St. Lawrence River tributary. The Ottawa River waters are brown, enriched in chromatic dissolved organic matter, suspended sediments and phosphorus, resulting in low water clarity (Secchi 1-5 m). By Lake Saint-Pierre (402 km^2) ≈90 km downstream, the St. Lawrence River discharge adds up to 10500 m^3 s^{-1}, including 3 additional large tributaries (Richelieu, Yamaska and Saint-François; discharge: 434, 86 and 168 m^3 s^{-1}, respectively) contributing to its large water level range (1.31 m to 2.26 m annually), low water clarity (Secchi 0.1-3 m) and high sediment accumulation rate (Table 1). The watershed of Lake Saint-Pierre is rural with a low population density (10-25 hab. km^{-2}). Wetland area differs substantially among the 3 fluvial lakes with 4100 ha for level-stabilized Lake Saint-François, 950 ha for the heavily urbanized Lake Saint-Louis and 18350 ha for Lake Saint-Pierre, which presents a more natural shoreline and flow regime. In addition to discharge regulation, the St. Lawrence River has also been considerably modified by human along its course with the dredging and channelling for ship traffic, creation of islands, and deepening of the Montreal harbor (Bibeault and Hudon 2007).

Sampling

Sampling was undertaken in the littoral zone potentially colonized by submerged plant communities where the water depth was <2.5 m (Hudon et al. 2000). Sampling sites were selected in areas upstream, within, and downstream of the inflow of tributaries to the St. Lawrence River. Sampling to describe the biomass of submerged plant communities and environmental characteristics of the St. Lawrence River was conducted in the period of maximum macrophyte biomass (August 19-September 18, 2008) (Vis et al. 2006). At each site, we measured water depth (z) (m), temperature (° C), dissolved oxygen (%), pH, conductivity ($\mu S\ cm^{-1}$) (YSI 103 600 XLM, Yellow Springs, Ohio) and the light extinction coefficient (k) (m^{-1}) (LI-COR LI-190SA air and underwater LI-193SA spherical sensor, Lincoln, Nebraska). At each site, water samples were taken just below the surface and unfiltered sub-samples were used for analyses of suspended matter (SPM, American Public Health Association 1995), total phosphorus (TP) and total nitrogen (TN) (Environment Canada 2005). Filtered subsamples (Whatman GF / C, GE Healthcare Bio-Sciences AB, Sweden) were analyzed for total dissolved phosphorus (TDP), NO_2-NO_3, NH_4^+, dissolved organic carbon (DOC) and color (Pt / Co) (Environment Canada 2005). TP and TDP were determined by acid digestion followed by colorimetry with ammonium molybdate. TN was analyzed after persulfate digestion with a LACHAT Continuous Flow Quick-Chem 8000 ion analyzer (Loveland, Colorado). NO_2-NO_3 was measured by reducing nitrate to nitrite in a cadmium column prior to colorimetry; NH_4^+ was analyzed by colorimetry after the addition of sodium nitroprusside and sodium phenate. DOC was oxidized to carbon dioxide by the addition of persulfate prior to infrared detection (Shimadzu TOC-5000; Shimadzu Corporation, Japan) (Environment Canada 2005).

Dissolved inorganic nitrogen (DIN) was calculated as the sum of NO_2-NO_3 and NH_4^+ concentrations. Distance of the closest upstream sampled tributary was measured (MapInfo Professional v8.5, Pitney Bowes Inc, Connecticut) to represents the local effect of tributary over water quality.

Biomasses of benthic PP (macrophytes, cyanobacterial mats and, epiphyton) was estimated quantitatively using a double-headed rake dragged over a length of 1 meter on the bottom of the St. Lawrence River (Kenow et al. 2007; Yin et al. 2000). Biomass was averaged from collections made in front and on both sides of the boat. Macrophytes collected simultaneously with epiphytes and filamentous algae were brought back to the laboratory for cleaning, sorting, identification, and measurement of wet mass (WM) and conversion to dry mass (DM) using previously established conversion factors (Hudon et al. 2012). The algae mats were dominated by the cyanobacterium *Lyngbya wollei* (Levesque et al. 2012). The epiphyton biomass (µg of chla mg^{-1} DM on macrophytes leaves) was estimated by manually dislodging epiphytes of 10 leaves of vascular macrophytes (generally *Vallisneria americana*), drying the leaves at 50° C, measuring their dry mass (± 0.1 mg) and measuring chlorophyll-a of epiphyton following cold ethanol extraction and spectrometry (Stainton et al. 1977).

Statistical analysis

Environmental variables – Physical, chemical and biological variables (biomass) of the sites in the littoral zone and at the mouth of tributaries of our three fluvial lakes were compared separately among lakes using Kruskal-Wallis nonparametric analysis of variance (ANOVA; function kruskal.test of package stats) followed by multiple comparisons of medians (function kruskalmc of package pgirmess) (Giraudoux 2011) in the R statistical language (R Development Core Team 2011, Austria). In addition, sites within littoral zone and at the mouth of the tributaries for the same fluvial lake were compared using the Wilcoxon rank sum in the same fashion. Water depth was not included in the analysis on the basis that the sampled sites were selected to have a depth in the 0.5-2 m range. Temperature, dissolved oxygen and pH were excluded because of their high daily variation.

Variability among sites of the littoral zone was explored by principal component analysis (PCA) using the FactoMineR library (Husson et al. 2010) in R. All variables were reduced to unit variance by standardization in order to facilitate the comparison of variables with different scales (Legendre and Legendre 2012).

Benthic PP analysis – We determined the influence of environmental variables and their spatial component on the benthic primary producer community using redundancy analysis (RDA) and variation partitioning (Borcard et al. 1992). Vegetation biomass data were transformed using the Hellinger transformation to prevent similarity to reflect double zeros, eliminate the differences of total biomass among sites and, because it includes a square-root transformation, reduce the importance of the most abundant vegetation types, as recommended for RDA (Legendre and Gallagher 2001). We also evaluated environmental and spatial control for individual functional groups of benthic PP using multiple regressions on $\log_{10}$ transformed biomass.

Spatial structure was modeled hierarchically at three levels: 1) at the fluvial scale using a linear trend in the x coordinates (longitude) of the sampling sites, 2) at the among-lake scale by using two binary variables to represent the three St. Lawrence River fluvial lakes, and 3) at the within-lake scale with Moran's eigenvector maps (MEM) (Borcard and Legendre 2002). MEM produce a group of orthogonal spatial variables from the geographic distances among the sampling sites (Dray et al. 2006). These variables model spatial variation at different scales and can be used as explanatory variables in RDA and regression (Borcard et al. 2011). Specifically, each fluvial lake was modelled separately with a set of MEM variables which were arranged into blocks, one for each lake. For each fluvial lake, the minimum and maximum distance between two sampling sites acted as the spatial detection range: Saint-Francois (10.1 -32.6 km), Saint-Louis (5.5 – 11.0 km) and Saint-Pierre (12.0 - 67.8 km). The detection range reflected lake size as well as the number of tributaries and distance between them in each lake. Significant MEM variables were then used to define the scale of the spatial patterns in benthic PP.

Forward selection was applied separately to the environmental and MEM variables to reduce the number of variables before RDA or regression. Variation in vegetation biomass was decomposed (Borcard et al. 1992) among environmental variables, river scale, among-lake and within-lake scales using the varpart function of the vegan package in R (Oksanen et al. 2013).

Results

Biomass of benthic primary producers

Macrophyte composition was dominated by *Vallisneria americana* through the whole study area, with the presence of *Elodea canadensis* in all tributaries and of various other taxa in St. Lawrence River littoral zone. Macrophytes represented the most abundant vegetation throughout the study area (Table 2) and showed a clear decreasing trend along the river continuum, nearly disappearing in Lake Saint-Pierre tributaries (Fig. 2). Epiphyton comprised a mixture of diatoms, filamentous Chlorophytes, cyanobacteria and debris loosely attached to the surface of vascular macrophytes. Epiphyte biomass tended to increase downstream in the littoral zone, but dropped in the increasingly turbid tributaries found within each successive fluvial lake (Fig. 2). Cyanobacterial mats were largely comprised of the filamentous, non-heterocyst taxon *Lyngbya wollei*; mats were absent from Lake Saint-François and their biomass increased downstream; they were first observed in the Ottawa River and Lake Saint-Louis and reached their highest biomass in Lake Saint-Pierre (Table 2 and Fig. 2).

Environmental variables

St. Lawrence River water quality changed markedly over its 250-km-long course through Lake Saint-François, Lake Saint-Louis and Lake Saint-Pierre. As expected by its position ≈175 km downstream of Lake Ontario and Lake St. Lawrence, just below Moses-Saunders dam, Lake Saint-François was clear (light extinction coefficient of 0.5 m^{-1}), with low suspended matter and DOC concentrations (Table 3). By the time St. Lawrence River reached Lake Saint-Pierre, located farthest downstream, large increases in water colour (5x), suspended matter (10x) and DOC (2x) were observed (Table 3). These conditions resulted in a sharp decrease in light penetration downstream, from > 50% of incident light reaching the bottom in Lake Saint-François to < 5% in Lake Saint-Pierre. With downstream advection, St. Lawrence River water also became enriched in nutrients, showing a 2.5-fold increase in both dissolved N and P.

For Lake Saint-François, comparison of the water quality between St. Lawrence River littoral zone and tributaries for each fluvial lake showed that tributaries were significantly more turbid and rich in DOC than St. Lawrence River waters. In contrast, for lakes Saint-Louis and Saint-Pierre, both inflowing tributary waters and St. Lawrence River littoral areas were increasingly turbid and nutrient-rich moving downstream (Table 3). Although conductivity was highly variable within each fluvial lake and among tributaries, it tended to decrease along the longitudinal river axis. Tributaries from Lake Saint-Pierre exhibited particularly high concentrations of suspended matter, DIN and DIN:TDP ratio as well as the highest range of conductivity values (Table 3). Poor water quality in tributaries exerts a cumulative impact and explain the progressive downstream degradation of the St. Lawrence River water quality.

We explored the relationship between the physical, chemical and spatial variables of the St. Lawrence River littoral zone along the downstream gradient by PCA. The first two principal components captured 62% of the total variance of the 13 standardized variables (Fig. 3A). The contrasting optical properties of water masses from Lake Saint-François (high conductivity, clear waters) and of Lake Saint-Louis and Lake Saint-Pierre (low conductivity, brown, turbid waters) was shown by the strong negative relation between conductivity and light penetration with color and DOC along the first PCA axis (49%). In addition, the concentrations of all forms of N and P were grouped together along the first axis and were strongly associated with water optical properties (colour, DOC, SPM). The second axis (13%) was driven by the opposition between DIN: TDP and distance to nearest upstream tributary.

Environmental and spatial variables controlling biomass of benthic PP

The combined influence of all environmental variables and spatial structure (fluvial, regional and lake scale) explained 61% ($R^2_{adj.}$) of the variation in the biomass of the benthic primary producers of the St. Lawrence River. The first axis (R^2_{adj} = 57%) contrasted high biomass of macrophytes found in Lake Saint-François and epiphyton which was dominant in Lake Saint-Pierre at the downstream end of the fluvial gradient (Fig. 3B). In addition, the first axis showed the increase in DOC and nutrients (TN and TP) and decrease in transparency (color and light extinction coefficient) from Lake Saint-François to Lake Saint-Pierre. The correlation between benthic PP and MEM variables LSF-1 and LSF-3 (left side of axis I) indicates a spatial pattern of enhanced plant growth at distances in the order of 16-33 km downstream of tributary enrichment. The second axis (4% of explained variation) related the biomass of *L. wollei* to a low DIN:TDP ratio and a long distance to the closest upstream tributary. Another regression analysis carried on *L. wollei* only (not shown), revealed that its biomass followed a spatial pattern at the ≈8-11 km scale in Lake Saint-Louis. Following a forward selection on environmental variables, conductivity and TP were retained and the model still explained 59% ($R^2_{adj.}$) of the variation in the biomass of the benthic primary producers of the St. Lawrence River (not shown).

Since environmental conditions were spatially structured, most of the explanatory power resided in their intersection (22%; Table 4). Environmental variables (7%) and within-lake (15%) scale were important components on their own, but taken together also explained 5.5% of biomass of benthic PP. Investigation of specific environmental/spatial factors controlling each group of benthic PP revealed that macrophyte biomass was positively related to conductivity ($R^2_{adj.}$ = 37%; Table 4), which was spatially structured at all scales ($R^2_{adj.}$ = 11%), but also important on its own (18%). Rising epiphyton biomass coincided with rising light extinction coefficient (i.e. increasing turbidity) and rising DIN:TDP ratio ($R^2_{adj.}$ = 15%), both largely modulated by within-lake differences between littoral sites and those influenced by local tributary inflow ($R^2_{adj.}$ = 7%). *Lyngbya wollei* rising biomass was best correlated to rising DOC and dropping NH_4^+ ($R^2_{adj.}$ = 32%), all of which showed a clear downstream gradient. The spatial structure within lake alone was important for all vegetation groups with 21% of biomass variation explained for both macrophytes and epiphyton and to a lesser extent for *Lyngbya* with 13% of biomass variation.

Discussion

In this study we compared the littoral zone of three fluvial lakes located along a fluvial continuum providing a natural, three-level nested design (fluvial scale, among lakes and within lakes) to understand the environmental control of benthic primary producer biomass. Water quality in the tributaries of the St. Lawrence River reflected land use and the geology of their drainage basins as their turbidity (light extinction coefficient, SPM, DOC) and DIN:TDP increased along the longitudinal river axis. We expected that biomass variation of benthic PP would be both environmentally and spatially controlled at the within-lake scale, which turned out to be the case; that finding will allow us to revisit the principles underlying the multi-scale functioning of large rivers.

Factors controlling the biomass of benthic primary producers

Water conductivity is often the most important environmental variable controlling macrophytes (Alahuhta and Heino 2013; Capers et al. 2010; O'Hare et al. 2012) and benthic algae (Biggs 1995) at multiple scales. The gradient of apparently decreasing conductivity in the littoral zone of each fluvial lake is likely related to differences in geology among individual sub-watersheds. Lake Saint-Francois is characterized by waters originating from the Great Lakes in the interior lowlands (high conductivity). Lake Saint-Louis is the point of confluence of the Ottawa River, which drains the Canadian Shield, adding a major contribution of low-conductivity waters to the St. Lawrence River north shore. Lake Saint-Pierre receives tributaries draining the Canadian Shield to the north and the Appalachian Mountains to the south. Longitudinal changes in land use further amplify the downstream degradation in water quality (Biggs 1995): from the rural and forested section around Lake Saint-François, the St. Lawrence River flows through the heavily urbanized area of metropolitan Montreal around Lake Saint-Louis, eventually reaching the fertile farmlands surrounding Lake Saint-Pierre. The combined effects of geology and land use explain the downstream gradient of decreasing conductivity and rising turbidity and TP we reported in this study.

As hypothesized, each type of benthic PP exhibited a specific response to water quality which was structured across multiple spatial scales. The association of TP with the biomass of each benthic PP reflected the nutrient acquisition strategy of the different functional groups. Macrophytes were prevalent in the clear, low TP waters of upstream littoral Lake Saint-François since they rely primarily on sediment nutrients via root absorption (Barko and Smart 1986; Carignan and Kalff 1980). Epiphytic biomass was highest in downstream Lake Saint-Pierre, where local tributaries increased nutrient concentrations in the water column (Vadeboncoeur and Steinman 2002). Biomass of epiphyton was positively associated with DIN:TPD, reflecting the degradation of the water quality of tributaries of the St. Lawrence River along the river continuum and showing that tributary confluences are key ecological nodes (Thorp et al. 2006). Similarly, a study of seven watersheds with varying agricultural use (12%-80%) found a stimulatory effect of tributary loadings on loosely attached algae (Makarewicz et al. 2007). For epiphytes, the positive correlation between biomass and the water extinction coefficient was likely achieved by the growth of epiphytes on macrophytes reaching towards the surface (Vis et al. 2006), in spite of the turbid conditions resulting from the high concentration of SPM brought by tributaries. Tributaries also supplied high DOC and nutrients concentrations favorable to cyanobacterial mats, either directly from the overlying water or indirectly via mineralization within the mat (Stevenson et al. 1996). DOC and NH_4^+ were also previously documented as environmental factors controlling the distribution and biomass of cyanobacterial mats in the St. Lawrence River (Levesque et al. 2012; Levesque et al. 2015).

Although the importance of direct environmental selection was only meaningful for the benthic PP community and specifically for macrophytes, a large portion of the variation was explained by environmental variables that were structured spatially at all scales studied (fluvial scale, among lakes and within lakes) a common feature in similar studies (Alahuhta and Heino 2013; Capers et al. 2010; O'Hare et al. 2012). The importance of the within-lake scale alone for the whole benthic community and each functional group might also be indicative of the influence of autogenic biological processes (e.g. competition, grazing) and that environmental factors act at smaller scale (<10 km) than used in our study (Legendre and Legendre 2012).

From a management perspective, our results indicate that reduction in SPM and nutrient loads from tributaries through better management practice (BMPs), could improve the St. Lawrence River water quality and benthic habitats 16 to 33 km downstream of the river mouth, depending on their discharge and location along the St. Lawrence River continuum. In addition, our study revealed that the abundance of *L. wollei* mats fluctuated at distances ≈8-11 km. Our multi-level approach allowed us to detect which environmental factors influence benthic PP and at what scale they act and additionally to take into account the strong effect of human actions across spatial scales (Allan 2004) in order to preserve the integrity of the benthic primary producer community.

Part of the unexplained variation in our general model could result from the high variation in community organisation, originating from stochastichydro-climatic disturbance events disrupting patches of benthic PP (Capers et al. 2010; Thorp et al. 2006). Such events, which can include water level and discharge variations, drought events, ice conditions, strong winds and waves, increase along the downstream direction in the St. Lawrence River. Lake Saint-Francois is largely stabilized and receives a small number of tributaries; Lake Saint-Louis level and water quality both vary under the influence of the Ottawa River and municipal discharge points. Of all St. Lawrence River fluvial lakes, Lake Saint-Pierre showed the highest spatial and temporal variability in level, discharge and water quality, resulting from the combined influences of the Ottawa River and multiple other tributaries (Table 1). The effect of such stochastic events are exemplified by the extremely low water levels experienced in 2007 in the St. Lawrence River, which may have amplified the among-lake differences in benthic PP growing in the shallow littoral zone. Because submerged macrophytes subsistence rely on buried belowground structures (Wetzel 2001) they are susceptible to water level decline and sediment dry-out as shown by the decrease of macrophytes after a 1-year drop in water level in the St. Lawrence River (Hudon 1997). Given that water level variations increase as one moves downstream in the St. Lawrence River, low level/discharge events should exert an increasingly high impact on benthic PP in Lake Saint-François than in Lake Saint-Louis and Lake Saint-Pierre. Stochastic events can therefore interrupt the annually repeated succession ruled by seasonal replacements of species. This interruption allows dispersal to take on a more important role where species colonized a previously disturbed environment to fill empty niches (Thorp et al. 2006).

Revisiting concepts addressing spatial gradients in river systems

As predicted by the RCC (Vannote et al. 1980), the littoral zone of the St. Lawrence River became progressively more turbid, enriched in DOC and in nutrients (N and P, both in dissolved and total concentration) along its downstream course. Overall, as predicted, benthic PP community biomass decreased along the river continuum (Vannote et al. 1980), driven by a strong decrease of macrophytes, although cyanobacterial mats and epiphyton showed opposite trends. It should nevertheless be pointed out that the decrease in macrophyte biomass did not lead to major changes in the composition of vascular plant communities along the fluvial gradient.

The prediction of the serial discontinuity concept, stating that an increase in light reaching the bottom and in submerged vascular macrophyte biomass is expected following a dam on the lower reach of a river was verified. We indeed found high biomass of macrophytes in Lake Saint-François, downstream of the Moses-Saunders power dam (Ward and Stanford 1983), but water clarity in the upper St. Lawrence River also results from the fact that the Great Lakes act as a huge sedimentation basin. Although large wetland areas were observed around downstream Lake Saint-Pierre, as predicted by the serial discontinuity concept extension (Ward and Stanford 1995), the positive gradient of wetland surface area was disrupted by wetland destruction in the heavily urbanized Lake Saint-Louis. These results indicate that anthropogenic activities have had major impacts on the St. Lawrence River fluvial landscape, despite the increasing range of water level variations and discharge with the distance downstream (Table 1). The local impact of anthropogenic perturbations such as dams, nutrients inputs and shore modifications produce a patchy structure (Cushing et al. 2006) both in terms of water physico-chemistry and benthic PP community composition. In summary, the spatial changes across the St. Lawrence River fluvial lakes are partially consistent with the presence of a fluvial gradient along the St. Lawrence River longitudinal axis but are best described by an assemblage of heterogeneous patches induced by human activities at small (tributaries) and large (dams) scales (Thorp et al. 2006). Given the major importance of submerged macrophytes as habitat for microfauna and fish that feed on them, water quality of all the St. Lawrence River tributaries, regardless of their size, induces a significant cumulative impact on river ecosystems at the fluvial scale. Our study shows that the sum of local tributary effects exerts considerable overall pressures on river ecosystems and that conversely, local-scale management of individual, albeit small watersheds, can markedly improve local ecological condition of the St. Lawrence River.

Acklowledgements

Funding was provided by the St. Lawrence Action Plan and Environment and Climate Change Canada (C.H.). The authors thank Antonella Cattaneo, Bernadette Pinel-Alloul, Roxanne Maranger, Jan R. Stevenson and two anonymous reviewers for their insightful comments on the manuscript. We also thank Jean-Pierre Amyot and Lisa Gualtieri for help with field data collection and the laboratory staff of the St. Lawrence Centre (LEEQ-ECCC) for water quality analyses. François Boudreault (ECCC) assembled and drafted the location map.

References

Alahuhta J, Heino J (2013) Spatial extent, regional specificity and metacommunity structuring in lake macrophytes J Biogeogr 40:1572-1582 doi:10.1111/jbi.12089

Allan JD (2004) Landscapes and riverscapes: The influence of land use on stream ecosystems Annual Review of Ecology Evolution and Systematics 35:257-284 doi:10.1146/annurev.ecolsys.35.120202.110122

American Public Health Association. 1995. Standard methods for the examination of water and wastewater. 19th edition edn. American Public Health Association, Washington, D.C.

Barko JW, Hardin DG, Matthews MS (1982) Growth and morphology of submersed freshwater macrophytes in relation to light and temperature Canadian Journal of Botany 60:877-887 doi:doi:10.1139/b82-113

Barko JW, Smart RM (1986) Sediment-related mechanisms of growth limitation in submerged macrophytes Ecology 67:1328 1340 doi:10.2307/1938689

Bibeault J-F, Hudon C (2007) Water availability: An overview of issues and future challenges for the St. Lawrence River Quebec Studies 42:75-90

Biggs BJF (1995) The contribution of flood disturbance, catchment geology and land-use to the habitat template of periphyton in stream ecosystems Freshwater Biology 33:419-438 doi:10.1111/j.1365-2427.1995.tb00404.x

Borcard D, Gillet F, Legendre P (2011) Numerical ecology with R. Use R! series. Springer Science, New York, New York. doi:10.1007/978-1-4419-7976-6

Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices Ecological Modelling 153:51-68 doi:10.1016/s0304-3800(01)00501-4

Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004) Dissecting the spatial structure of ecological data at multiple scales Ecology 85:1826-1832 doi:10.1890/03-3111

Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation Ecology 73:1045 1055 doi:10.2307/1940179

Capers RS, Selsky R, Bugbee GJ (2010) The relative importance of local conditions and regional processes in structuring aquatic plant communities Freshwater Biology 55:952-966 doi:10.1111/j.1365-2427.2009.02328.x

Carignan R, Kalff J (1980) Phosphorus sources for aquatic weeds - water or sediments Science 207:987-989 doi:10.1126/science.207.4434.987

Carignan R, Lorrain S (2000) Sediment dynamics in the fluvial lakes of the St. Lawrence River: accumulation rates and characterization of the mixed sediment layer Canadian Journal of Fisheries and Aquatic Sciences 57:63-77 doi:10.1139/cjfas-57-S1-63

Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics Ecology letters 8:1175-1182 doi:10.1111/j.1461-0248.2005.00820.x

Cushing CE, Cummins KW, Minshall GW (2006) River and Stream Ecosystems of the World. University of California Press,

Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM) Ecological Modelling 196:483-493 doi:10.1016/j.ecolmodel.2006.02.015

Duarte CM, Kalff J (1986) Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities Limnol Oceanogr 31:1072 1080

Elwood JW, Newbold JD, O'Neill RV, Van Winkle W (1983) Resource spiralling: an operational paradigm for analyzing lotic ecosystems. In: Fontaine TD, Bartell SM (eds) The Dynamics of Lotic Ecosystems. Ann Arbor Science, Ann Arbor, USA, pp 3-27

Environment Canada. 2005. Manuel des methodes d'analyses (annexe B). . Environment Canada, Quebec Region, Scientific and Technical Services Section, St. Lawrence Centre, Montreal, Quebec, Canada

Environment Canada. 2012. Water Survey Canada: Hydat database. Environment Canada, Ottawa, Ontario, Canada.

Forman RTT, Godron M (1986) Landscape ecology. John Wiley & Sons, New York, USA

Franklin P, Dunbar M, Whitehead P (2008) Flow controls on lowland river macrophytes: A review Science of the Total Environment 400:369 378 doi:10.1016/j.scitotenv.2008.06.018

Gallego I, Davidson TA, Jeppesen E, Perez-Martinez C, Fuentes-Rodriguez F, Juan M, Casas JJ (2014) Disturbance from pond management obscures local and regional drivers of assemblages of primary producers Freshwater Biology 59:1406-1422 doi:10.1111/fwb.12354

Giraudoux P (2011) Data analysis in ecology R package version 1.5.2. http://cran.r-project.org/web/packages/pgirmess/index.html.

Gouvernement du Québec (2010) Répertoire des municipalités. Ministère des Affaires municipales et de l'Occupation du territoire, Gouvernement du Québec. http://www.mamrot.gouv.qc.ca/repertoire-des-municipalites/. Accessed 29 September 2015

Hilton J, O'Hare M, Bowes MJ, Jones JI (2006) How green is my river? A new paradigm of eutrophication in rivers Science of the Total Environment 365:66-83 doi:10.1016/j.scitotenv.2006.02.055

Hudon C (1997) Impact of water level fluctuations on St. Lawrence River aquatic vegetation Canadian Journal of Fisheries and Aquatic Sciences 54:2853-2865 doi:10.1139/cjfas-54-12-2853

Hudon C, Carignan R (2008) Cumulative impacts of hydrology and human activities on water quality in the St. Lawrence River (Lake Saint-Pierre, Quebec, Canada) Canadian Journal of Fisheries and Aquatic Sciences 65:1165 1180 doi:10.1139/f08-069

Hudon C et al. (2012) Oligotrophication from wetland epuration alters the riverine trophic network and carrying capacity for fish Aquat Sci 74:495 511 doi:10.1007/s00027-011-0243-2

Hudon C, Lalonde S, Gagnon P (2000) Ranking the effects of site exposure, plant growth form, water depth, and transparency on aquatic plant biomass Canadian Journal of Fisheries and Aquatic Sciences 57:31-42 doi:10.1139/cjfas-57-S1-31

Husson F, Josse J, Le S, Mazet J (2010) Multivariate exploratory data analysis and data mining with R. R package version 1.14. http://cran.r-project.org/web/packages/FactoMineR/index.html.

Jeppesen E, Søndergaard M, Søndergaard M, Christoffersen K (1998) The structuring role of submerged macrophytes in lakes. Springer, New York

Jones JI, Young JO, Eaton JW, Moss B (2002) The influence of nutrient loading, dissolved inorganic carbon and higher trophic levels on the interaction between submerged plants and periphyton J Ecol 90:12-24 doi:10.1046/j.0022-0477.2001.00620.x

Junk JW, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems Canadian Special Publication of Fisheries and Aquatic Sciences 106: 110-127

Kenow KP, Lyon JE, Hines RK, Elfessi A (2007) Estimating biomass of submersed vegetation using a simple rake sampling technique Hydrobiologia 575:447 454 doi:10.1007/s10750-006-0284-z

Lacoul P, Freedman B (2006) Environmental influences on aquatic plants in freshwater ecosystems Environ Rev 14:89-136 doi:10.1139/a06-001

Legendre P, Gallagher E (2001) Ecologically meaningful transformations for ordination of species data Oecologia 129:271-280 doi:10.1007/s004420100716

Legendre P, Legendre L (2012) Numerical ecology. 3rd english edn. Elsevier Science BV, Amsterdam, the Netherlands

Levesque D, Cattaneo A, Hudon C, Gagnon P (2012) Predicting the risk of proliferation of the benthic cyanobacterium *Lyngbya wollei* in the St. Lawrence River Canadian Journal of Fisheries and Aquatic Sciences 69:1585 1595 doi:10.1139/f2012-087

Levesque D, Hudon C, Amyot J-P, Cattaneo A (2015) Wave exposure and current regulate biomass accumulation of the benthic cyanobacterium *Lyngbya wollei* in a large fluvial lake Freshw Sci 34:867-880

Makarewicz JC, D'Aiuto PE, Bosch I (2007) Elevated nutrient levels from agriculturally dominated watersheds stimulate metaphyton growth Journal of Great Lakes Research 33:437-448 doi:10.3394/0380-1330(2007)33[437:enlfad]2.0.co;2

Mikulyuk A, Sharma S, Van Egeren S, Erdmann E, Nault ME, Hauxwell J (2011) The relative role of environmental, spatial, and land-use patterns in explaining aquatic macrophyte community composition Canadian Journal of Fisheries and Aquatic Sciences 68:1778-1789 doi:10.1139/f2011-095

Ministère des affaires municipales. 1998. Répertoire des municipalités du Québec. Presses de l'Université du Québec., Québec

Morrice JA, Kelly JR, Trebitz AS, Cotter AM, Knuth ML (2004) Temporal Dynamics of Nutrients (N and P) and Hydrology in a Lake Superior Coastal Wetland Journal of Great Lakes Research 30, Supplement 1:82-96 doi:http://dx.doi.org/10.1016/S0380-1330(04)70379-2

O'Hare MT, Gunn IDM, Chapman DS, Dudley BJ, Purse BV (2012) Impacts of space, local environment and habitat connectivity on macrophyte communities in conservation lakes Diversity and Distributions 18:603-614 doi:10.1111/j.1472-4642.2011.00860.x

Oksanen J et al. (2013) vegan: Community Ecology Package. R package version 2.0-10. http://cran.r-project.org/package=vegan.

Sand Jensen K (1989) Environmental variables and their effect on photosynthesis of aquatic plant-communities Aquat Bot 34:5-25 doi:10.1016/0304-3770(89)90048-x

Stainton MP, Capel MJ, Armstrong FAJ (1977) The chemical analysis of fresh water. Canada Fisheries and Marine Service, Winnipeg, Manitoba, Canada

Stevenson RJ, Bothwell ML, Lowe RL (1996) Algal Ecology: Freshwater Benthic Ecosystem. Elsevier, San Diego, California

Thorp JH, Thoms MC, Delong MD (2006) The riverine ecosystem synthesis: Biocomplexity in river networks across space and time River Research and Applications 22:123-147 doi:10.1002/rra.901

Vadeboncoeur Y, Steinman AD (2002) Periphyton function in lake ecosystems TheScientificWorldJournal 2:1449-1468 doi:10.1100/tsw.2002.294

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) River continuum concept Canadian Journal of Fisheries and Aquatic Sciences 37:130-137 doi:10.1139/f80-017

Vis C, Hudon C, Carignan R (2006) Influence of the vertical structure of macrophyte stands on epiphyte community metabolism Canadian Journal of Fisheries and Aquatic Sciences 63:1014-1026 doi:10.1139/f06-021

Ward JV, Stanford JA (1983) The serial discontinuity concept of lotic ecosystems. In: T.D. F, Bartell SM (eds) Dynamics of Lotic Ecosystems. Ann Arbor Scientific Publishers, Ann Arbor, USA, pp 29–42

Ward JV, Stanford JA (1995) The serial discontimuity concept - Extending the model to floodplain rivers Regulated Rivers-Research & Management 10:159-168 doi:10.1002/rrr.3450100211

Wetzel RG (2001) Limnology: Lake and River Ecosystems. 3rd edn. Academic Press, New York

Yin Y, Winkelman JS, Langrehr HA (2000) Long term resource monitoring program procedures: aquatic vegetation monitoring. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin

Table 1 Comparison of the attributes potentially affecting the abundance, composition and scale of distribution of benthic primary producers in the three fluvial lakes of the St. Lawrence. See figure 1 for position of each fluvial lake within the St. Lawrence River continuum

Functional attribute	Lake Saint-François	Lake Saint-Louis - lower Ottawa R	Lake Saint-Pierre
St. Lawrence River discharge ($m^3\ s^{-1}$)[f]	7500	9500	10500
Total fluvial lake area (km^2)[c]	235	140	402
Annual (1998-2008) Water Level variation (m)[f]	0.09-0.28, largely stabilized	0.53-1.42	1.31-2.26
Major tributaries (Mean annual tributary discharge, $m^3\ s^{-1}$) [a]	Raquette, Saint-Régis rivers (< 25, < 10)	Ottawa Chateauguay rivers (1838, 37),	Richelieu, Yamaska, Saint-François rivers (434, 86, 168)
Population density (hab km^{-2})[b]	100-500	>500	10-25
Shoreline use	Rural	Urban	Wetlands
Connectivity with floodplain	Low because of stabilized water level	Low because of heavily urbanized shorelines	High because of high range of level and natural wetlands along the shoreline
Littoral areas (defined as z < 4.5 m, km^2) (% of total area)[c]	176 (75%)	100 (71%)	249 (62%)
Total area of wetlands (ha)[d]	4100	950	18350
Mean Depth (m)[c]	5.1	3.4	2.7
Water clarity (Secchi Depth range, m)[e]	5-10	1-5	0.1-3
Sediment accumulation (kg m^{-2} $year^{-1}$)[c]	3.2	6.7	12.1

[a]from Hudon and Carignan (2008); [b]from Répertoire des Municipalités du Québec (2010); [c]from Carignan and Lorrain (2000); [d]from http://www.qc.ec.gc.ca/csl/fich/fich001_002_e.html#overview; [e]from Hudon et al. (2000); [f]from Environment Canada (2012)

Table 2 Median biomass and range for each of the three major types of benthic primary producers collected in the St. Lawrence River (SLR) fluvial lakes and their tributaries

	Lake St. François		Lake St. Louis		Lake St. Pierre	
	SLR littoral (N=11)	**Tributaries (N=9)**	**SLR littoral (N=6)**	**Tributaries (N=10)**	**SLR littoral (N=26)**	**Tributaries (N=15)**
Dominant macrophyte taxa	*Vallisneria americana, Heteranthera dubia*	*Vallisneria americana, Elodea canadensis*	*Vallisneria americana, Alisma plantago-aquatica*	*Vallisneria americana, Elodea canadensis*	*Vallisneria americana, Potamogeton richardsonii*	*Vallisneria americana, Elodea canadensis*
Macrophytes biomass (g DM m^{-2})	182 (1-345)a	165 (11-277)*a*	30 (9-75)ab	67 (5-176)*a*	**26 (0-169)b**	**0 (0-30)*b***
Epiphyton biomass (µg of chla mg^{-1} DM of macrophytes)	642 (106-5790)a	1219 (250-4694)*a*	538 (386-1109)a	955 (127-5305)*a*	**1090 (164-7623)a**	**0 (0-2210)*b***
Cyanobacterial mats biomass (g DM m^{-2})	0 (0-0)a	0 (0-0)*a*	2 (0-24)ab	0 (0-16)*a*	**0 (0-46)b**	**0 (0-0)*b***

Results of three comparison tests based on Kruskal–Wallis nonparametric analysis of variance (ANOVA) followed by multiple comparisons of medians. Letters identify significantly different groups ($p < 0.05$) for each comparison: 1) between-lake comparisons (normal letters); 2) between littoral zone and tributary mouth for all lakes (italic letters); 3) between littoral zone and tributary mouth within each lake (bold characters)

Table 3 Median values (range) of the chemical and physical water quality characteristics in the St. Lawrence River (SLR) fluvial lakes and tributaries (See Table 2 for the key to statistical comparisons).

	Lake St. François		**Lake St. Louis**		**Lake St. Pierre**	
	SLR littoral (N=11)	**Tributaries (N=9)**	**SLR littoral (N=6)**	**Tributaries (N=10)**	**SLR littoral (N=26)**	**Tributaries (N=15)**
Conductivity (µS cm^{-1})	261 (23-282)	244 (50-565)	161 (64-253)	124 (67-253)	130 (72-259)	172 (27-597)
Light extinction coef. (m^{-1})	**0.5 (0.4-1.5)a**	**1.2 (0.6-2.0)*a***	1.0 (0.4-2.1)ab	1.8 (0.5-2.3)*ab*	2.1 (0.8-3.5)b	2.4 (1.2-5.1)*b*
Color (Pt/Co)	**9 (2-16)a**	**21 (6-80)**	36 (6-55)ab	47 (7-59)	46 (9-71)b	47 (11-206)
SPM (mg L^{-1})	1 (1-9)a	1 (1-4)*a*	2 (1-5)a	4 (1-12)*a*	11 (2-48)b	18 (2-170)*b*
Total Nitrogen (µg N L^{-1})	435 (315-495)a	508 (370-1085)	440 (370-1000)ab	510 (360-1030)	622 (365-885)b	670 (353-4620)
DIN (µg N L^{-1})	102 (22-183)a	64 (20-246)*a*	123 (104-217)ab	106 (25-643)*a*	241 (26-486)b	262 (88-4577)*b*
NH_4^+ (µg N L^{-1})	11 (7-15)a	8 (5-41)*a*	14 (12-37)ab	18 (9-69)*ab*	21 (2-96)b	27 (8-757)*b*
Total Phosphorus (µg P L^{-1})	13 (7-35)a	33 (10-44)	20 (11-56)ab	28 (12-64)	40 (16-68)b	40 (13-138)
TDP (µg P L^{-1})	8 (5-23)a	20 (6-37)	13 (6-48)ab	16 (8-40)	20 (10-34)b	19 (7-67)
DIN: TDP (by mass)	14 (2-24)	3 (1-18)*a*	9 (5-21)	6 (2-23)*ab*	10 (2-18)	15 (5-68)*b*

DOC (mg C L^{-1})	**2.7 (2.3-4.12)a**	**4.8 (2.9-10.9)**	5.6 (2.4-7.0)ab	7.1 (2.3-7.4)	6.3 (2.8-7.1)b	5.9 (3.4-12.6)

Table 4 Variation partitioning (R^2_{adj} x 100) of benthic PP community biomass and individual group biomass using environmental factors, fluvial scale, among-lake and within-lake scale variables subsets

		Benthic PP community	Macrophytes	Epiphyton	Cyanobacterial mats
	Overall model	58.9^{***}	63.7^{***}	36.9^{***}	58.9^{***}
Individual models	Environment	$39.7^{***(a)}$	$36.9^{***(b)}$	$15.4^{**(c)}$	$31.8^{***(d)}$
	Fluvial scale	26.4^{**}	20.2^{***}	4.0^{NS}	21.3^{**}
	Among-lake scale	30.9^{***}	16.1^{*}	6.6^{NS}	19.0^{**}
	Within-lake scale	48.1^{***}	38.9^{***}	29.1^{**}	58.4^{***}
Pure fractions	Environment	7.0^{*}	17.7^{***}	0.1^{NS}	0.0^{NS}
	Fluvial scale	0.2^{NS}	3.8^{*}	0.0^{NS}	0.0^{NS}
	Among-lake scale	0.1^{NS}	0.7^{*}	0.0^{NS}	0.0^{NS}
	Within-lake scale	14.9^{***}	21.1^{***}	21.3^{**}	12.7^{**}
Fractions explained jointly (Not testable)	Environment ∩ Fluvial scale	0.0	0.0	2.0	0.1
	Environment ∩ Among-lake	2.3	0.0	4.3	0.1
	Environment ∩ Wihin-lake scale	5.5	3.2	6.8	12.7
	Environment ∩ Fluvial scale ∩ Among-lake	0.0	2.3	1.5	0.0
	Environment ∩ Fluvial scale ∩ Within-lake	0.4	1.7	0.2	8.0
	Environment ∩ Among-lake ∩ Within-lake	2.7	0.7	0.5	6.4
	Fluvial scale ∩ Among-lake	1.2	0.2	0.0	0.3

	Fluvial scale ∩ Within-lake	0.0	0.0	0.0	7.4
	Among-lake ∩ Within-lake	0.0	0.0	0.0	6.7
	Fluvial scale ∩ Among-lake ∩ Within-lake	2.4	0.9	0.3	0.0
	Env ∩ Fluvial scale ∩ Among-lake ∩ Within-lake	22.2	11.3	0.0	4.5

Note - * $p < 0.05$, ** $p<0.01$, ***$p < 0.001$, NS not significant. Intersections (fractions explained jointly) are not mathematically testable. Variables included in the environmental component following forward selection (a) conductivity and TP; (b) conductivity; (c) DIN: TDP and light extinction coefficient; (d) DOC and NH_4^+.

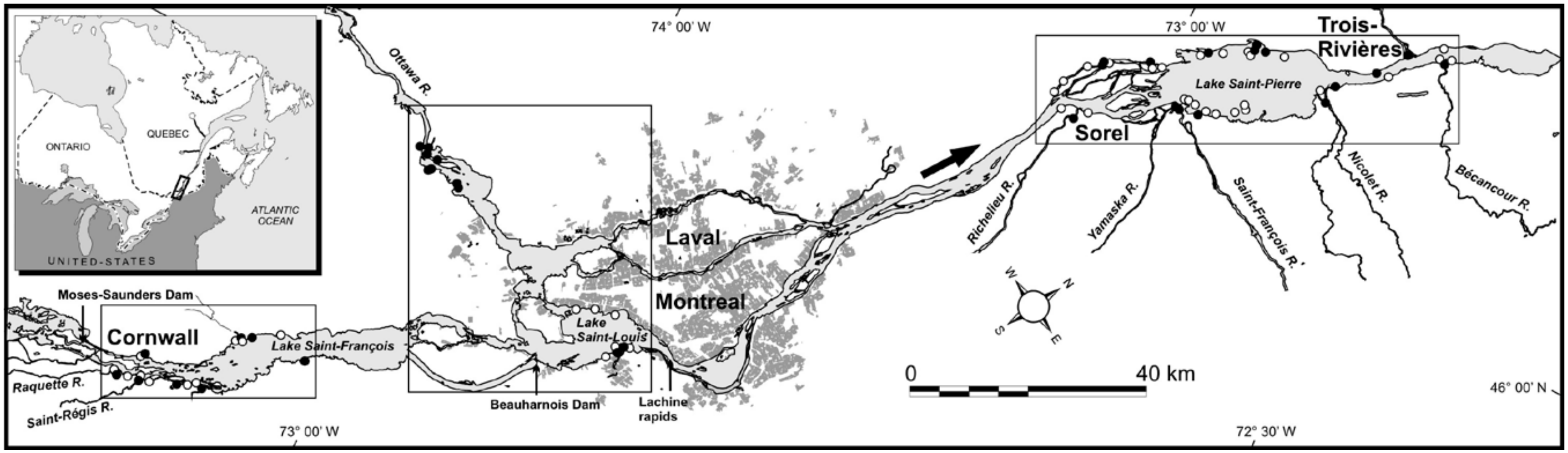
Figure captions

Fig. 1 Map of the study area showing, for each major sampling region, the location of littoral sites (open circles) and tributaries (full circle). Boxes indicate the three fluvial lakes under study: Lake Saint-François (11 littoral and 9 tributary sites); the Ottawa River and Lake Saint-Louis (6 littoral and 10 tributary sites), and Lake Saint-Pierre (26 littoral and 15 tributary sites).

Fig. 2 Vertical bar plot of the biomass of a) submerged macrophytes, b) epiphyton, and c) cyanobacterial mats against distance from the Moses-Saunders power dam, for each major sampling regions (black horizontal bars). The top panel (vertical black bars) of each plot represents biomass in the St. Lawrence River littoral sites and the bottom panel (vertical grey bars), the biomass sampled downstream of the mouth of tributaries. LSF = Lake St. François, LSL = Lake St. Louis and LSP = Lake St. Pierre.

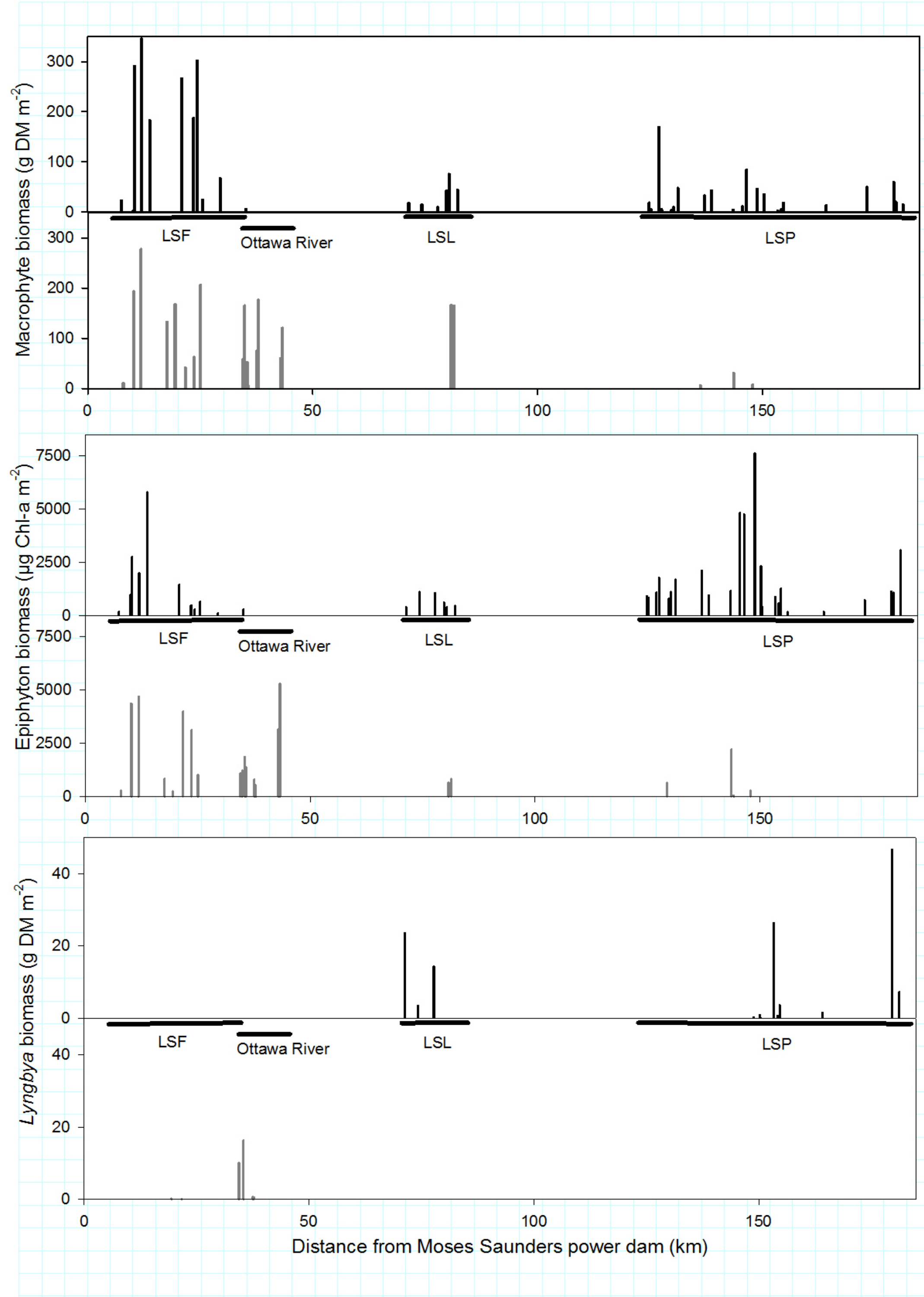
Fig. 3 a Principal component analysis (PCA) biplot based on correlations among the physical and chemical variables of the littoral sites (N = 43) of the St. Lawrence River. Arrows represent environmental variables (SPM = concentration of suspended particulate matter, dist. near. tributary = distance to the nearest upstream tributary, LSF = Lake St. François, LSL = Lake St. Louis and LSP = Lake St. Pierre.). White circles represent the centroids of the states of the qualitative variable fluvial lake.

b Redundancy analysis (RDA) with type 2 scaling for all environmental variables; biomass of benthic PP was Hellinger-transformed (full circles). Quantitative environmental and spatial variables selected by forward selection (arrows) and centroids of qualitative variables (full triangles) are also shown.



74° 00' W
73° 00' W
Trois-
Rivières
Ottawa R.
ONTARIO
QUEBEC
ATLANTIC OCEAN
UNITED-STATES
Lake Saint-Pierre
Sorel
Laval
Montreal
Moses-Saunders Dam
Cornwall
Lake Saint-François
Lake Saint-Louis
Raquette R.
Saint-Régis R.
Beauharnois Dam
Lachine rapids
Richelieu R.
Yamaska R.
Saint-François R.
Nicolet R.
Bécancour R.
0
40 km
46° 00' N
73° 00' W
72° 30' W

Figure 1.



Macrophyte biomass (g DM m^{-2})
300
200
100
0
LSF
Ottawa River
LSL
LSP
0
50
100
150
Epiphyton biomass (µg Chl-a m^{-2})
7500
5000
2500
Lyngbya biomass (g DM m^{-2})
40
20
Distance from Moses Saunders power dam (km)

Figure 2

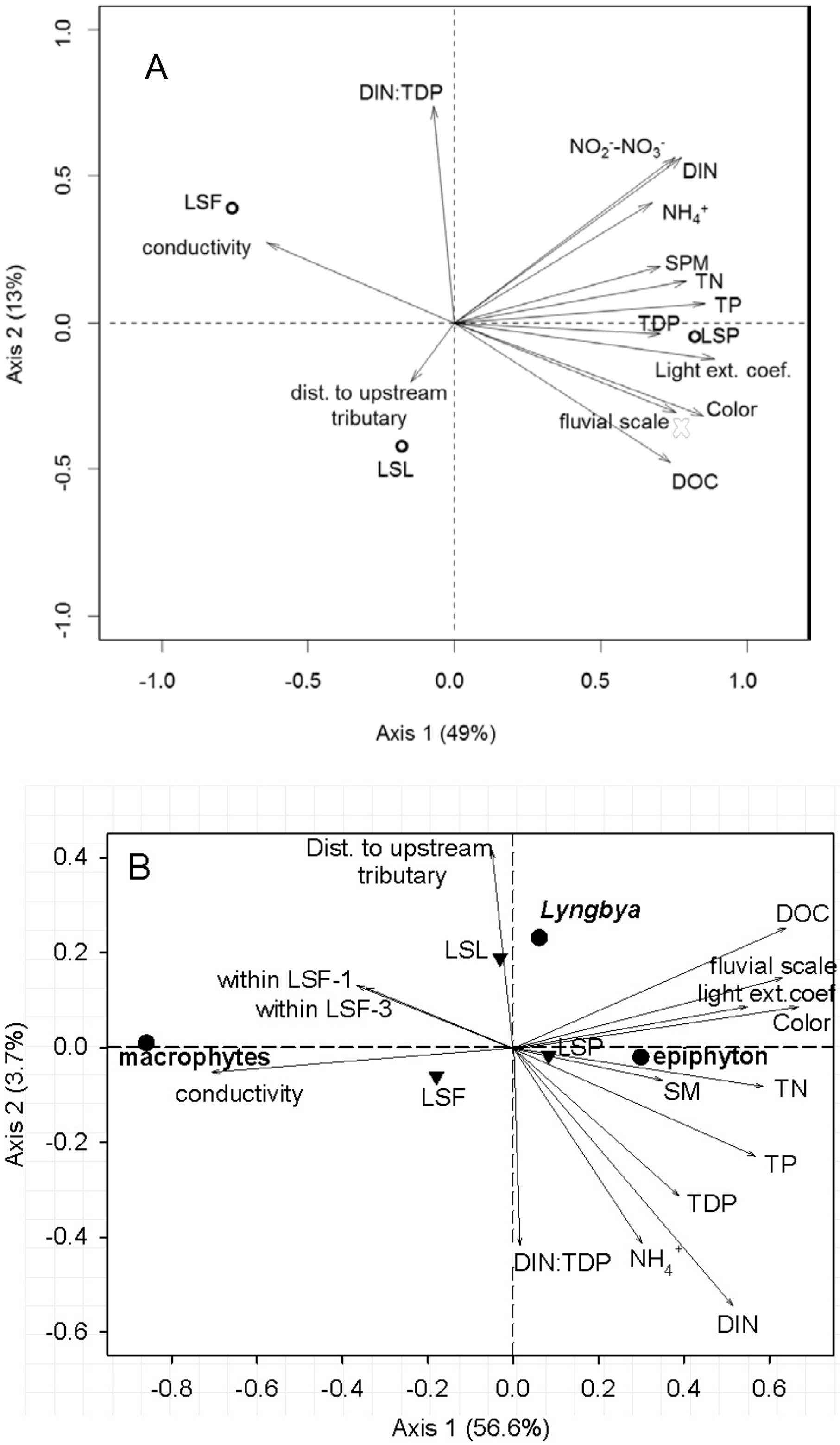

A
DIN:TDP
NO_2^--NO_3^-
DIN
NH_4^+
LSF
conductivity
SPM
TN
TP
TDP
LSP
Light ext. coef.
dist. to upstream tributary
Color
fluvial scale
LSL
DOC
Axis 2 (13%)
Axis 1 (49%)
B
Dist. to upstream tributary
Lyngbya
DOC
LSL
within LSF-1
within LSF-3
fluvial scale
light ext.coef
Color
macrophytes
LSP
epiphyton
conductivity
LSF
SM
TN
TP
TDP
DIN:TDP
NH_4^+
DIN
Axis 2 (3.7%)
Axis 1 (56.6%)

Figure 3