

Using the landscape morphometric context to resolve spatial patterns of submerged macrophyte communities in a fluvial lake

Rosalie Léonard · Pierre Legendre ·
Martin Jean · André Bouchard

Received: 5 February 2007 / Accepted: 4 October 2007 / Published online: 23 October 2007
© Springer Science+Business Media B.V. 2007

Abstract This study investigates the spatial heterogeneity of macrophyte communities in a fluvio-lacustrine landscape. We analysed the importance of the geomorphological point/bay pattern in structuring aquatic plant assemblages inside a 20-km-long littoral segment of a large fluvial lake. The abundance of 21 macrophyte species was surveyed in 232 quadrats along 24 transects perpendicular to the lakeshore. Two contrasting plant communities were identified, corresponding to the bay and point morphology of the study zone: a bay community characterized by *Chara* sp. and a point community dominated by *Butomus umbellatus* f. *vallisneriifolius*, *Vallisneria americana*, *Potamogeton richardsonii* and *Myriophyllum* sp. We subsequently investigated the spatial patterns within the bay and point communities. From a dataset containing local environmental variables, landscape morphometric descriptors, and

spatial geographical positions of the sampling sites, variation partitioning of the species abundance table showed that more than two-thirds of the explained variation was spatially structured. Around half of the spatially structured variation was due to the spatially structured environment. We identified important broad-scale patterns in the vegetation correlated to the local environmental variables, mainly depth and sediment richness. The remaining half of the spatially structured variation in the aquatic plant communities was explained by the landscape morphometric context; shoreline complexity of the bay or point, relative width, duration of wind exposure, and fetch were the landscape descriptors explaining most of this variation. Our results indicate that the landscape morphometric context can resolve as much spatial patterning as environmental variables and should be considered when studying a large lake ecosystem.

R. Léonard (✉) · P. Legendre
Département de sciences biologiques, Université de
Montréal, C.P. 6128, succursale Centre-Ville, Montréal,
QC, Canada H3C 3J7
e-mail: rosalie.leonard@umontreal.ca

M. Jean
Centre Saint-Laurent, Environnement Canada, 105 rue
McGill, 4e étage, Montréal, QC, Canada H2Y 2E7

A. Bouchard
Institut de recherche en biologie végétale, Université de
Montréal, 4101 Sherbrooke Est, Montréal, QC, Canada
H1X 2B2

Keywords Lake Saint-François ·
St. Lawrence River ·
Submerged macrophyte communities ·
Variation partitioning · Spatial patterns ·
Landscape morphometric context

Introduction

Ecological studies now regularly recognize the potential importance of spatial heterogeneity (Turner 2005) and spatially structured interactions between the biological and physical components of ecosystems.

Spatial heterogeneity in the physical environment generates a great deal of diversity in communities and in ecological processes (Legendre and Fortin 1989). In macrophyte beds, the assemblage of different plant species—each having its own propagation, competition and resource utilization strategies—can result in a variety of responses to the heterogeneous patterns inherent in the underwater landscape.

Landscape ecology examines the interrelationships between spatial patterns and ecological processes across scales (Turner et al. 2001; Wiens 2002). Although most landscape studies have focused on terrestrial systems, aquatic ecologists have long acknowledged the importance of spatial heterogeneity in determining biological dynamics underwater (Palmer et al. 2000). Limnologists have often used spatial approaches by including the catchment in the study of streams or lakes or by comparing similar geographically proximate aquatic systems (Allan and Johnson 1997; Magnuson and Kratz 2000). Studies have explored the ability of spatial variables, like the position of a lake within a landscape or the connectivity level among streams and lakes, to explain the variation in composition of aquatic communities (Kratz et al. 1997; Riera et al. 2000). In marine ecosystems, numerous studies (e.g. in seagrasses) have been addressing concepts such as spatial configuration of patches, scales, and fragmentation within the landscape (Bell and Fonseca 2006).

In submerged freshwater macrophytes communities, species distribution and productivity have been traditionally recognized to be modified by local environmental variables: available light (Chambers 1987; Chambers and Kalff 1987), water temperature (Pip 1989), water chemistry (Vestergaard and Sand-Jensen 2000), water velocity (Chambers et al. 1991), and sediment characteristics (Barko and Smart 1986; Barko et al. 1991). Studies have also investigated the influence of morphometric information such as water depth, littoral slope, and wind and wave exposure on aquatic plant communities (Duarte and Kalff 1986, 1988), suggesting the importance of the landscape morphology underwater. Recent studies have shown the importance of catchment characteristics (Mackay et al. 2003) and connectivity in the hydrological network in determining aquatic plant species composition (Aznar et al. 2003; Dahlgren and Erlén 2005; Demars and Harper 2005).

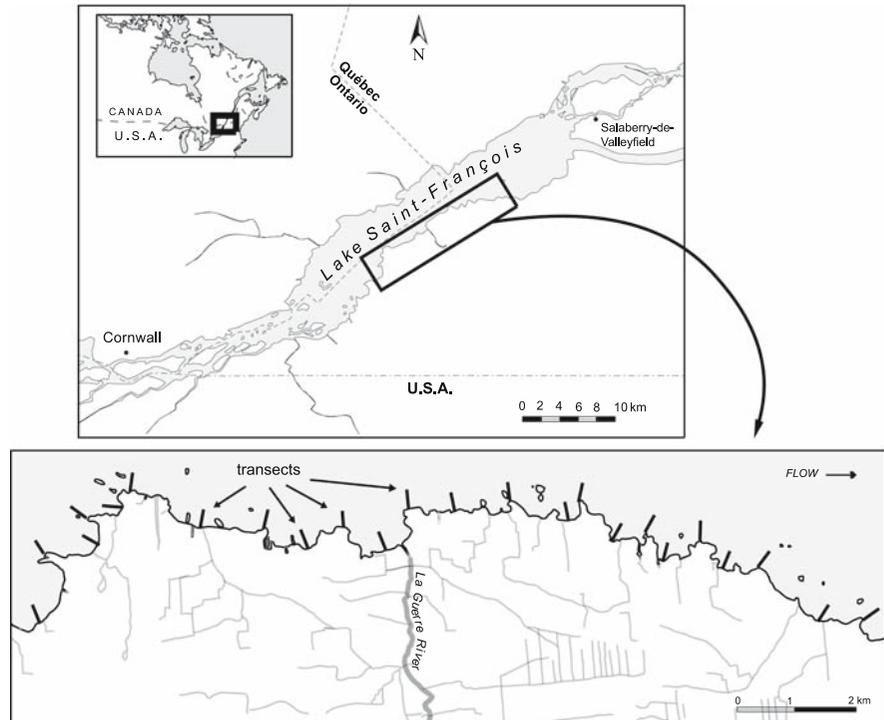
Building upon these findings, we investigated how a landscape approach could be applied to a fluvial lake (Lake Saint-François, St. Lawrence River, Canada). The first objective of this paper was to analyse the spatial heterogeneity of the macrophyte communities within the littoral zone of Lake Saint-François. Sampling transects were distributed on successive bays and points to evaluate the importance of the geomorphological pattern in structuring macrophytes communities. The second objective was to investigate how different landscape spatial variables—describing morphometric characteristics of each bay or point—could explain the variation in aquatic plant species distribution and abundance within the bay and point communities. This was addressed by answering the three following questions: (i) What are the main spatial patterns in the aquatic plant communities? (ii) How much of these patterns can be explained by spatially structured environmental variables? (iii) How much of these same patterns can be explained by the landscape morphometric context?

Methods

Study region

The site covers a 20-km-long section along the south shore of Lake Saint-François (Fig. 1), the first natural widening of the St. Lawrence River downstream of the Great Lakes. The lake extends over 50 km, with an average depth of 5.1 m and a maximum width of 8 km (Lorrain et al. 1993). The mean discharge of $7,500 \text{ m}^3 \text{ s}^{-1}$ consists essentially of the Great Lakes outflow (Morin et al. 2000). The lake is divided into an upstream deltaic section and a downstream fluvio-lacustrine section where our sampling sites were located. Waters are relatively clear (up to 10 m Secchi), with a low mean suspended sediment concentration, 2.2 mg l^{-1} (Rondeau 1993). Suspended sediment along the lake's south shore was found to be mainly a function of resuspension in shallow areas and the input from local tributaries (Lepage et al. 2000). The study area is located on either side of the La Guerre River, at the confluence of which a $9 \text{ m}^3 \text{ s}^{-1}$ capacity pumping station is seasonally used to drain the surrounding floodplain for agricultural purposes (Bouchard 2003); the

Fig. 1 Maps of Lake Saint-François showing the sampling area and transects positioned on successive alternating bays and points



unadjusted mean annual flow of the La Guerre River is $1.4 \text{ m}^3 \text{ s}^{-1}$ (Sylvestre 1989). The lakeshores shelter high and low marshes and large submerged macrophyte beds. Since the middle of the 19th century, the lake morphology has been profoundly modified by the construction of dams, dredging works, and locks used for commercial navigation and hydroelectricity production. Water regularization has transformed Lake Saint-François—originally with natural seasonal water level fluctuations of 1.2 m—into an essentially fixed stage system with an annual water level variation of *c.* 0.15 m (Morin et al. 2000).

Sampling and data collection

Two sampling campaigns were conducted from July to September 2002 and 2003. Twenty-four transects perpendicular to shore were positioned on successive alternating points and bays (12 points and 12 bays). Transects were positioned either at the extremity of the points or in the centre of bays along the shoreline. Ten quadrats of 25 m^2 were sampled along each transect (with the exception of two transects where only 6 quadrats were sampled), one quadrat every 25 m starting from shore, for a total of 232 quadrats.

In each quadrat, the cover of each macrophyte species was visually estimated during snorkelling dives. Species cover was grouped into 8 classes (1: [$<1\%$]; 2: [$1\text{--}5\%$]; 3: [$5\text{--}10\%$]; 4: [$10\text{--}20\%$]; 5: [$20\text{--}30\%$]; 6: [$30\text{--}50\%$]; 7: [$50\text{--}75\%$] and 8: [$75\text{--}100\%$]). Species nomenclature followed Crow and Hellquist (2000a, b).

Four data tables regrouped the different explanatory variables measured or estimated:

- i) *Time*. In order to isolate temporal variation from the data analysis, the table included the sampling year and month, coded as binary variables (2002 or 2003; July, August, or September).
- ii) *Local environment*. The matrix included 7 environmental variables measured in all 232 quadrats. Water depth, mean water velocity (averaged over 20 s) at 40% of the depth from the bed, water temperature, pH, and conductivity were sampled using a Marsh-McBirney Flo-Mate™ Model 2000 electromagnetic flowmeter and a YSI® Model 63 multi-probe. Rock cover percentage was visually estimated. The bed slope perpendicular to shore was estimated from depth measurements. Exploratory water transparency measurements (Secchi disk) confirmed

the high water clarity of Lake Saint-François: visibility was maximal over all sites, down to a depth of 5 m. From a 94-quadrat subset, a complementary data table regrouped 9 sediment variables measured from surface sediment samples collected in October 2003 in 4 quadrats per transect (quadrats at 0, 75, 150 and 225 m from shore). Sediment sampling depth (top 10 cm from sediment surface) corresponded to the plant-rooting zone observed in the field. Sediment samples were air dried and sieved (2 mm) prior to a hydrometer particle-size analysis (percentage of sand, silt, and clay). Sediment bio-available nutrient contents—phosphorus (P), potassium (K), magnesium (Mg), and calcium (Ca)—were measured by spectrophotometric atomic emission with argon plasma (Perkin Elmer Optima 4300 DVTM) after a Mehlich III extraction (Mehlich 1984). Nitrogen (N) content was measured by combustion (LECO CNS 2000TM); organic matter content was determined by incineration (lost on ignition) at 375°C. Sediment pH and cation exchange capacity (CEC) were also measured.

- iii) *Spatial geographical position.* The geographical position of the sampling sites consisted of two spatial descriptors equivalent to X and Y Cartesian coordinates. The X coordinate represented the streamwise transect position alongshore—following the SW-NE flow (Fig. 1). The Y coordinate corresponded to the perpendicular distance away from shore. The X coordinate was subjected to a spectral decomposition by computing a Principal Coordinates of Neighbour Matrices (PCNM) analysis (Borcard and Legendre 2002; Borcard et al. 2004). To construct the PCNM functions, we created a matrix of Euclidean distances among the transects along the shore. The ‘give.thresh’ function of the ‘spacemakeR’ library (Dray 2006) for the R statistical language (R Development Core Team 2006) was used to truncate the matrix and retain the distances between neighbouring sites. Distances larger than the threshold value were replaced by an arbitrarily large distance following Borcard and Legendre (2002). A principal coordinate analysis of the modified distance matrix was computed using the ‘pcnm’ function of the ‘spacemakeR’ library; only the

coordinates corresponding to positive eigenvalues were kept. The resulting PCNM variables corresponded to a series of sinusoids with decreasing periods, modelling broad to fine-scale patterns among transects. The Y coordinate was used to construct monomial function terms up to the third degree, computed from the centred Y coordinate (Legendre and Legendre 1998). The monomials were used instead of PCNMs because of the irregular number of quadrats per transect.

- iv) *Landscape morphometric context.* The data table regrouped 9 variables (Table 1) collected for each transect (and the associated bay or point) from 1:20,000 digitized topographic maps (Gouvernement du Québec 1999). The morphology of each bay and point was characterized by its width, length, and relative width. The fractal dimension of the shoreline (for each bay and point) was measured to represent its complexity. The effective fetch and a wind exposure duration variable were estimated for each transect from 4,400 hourly observations of wind speed and orientation recorded during the sampling months at the local meteorological station (Saint-Anicet station, 45°08' N, 74°21' W, Environment Canada); the median dominant wind direction was estimated to be 240° (WSW). A semiquantitative variable was used to describe the distance, number, and size of islands. To characterize the effect of local small-scale watersheds, we estimated the distance of each transect to the closest upstream watercourse and the watercourse order.

Data analysis

Two sets of analyses were employed to investigate the research questions. First, K-means partitioning, indicator value analysis and redundancy analysis (RDA) were performed on all sampled quadrats to characterize general heterogeneity patterns in the vegetation data. The results were compared to the landscape geomorphological point and bay pattern. Secondly, a variation partitioning between the spatial, environmental, and landscape matrices was conducted separately for points and bays. This analysis

Table 1 Single variables from the landscape morphometric context characterizing each transect located in a bay or on a point

Variable	Data collection
Width	(a) For bays: distance in meters between the extremities of the two neighbouring points. (b) For points: distance in meters between the furthest points inland of the two neighbouring bays
Length	Height in meters of the triangle formed (a) for bays: by the two extremities of the two neighbouring points and the furthest point inland of the bay, or (b) for points: by the furthest points inland of the two neighbouring bays and the extremity of the point
Relative width	Ratio length/width
Shoreline complexity	Fractal dimension of the shoreline of each bay or point measured using rulers of 400 m, 200 m, 100 m, and 50 m
Fetch	Effective fetch computed for each transect, following Håkanson (1981)
Duration of wind exposure	Semiquantitative variable (range = 1 to 4) using the number of wind exposure hours (for all wind speeds combined) estimated from the range of azimuths exposing each transect and the recorded frequencies (in number of hours) per azimuth (in blocks of 10°)
Islands	Semiquantitative variable (range = 1 to 3) describing the distance, number, and size of islands inside an 800 m radius from each transect, from south to north azimuths (the length of the radius corresponds to the mean distance between transects)
Distance to watercourse	Distance in meters of each transect to the closest upstream watercourse, calculated along a streamwise gradient linking the first quadrat of every transect to the watercourse
Order of watercourse	Order of each transect to the closest upstream watercourse

(i) identified the main scales of spatial variation in the vegetation between transects (PCNMs) and along transects between quadrats (monomials) and (ii) measured the relative importance of the local environment versus the landscape morphometric context in explaining the variation within the bay and point communities.

The species abundance table was transformed using the Hellinger transformation (square root of the relative abundance of each species in the quadrat) in order to make the data, containing many zeros, amenable to analysis by methods preserving Euclidean distances (Legendre and Gallagher 2001). With this transformation, the influence of uncommon species was not overestimated. A K-means non-hierarchical partitioning analysis was performed using 250 random starting configurations. The significant indicator species of each group were identified by an indicator value analysis ('duleg' function of the R 'labdsv' library, Roberts 2006) based on a combination of the specificity and the fidelity of each species to a group (Dufrêne and Legendre 1997). The main environmental variables

linked to vegetation heterogeneity were determined by a RDA of the vegetation data constrained by the local environment matrix (and controlling for temporal variables) conducted using the 'rda' function of the R 'vegan' library (Oksanen et al. 2006).

Variation partitioning was performed through multiple RDAs (Borcard et al. 1992; Borcard and Legendre 1994) to estimate the fraction of variation of the vegetation data attributable to the four different explanatory tables: (i) *time* (which was treated as a covariable and not further analysed); (ii) *spatial geographical position*; (iii) *local environment*; and (iv) *landscape morphometric context*. Adjusted bi-multivariate redundancy statistics (R_a^2) were computed by the 'varpart' partitioning function of the R 'vegan' library. The R_a^2 statistics were shown to produce unbiased estimates of the contributions of the independent variables to the explanation of the response variables, correcting for the number of objects and explanatory variables in the analysis (Peres-Neto et al. 2006). The adjusted form corrects for the explanation that would be provided by the same number of random explanatory variables

measured over the same number of observation points. RDA fitted sites scores were obtained using CANOCO version 4.5 (ter Braak and Šmilauer 2002). A second partitioning analysis was carried out to include the sediment characteristics, which were sampled in 4 quadrats per transect (instead of 10 in the full model).

For all RDAs, a forward selection of the significant explanatory variables was performed using Monte Carlo permutation tests (999 random permutations), retaining the variables with $P \leq 0.05$; this was computed from the 'forward.sel' function available in the R 'packfor' library (Dray 2004) or from CANOCO when using covariables.

Results

General results: spatial heterogeneity in Lake Saint-François

Twenty-one aquatic plant species were identified in the sampled sites. The assemblages were dominated by *Vallisneria americana*, *Chara* sp., and *Butomus umbellatus* f. *vallisneriifolius*, present in 90%, 55%, and 46% of the quadrats respectively (Table 2). *Potamogeton richardsonii* was found in 71% of the sites but was not dominant within these sites; it was rather found as a companion species (median class: 5–10%). *Ranunculus tricophyllus*, *Scirpus acutus*, *Lemna trisulca*, *P. nodosus*, and *Sagittaria cuneata* were observed in <5% of the sites.

The Calinski-Harabasz statistic (from the K-means analysis partitioning the sites based on vegetation abundance) indicated that the optimal division of quadrats, in the least-squares sense, was in two groups. These two groups served as the basis for an indicator species analysis, from which 13 of the 21 macrophyte species were found to be significant indicators of one of the two groups (Table 2). The best indicator for the first group was *Chara* sp., while the second group was characterized by *Butomus umbellatus*, *Myriophyllum* sp., *Vallisneria americana*, and *Potamogeton richardsonii*. The partition in two groups was highly similar (simple matching coefficient, $S_1 = 0.78$) to the bay/point landscape pattern. The RDA constrained by the local environment showed the same segregation between macrophyte species from bays and points. From the

group of significant explanatory variables selected using the forward selection procedure ($P \leq 0.05$), depth, water velocity and slope were the variables with the highest correlation with the first RDA axis which explained 22% of the variation ($r = 0.74$, 0.31 and 0.28, respectively). The same analysis performed on the sediment-data subset showed the importance of the P content ($r = 0.59$ with the first RDA axis). Table 3 presents an overview of the differences between bay and point sites for the RDA main structuring environmental variables: bay sites were generally shallower than point sites, with lower water velocity; quadrats sampled on points were characterized by a stronger slope and richer sediments (i.e., higher P content).

Spatial patterns within bay and point communities

Considering the strongly contrasted species distributions, the variation partitioning analyses were conducted on the bay and point sites separately. The RDA model, which included the significant explanatory variables from the geographical position, local environment, and landscape morphometric context (Table 4), was found to explain 37% and 35% (R_a^2) of the total variation in the submerged plant assemblages of bays and points, respectively (Fig. 2). The temporal patterns—annual and seasonal (sampling year and month)—were not included in Fig. 3 for clarity; it explained an additional 9% of the total variation in bays and 13% in points.

More than two-thirds of the variation explained by our model was spatially structured (Fig. 2). The broad-scale PCNMs 1 and 2 were the dominating spatial variables, as they had the highest correlations with the first canonical axes of the RDA constrained by the spatial descriptors (for bays: PCNM 1, $r = -0.35$ and PCNM 2, $r = 0.43$; for points: PCNM 1: $r = -0.66$). PCNMs 1 and 2 described a southwest/northeast pattern dividing the study area in its centre, which corresponds to the La Guerre River confluence (located 8.95 km downstream from the first transect along the lakeshore, Fig. 1). The first canonical RDA axes explained an important part of the variance of *Chara* sp. (38% in bays and 47% on points) and of *B. umbellatus* f. *vallisneriifolius* (29% in bays and 59% on points), two dominant species in the sampled sites. Maps of the two species' standardized abundances

Table 2 Frequency, median cover class, maximum cover class, *K-Means* group (A or B) and indicator value (*IndVal*) for each sampled aquatic plant species

Species	Occurrence frequency in the quadrats (%)	Median cover class for quadrats colonized by the species (%)	Maximal cover class (%)	K-means group	Indicator value (%)	$P \leq 0.05$
<i>Vallisneria americana</i> Michx.	89.7	30–50	75–100	B	62.5	*
<i>Potamogeton richardsonii</i> (A. Benn.) Rydb. ^a	71.2	5–10	75–100	B	49.5	*
<i>Chara</i> sp.	54.5	50–75	75–100	A	94.1	*
<i>Butomus umbellatus</i> f. <i>vallisnerifolius</i> (L.) Sagorski Glöck	45.5	30–50	75–100	B	74.0	*
<i>Neajas flexilis</i> (Willd.) Rostk. & Schmidt	41.2	1–5	75–100	B	26.8	NS
<i>Myriophyllum</i> sp.	41.6	<1	20–30	B	51.8	*
<i>Potamogeton friesii</i> Rupr. ^b	40.3	1–5	75–100	B	22.4	NS
<i>Stuckenia pectinata</i> (L.) Börner (= <i>Potamogeton pectinatus</i> L.)	28.3	1–5	75–100	A	26.3	*
<i>Heteranthera dubia</i> (Jacq.) MacMill.	25.8	<1	30–50	B	28.0	NS
<i>Alisma graminea</i> Lej.	23.2	1–5	50–75	B	13.0	NS
<i>Nitella</i> sp.	22.3	1–5	75–100	A	24.3	*
<i>Elodea canadensis</i> Michx.	16.3	<1	1–5	B	27.1	*
<i>Ceratophyllum demersum</i> L.	14.6	<1	1–5	B	16.2	NS
<i>Potamogeton gramineus</i> L.	13.3	5–10	75–100	A	14.9	*
<i>Potamogeton illinoensis</i> Morong	6.9	1–5	75–100	A	3.5	NS
<i>Sagittaria graminea</i> Michx.	6.9	1–5	5–10	A	14.8	*
<i>Ranunculus tricophyllus</i> Chaix	3.0	<1	1–5	B	2.9	NS
<i>Scirpus acutus</i> Muhl.ex Bigelow	2.1	1–5	1–5	A	4.6	*
<i>Lemna trisulca</i> L.	1.3	<1	1–5	A	1.4	NS
<i>Potamogeton nodosus</i> Poir.	0.4	<1	<1	A	0.9	NS
<i>Sagittaria cuneata</i> E. Sheld.	0.4	<1	<1	A	0.9	NS

^a Can include *P. perfoliatus* L.^b Can include *P. zosteriformis* Fernald

*: significant, NS: non-significant

Probabilities for the IndVal analysis were calculated by a Monte-Carlo test (999 permutations)

Table 3 Mean (\pm standard errors) and range of the main environmental variables comparing the bay and point sampling sites

Variables	Bays	Points	Range
Depth (m)	1.44 (\pm 0.07)	2.73 (\pm 0.11)	0.32–5.40
Slope ($^{\circ}$)	0.55 (\pm 0.05)	1.03 (\pm 0.10)	0–5
Water velocity (m s $^{-1}$)	0.02 (\pm 0.001)	0.08 (\pm 0.009)	0–0.23
Sediment P (μ g g $^{-1}$)	17.9 (\pm 1.8)	27.0 (\pm 1.6)	2.5–58

show their highly contrasted distributions—following the upstream and downstream pattern (Fig. 3).

The spatially structured environment

Around half of the spatially structured variation in the vegetation data was due to the spatially structured environment (Fig. 2). Maps of the fitted site scores on the first canonical axes of the RDA constrained by the local environmental variables (Fig. 4) show two main trends: a distance-to-shore gradient superimposed onto the previously identified upstream/downstream pattern along the shore. Depth was the variable with the highest correlation with these trends, having correlation values with the first canonical axes of $r = 0.71$ for bays and $r = -0.63$ for points. In order to detail the spatial patterns, we subsequently estimated correlation coefficients between the first RDA axes (constrained by the local environment) and the geographical variables. For bays, the distance to shore and the broad- and fine-scale spatial descriptors PCNMs 1, 2 and 7 were the dominant variables related to the patterns observed on the plotted fitted sites scores (Fig. 4), having correlation values with the first RDA axis of $r = 0.48, 0.33, 0.30,$ and $0.44,$ respectively. For points, the broad scale spatial descriptor PCNM 1 was highly correlated with the first canonical axis ($r = -0.45$).

To investigate the spatial structure in the macrophyte communities linked to substrate quality, two partial RDAs (for point and bay sites) were computed from the 94-quadrat data subset sampled for sediment analysis. To be able to compare the results with the previous analyses, the RDAs were performed on the sets of variables previously selected using the 232 quadrats. Separate forward selection procedures were used to determine the significant sediment variables

(Table 5); only P content was selected for the bay sites, and K content, silt %, organic matter, and CEC for point sites. We can however note that in bays, the unselected silt %, organic matter, and N content were highly correlated with P content ($r = 0.64, 0.83, 0.79,$ respectively) while in points the unselected P and Mg were well correlated with K content ($r = 0.64$ and $0.75,$ respectively).

Through variation partitioning, it was possible to determine that a large portion—74% for bays and 95% for points—of the spatially structured variation in the vegetation explained by the sediments characteristics was correlated to the spatial patterns previously identified using the local environmental matrix. This can be explained by the fact that the significant sediment variables for both bay and point datasets were correlated with depth (in bays: P, $r = 0.68$; in points: K, $r = 0.47,$ silt, $r = 0.47,$ and organic matter, $r = 0.42$). Thus, the predominant vegetation upstream/downstream pattern, identified using the environmental variables (mainly depth), could also be detected in the distribution of sediment characteristics. Among bay sites, sediment P content rose from 11% upstream of the La Guerre River to 24% downstream. In point sites, the silt % and K content increased from 9% and 131 μ g g $^{-1}$ upstream of the river to 39% and 164 μ g g $^{-1}$ downstream.

The landscape morphometric context

As shown in Fig. 2, around half of the spatially structured variation in species distributions for both bay and point sites could not be explained by the environmental variables. However, it was almost completely resolved by including the landscape morphometric context. Whereas the broad-scale PCNMs 1 and 2 were overall the best spatial variables to describe the spatially structured environment, a new forward selection showed that the contributions of the spatial descriptors were all relatively similar when controlling for the environmental variables; this indicated that no scale (PCNMs or monomials) was predominant in the purely spatial landscape fraction.

For bay sites, shoreline complexity, relative width, duration of wind exposure, and fetch were the landscape descriptors with the largest marginal effects on macrophyte species distributions ($R^2 = 0.12, 0.07,$

Table 4 Forward selection of explanatory variables in the local environment, landscape, space, and time data tables for bay and point sites

Data table	Variables			Fraction of explained variation for bay sites			Fraction of explained variation for point sites		
		Marginal effect	Selection order	Marginal effect	Conditional effect	Selection order	Marginal effect	Conditional effect	Selection order
Local environment	Depth	0.18	1	0.18***	0.11	1	0.11***	0.11***	1
	Water temperature	0.08	2	0.04***	0.03	3	0.03***	0.03***	3
	Water pH	0.02	3	0.02***	–	–	NS	NS	–
	Rock cover percentage	0.05	4	0.02*	0.04	2	0.05***	0.05***	2
	Slope	0.02	5	0.01**	0.01	6	0.02*	0.02*	6
	Water velocity	–	–	NS	0.03	4	0.03***	0.03***	4
	Water conductivity	–	–	NS	0.01	5	0.02**	0.02**	5
	Complexity	0.12	1	0.12***	0.06	1	0.06***	0.06***	1
	Relative width	0.07	2	0.08***	0.05	3	0.04***	0.04***	3
	Duration of wind exposure	0.06	3	0.06***	0.04	5	0.04***	0.04***	5
	Width bay/point	0.03	4	0.02**	0.03	8	0.04***	0.04***	8
	Length bay/point	0.05	5	0.02**	0.03	7	0.03***	0.03***	7
	Islands	0.04	6	0.02**	0.04	6	0.03***	0.03***	6
Landscape	Watercourse order	0.03	7	0.03***	0.04	2	0.05***	0.05***	2
	Fetch	0.06	8	0.02**	0.02	4	0.07***	0.07***	4
	Distance to watercourse	0.02	9	0.02**	0.03	9	0.05***	0.05***	9
	PCNM 1	0.10	1	0.10***	0.10	1	0.10***	0.10***	1
	PCNM 2	0.05	2	0.05***	0.02	9	0.02**	0.02**	9
	PCNM 6	0.04	3	0.04***	0.08	2	0.08***	0.08***	2
	PCNM 7	0.03	4	0.03***	0.02	6	0.02***	0.02***	6
	PCNM 4	0.03	5	0.03***	0.04	4	0.04***	0.04***	4
	PCNM 5	0.03	6	0.03***	0.05	3	0.05***	0.05***	3
	Y ²	0.02	7	0.02**	–	–	NS	NS	–
	Y	0.02	8	0.02**	0.02	8	0.02***	0.02***	8
	PCNM 3	0.02	9	0.02**	0.02	7	0.02***	0.02***	7
	PCNM 8	–	–	NA	0.03	5	0.03***	0.03***	5
Time	September	0.08	1	0.08***	0.04	3	0.02*	0.02*	3
	July	0.06	2	0.03**	0.09	1	0.09***	0.09***	1
	August	0.03	3	–	0.05	4	–	–	4
	Year	–	–	NS	0.04	2	0.04***	0.04***	2

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$. NS: non-significant, NA: non-available

The explained variation R^2 (marginal effect), the conditional effect, and the level of significance (P -value) of each variable were computed using Monte Carlo permutations tests (999 permutations). The conditional effects were calculated for each explanatory table independently

Fig. 2 Venn diagrams representing the results of variation partitioning by RDA of (a) bay and (b) point vegetation response tables, between the local environmental, landscape morphometric context, and spatial explanatory tables. The fractions, representing R_a^2 are expressed as percentages

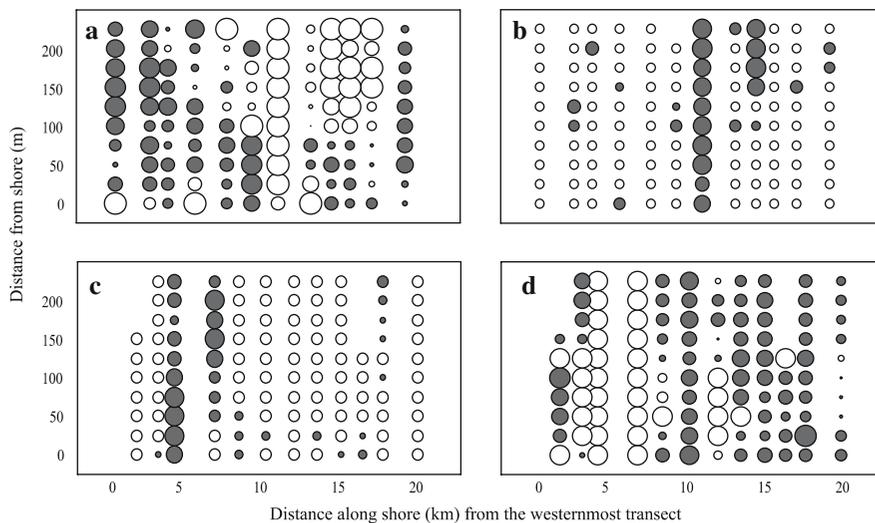
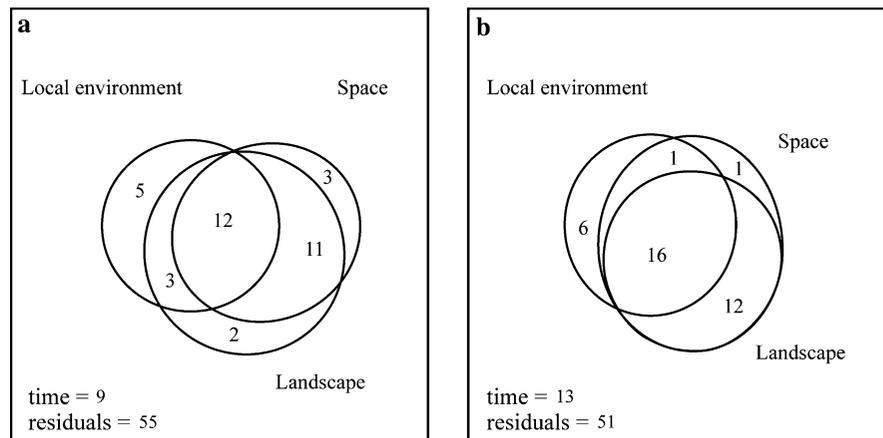


Fig. 3 Maps representing the standardized abundance values of *Chara* sp. and *Butomus umbellatus* f. *vallisneriifolius*. Each dot represents a sampled site, positioned along a transect from 0 m to 225 m from the shore (Y axis). The transects are positioned along a west-east gradient following the river flow, from the westernmost transect to the easternmost (X axis).

Filled bubbles represent positive standardized abundance values, open bubbles are negative values. Bubble sizes are proportional to the absolute values. (a and b) Bays: (a) *Chara* sp.; (b) *B. umbellatus* f. *vallisneriifolius*; (c and d) Points: (c) *Chara* sp.; (d) *B. umbellatus* f. *vallisneriifolius*

0.06 and 0.06, respectively, Table 4). These variables were all poorly correlated to one another, except for duration of wind exposure and fetch, which were almost collinear ($r = 0.95$). For point sites, shoreline complexity and relative width had the largest marginal effects ($R^2 = 0.06$ and 0.05 , respectively, Table 4) and were negatively correlated ($r = -0.45$). When controlling for the environmental variables, all landscape variables for both point and bay sites had marginal effects between 0.01 and 0.03.

Discussion

The geomorphological pattern in the landscape: a template for community structure

Our results highlight the large vegetation beta diversity in the submerged macrophyte beds of Lake Saint-François. The species composition responded strongly to the heterogeneous geomorphologic structure of the landscape; two

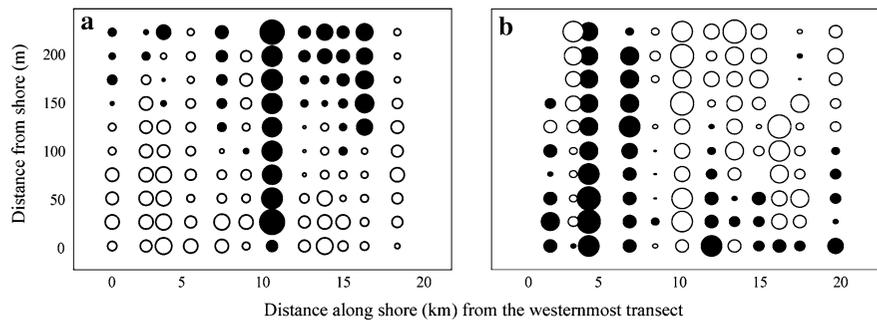


Fig. 4 Schematic maps of the fitted sites scores on the first canonical axis of the RDA of the vegetation data constrained by the environmental variables, after controlling for the effect of time. Each dot represents a sampled site, positioned along a transect from 0 m to 225 m from the shore (Y axis). The transects are positioned along a west-east gradient following

the river flow, from the westernmost transect to the easternmost (X axis). Filled bubbles represent positive fitted sites scores, open bubbles are negative values. Bubble sizes are proportional to the absolute values. **(a)** Bays: axis 1 accounts for 18% of the total variation in the species data. **(b)** Points: axis 1 accounts for 15% of the variation

Table 5 Forward selection of the explanatory sediment variables for bays and points separately

Data table	Variables	Fraction of explained variation (marginal effect)	Conditional effect	P-value
Bays	P	0.15	0.15	0.001
Points	K	0.12	0.12	0.001
	Silt %	0.09	0.06	0.001
	Organic matter	0.09	0.05	0.004
	CEC	0.06	0.04	0.015

The explained variation R^2 (marginal effect), the conditional effect, and the level of significance (P -value) of each variable were computed from Monte Carlo permutations tests (999 permutations). The conditional effect was calculated for each matrix independently

contrasted communities were found to represent the lake's succession of bays and points. Underlying the geomorphology, the depth and sediment gradients were shown to be important predictors of the species distributions between point and bay sites.

The community found in bays, which generally corresponded to shallow sites with nutrient-poor sediments, was dominated by *Chara* sp. As argued by Chambers and Kalff (1987) and Chambers (1987), bottom-dwellers such as *Chara* are favoured on infertile sediments, as opposed to canopy/erect species on rich sediments. Moreover, we observed the sampled shallow zones to correspond to high-energy areas. Wave-induced turbulent forces on the bed have been shown to increase with decreased water depth (Sand-Jensen 1989). The mean wave height during storms in Lake Saint-François was estimated to be between 0.70 m and 1.40 m (Frenette et al. 1989); the resulting energy was recognized to generate important fluctuating bottom currents in shallow zones.

Hudon et al. (2000) showed how exposed areas shallower than 2 m in the St. Lawrence River cannot support vertically developed aquatic plant assemblages. The importance of *Chara* in the shallow sampled sites could thus be attributed to its competitiveness in turbulent environments. The sampled *Chara* species had a small stature (<10 cm high); small charophytes were previously identified as being resistant to intense wave-action (Blindow 1992; Ali et al. 1999). The success of *Chara* in shallow sites could also be linked to the abundance of its propagules (Van den Berg et al. 2001), ensuring regeneration after winter in turbulent zones.

Point sites, dominated by *Vallisneria americana*, *Butomus umbellatus* f. *vallisneriifolius*, *Potamogeton richardsonii*, and *Myriophyllum* sp., corresponded to deeper zones of the lake characterized by richer sediments. The capacity of canopy producers (*Myriophyllum*) and erect species (*P. richardsonii*) to stretch from deeper sites allows them to avoid light

attenuation stress and benefit from higher nutrient availability. It was however shown that *V. americana* can compete successfully with canopy-producers and compensate for apparently disadvantageous morphological features by greater physiological adaptability to low light regimes (Titus and Adams 1979); such mechanism could explain the dominance of rosette-shaped angiosperms *V. americana* and *B. umbellatus* in deep quadrats. Moreover, many point sites were exposed to stronger currents than in bays, favouring streamlined species such as *V. americana* or *B. umbellatus*, with long, flexible strap-formed leaves that experience lower drag forces (Sand-Jensen 2003).

The dominance of *Chara* in shallow bay sites may seem to contradict studies showing that in clear lakes, charophytes have lower minimum light requirements than angiosperms, allowing them to colonize deeper sites (Middelboe and Markager 1997). However, we sampled along 250 m-long transects, which covered a range of depths between 0 m and 5 m. Considering that Hudon et al. (2000) have shown that angiosperms reach the 10-m isobath in Lake Saint-François, our sampling zone corresponded only to an intermediate zone where colonization limits were not yet critical in determining species distribution.

Spatial heterogeneity within bay and point communities

Lakes with complex morphometries such as Lake Saint-François, with isolated bays and tributary inflows, can present considerable within-lake spatial heterogeneity (Johnson and Ostrofsky 2004). Our results showed that an important part of the within-lake variation in macrophyte species distribution from Lake St-François was spatially structured, as the spatial geographic descriptors accounted for more than two-thirds of the explained variation. A marked southwest/northeast gradient (represented by broad-scale PCNMs) was observed in the species abundance data. This pattern corresponded to the upstream/downstream sections from the confluence of the La Guerre River. For both bays and points, the upstream (SW) part of the territory presented high abundances of *Chara* sp. whereas downstream (NE), we observed a dominance of *Butomus umbellatus*.

Are the spatial patterns mainly environmental?

The spatially structured environment was shown to be a main source of spatial patterning in the vegetation. The contrasted species distribution was primarily explained by depth and sediment richness, with a deeper and richer zone downstream from the La Guerre River confluence. The well-known confounded effect of depth and sediment characteristics is explained by the fact that most of the sediment organic matter, Ca, P, and fine particles tend to accumulate in deep areas of lakes rather than in the littoral high-energy zones affected by waves (Håkanson 1977; Kleeberg et al. 1999). Except for dredged channels, the deep parts of Lake Saint-François, away from the river thalweg, form sedimentation areas for fine material (Carignan and Lorrain 2000). Moreover, an increased turbidity at the confluence of the La Guerre River along the downstream lakeshore has often been observed (Sylvestre 1989). The La Guerre River is typical of watercourses in agricultural environments, i.e. turbid and with high concentrations of P, N and suspended material. Streaks of turbid water have been observed up to 15 km downstream of the river pumping station (Messier 1986). This enrichment of the littoral could contribute to the downstream changes in the plant community structure. However, the dynamic processes of sediment erosion, transport, and accumulation, acting at lake or river scales, must be taken into account.

Predicting submerged macrophyte species distribution using landscape variables

Our study outlines the importance of the fraction from the spatially structured variation in macrophyte species that could not be explained by environmental variables (14% of 26% for bays and 13% of 30% for points, Fig. 2). Similarly but at broader scale, Demars and Harper (2005) found a large part of the spatial structure of aquatic vegetation in a river network to be independent of local environmental factors. While residual spatial structures are often suggested to be linked to non-measured environmental and/or biological processes (Legendre and Legendre 1998), this study showed that the landscape morphometric context, using bays and points as ecological units,

could explain almost all of the remaining spatial variation (Fig. 2).

The macrophyte species distribution in Lake St-François was primarily influenced by the shoreline complexity, the relative width of bays or points, and the duration of wind exposure and fetch. The duration of wind exposure and fetch of each transect contributed to the morphometric description of the study area by orienting and characterizing the bays and points in relation to the SW-NE axis of dominant winds. When controlling for environmental variables (e.g. depth and sediment gradient), we removed the indirect effect of wind-induced waves, affecting nutrient availability through sediment erosion, and isolated their remaining direct effect on macrophyte growth through mechanical damage. However, as noted by Duarte and Kalff (1988), the shape of a lake can significantly deflect the wave direction from the prevailing wind direction. Therefore, wind direction measured at the lakeside meteorological station could be a poor indicator of wave direction at individual sites. In a study of littoral macrozoobenthos, Palomäki and Hellsten (1996) found the shape of the shoreline—they used the opening angle of the shoreline—to be a better predictor of wave action onto the shoreline than fetch. Similarly, it is possible that the relative width of bays or points from this study could influence the wave climate. Our results also highlighted the importance of the shoreline complexity, explaining 12% of the vegetation variance in bays and 6% in points. Since a higher shoreline complexity index implied a higher number of smaller bays and points within each landscape unit, we hypothesized the explained variation to be linked to habitat heterogeneity at finer scales.

While many studies have isolated the spatial structure of ecological data, the interpretation of the spatial component often remains overlooked. Our methodology proved to be a useful means of explaining the presence and shape of spatial patterns in communities. However, the interpretation of the landscape descriptors still had to be made with caution, considering they were primarily spatial variables, which do not necessarily have a direct “ecological effect” on communities. The influence of certain landscape variables on species distributions could originate from a correlation with variables not included in the study, such as anthropogenic pressure (boat circulation, proximity to the St. Lawrence

Seaway, houses and septic tank densities), biotic factors (competition, grazing pressure, or epiphytes), or processes linked to species propagation.

Conclusion

The present study showed that the geomorphological pattern of alternating bays and points in a large-lake landscape strongly structures its physical and biological components. Within this contrasted landscape, important broad-scale patterns in the vegetation were correlated to the spatially structured environment. However, our results indicated that the landscape morphometric context can resolve as much spatial patterning as the environmental variables and should be considered when studying a large-lake ecosystem. Investigating spatial patterns and landscape configuration in aquatic communities can provide useful insights on ecological processes operating at different scales.

Acknowledgements We would like to thank the Centre Saint-Laurent team from Environment Canada, especially M. Arseneau, G. Brault, and C. Lessard for fieldwork. We thank M. Pelletier for advice on sediment analysis, V. Champagne for the particle-size analysis, and J. Lacey for enriching discussions concerning the project. We are also grateful to H. Wagner, J. Vermaat and an anonymous reviewer for their insightful comments which helped to improve the manuscript. This study was supported by a Natural Science and Engineering Research of Canada scholarship to R.L., by NSERC grants to A.B. and to P.L., and by CSL funds to M.J.

References

- Ali MM, Murphy KJ, Langendorff J (1999) Interrelations of river ship traffic with aquatic plants in the River Nile, Upper Egypt. *Hydrobiologia* 415:93–100
- Allan JD, Johnson LB (1997) Catchment-scale analysis of aquatic ecosystems. *Freshw Biol* 37(1):107–111
- Aznar JC, Dervieux A, Grillas P (2003) Association between aquatic vegetation and landscape indicators of human pressure. *Wetlands* 23:149–160
- Barko JW, Smart RM (1986) Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecology* 67(5):1328–1340
- Barko JW, Gunnison D, Carpenter SR (1991) Sediment interactions with submersed macrophyte growth and community dynamics. *Aquat Bot* 41:41–65
- Bell SS, Fonseca MS (2006) Seagrass ecology: new contributions from a landscape perspective. In: Larkum AWD et al (eds) *Seagrasses: biology, ecology and conservation*. Springer, Netherlands, pp 625–645

- Blindow I (1992) Decline of charophytes during eutrophication: comparison with angiosperms. *Freshw Biol* 28:9–14
- Borcard D, Legendre P (1994) Environmental control and spatial structure in ecological communities: an example using oribatid mites (Acari, Oribatei). *Environ Ecol Stat* 1:37–61
- Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol Modell* 153:51–68
- Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004) Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85(7):1826–1832
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055
- Bouchard A (2003) Marie-Victorin, témoin expert dans une cause sur un marécage du lac Saint-François, le Saint-Laurent. *Le Naturaliste Canadien* 127:11–21
- 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. *Can J Fish Aquat Sci* 57(Suppl 1):63–77
- Chambers PA (1987) Light and nutrients in the control of aquatic plant community structure. II. *In situ* observations. *J Ecol* 75:621–628
- Chambers PA, Kalf J (1987) Light and nutrients in the control of aquatic plant community structure. I. *In situ* experiments. *J Ecol* 75:611–619
- Chambers PA, Prepas EE, Hamilton HR, Bothwell ML (1991) Current velocity and its effect on aquatic macrophytes in flowing waters. *Ecol Appl* 1:249–257
- Crow GE, Hellquist CB (2000a) Aquatic and wetland plants of northeastern North America: a revised and enlarged edition of Norman C. Fassett's *A Manual of Aquatic Plants*. Volume one—pteridophytes, gymnosperms and angiosperms: dicotyledons. The University of Wisconsin Press, Madison
- Crow GE, Hellquist CB (2000b) Aquatic and wetland plants of northeastern North America: a revised and enlarged edition of Norman C. Fassett's *A Manual of Aquatic Plants*. Volume two—angiosperms: monocotyledons. The University of Wisconsin Press, Madison
- Dahlgren JP, Ehrlén J (2005) Distribution patterns of vascular plants in lakes—the role of metapopulation dynamics. *Ecography* 28:49–58
- Demars BOL, Harper DM (2005) Distribution of aquatic vascular plants in lowlands rivers: separating the effects of local environmental conditions, longitudinal connectivity and river basin isolation. *Freshw Biol* 50:418–437
- Dray S (2004) packfor. R package version 0.0–6, <http://biomserv.univ-lyon1.fr/~dray/Software.html#packfor> (accessed March 2006)
- Dray S (2006) spacemaker: spatial modelling. R package version 0.0–3, <http://biomserv.univ-lyon1.fr/~dray/Software.html#spacemaker> (accessed June 2006)
- Duarte CM, Kalf J (1986) Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. *Limnol Oceanogr* 31(5):1072–1080
- Duarte CM, Kalf J (1988) Influence of lake morphometry on the response of submerged macrophytes to sediment fertilization. *Can J Fish Aquat Sci* 45:216–221
- Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366
- Frenette M., Barbeau C, Verette J-Ls (1989) Aspects quantitatifs, dynamiques et qualitatifs des sédiments du Saint-Laurent. Hydrotech inc., préparé pour Environnement Canada et le Gouvernement du Québec
- Gouvernement du Québec (1999) Ministère des ressources naturelles, *Cazaville, Huntingdon, Saint-Anicet and Salaberry-de-Valleyfield* [digitized map]. 1:20 000. MTM-zone 8, 31G01–200–0101, 0102, 0201, 0202. Québec : Direction de la cartographie topographique
- Håkanson L (1977) The influence of wind, fetch, and water depth on the distribution of sediments in Lake Vanern, Sweden. *Can J Earth Sci* 14:397–412
- Håkanson L (1981) *A manual of lake morphometry*. Springer-Verlag, Berlin Heidelberg
- Hudon C, Lalonde S, Gagnon P (2000) Ranking the effects of site exposure, plant growth form, water depth, and transparency on aquatic plant biomass. *Can J Fish Aquat Sci* 57(Suppl 1):31–42
- Johnson RK, Ostrofsky ML (2004) Effects of sediment nutrients and depth on small-scale spatial heterogeneity of submersed macrophyte communities in Lake Pleasant, Pennsylvania. *Can J Fish Aquat Sci* 61: 1493–1502
- Kleeberg A, Jendritzki D, Nixdorf B (1999) Surficial sediment composition as a record of environmental changes in the catchment of shallow Lake Petersdorf, Brandenburg, Germany. *Hydrobiologia* 408/409:185–192
- Kratz TK, Webster KE, Bowser CJ, Magnuson JJ, Benson BJ (1997) The influence of landscape position on lakes of northern Wisconsin. *Freshw Biol* 37:209–217
- Legendre P, Fortin MJ (1989) Spatial pattern and ecological analysis. *Vegetatio* 80:107–138
- Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280
- Legendre P, Legendre L (1998) *Numerical ecology*. Elsevier Science B.V., Amsterdam
- Lepage S, Biberhofer J, Lorrain S (2000) Sediment dynamics and the transport of suspended matter in the upstream area of Lake St. Francis. *Can J Fish Aquat Sci* 57(Suppl 1): 52–62
- Lorrain S, Jarry V, Guertin K (1993) Répartition spatiale et évolution temporelle des biphényles polychlorés et du mercure dans les sédiments du lac Saint-François; 1979–1989. Centre Saint-Laurent, Environnement Canada, Montréal, Québec
- Mackay SJ, Arthington AH, Kennard MJ, Pusey BJ (2003) Spatial variation in the distribution and abundance of submersed macrophytes in an Australian subtropical river. *Aquat Bot* 77:169–186
- Magnuson JJ, Kratz TK (2000) Lakes in the landscape: approaches to regional limnology. *Verh Internat Verein Limnol* 27:74–87
- Mehlich A (1984) Mehlich III soil extractant: a modification of Mehlich II extractant. *Commun Soil Sci Plant Anal* 15(12):1409–1416
- Messier G (1986) Rivière La Guerre: pré-étude environnementale. Rapport de Urgel Delisle et Associés. Pour le

- Ministère de l'agriculture, des pêcheries et de l'alimentation du Québec
- Middelboe AL, Markager S (1997) Depth limits and minimum light requirements of freshwater macrophytes. *Freshw Biol* 37:553–568
- Morin J, Boudreau P, Secretan Y, Leclerc M (2000) Pristine lake Saint-Francois, St.Lawrence River: hydrodynamic simulation and cumulative impact. *J Great Lakes Res* 26:384–401
- Oksanen J, Kindt R, Legendre P, O'Hara RB (2006) vegan: Community Ecology Package version 1.8–2, <http://cran.r-project.org/> (accessed January 2006)
- Palmer MA, Swan CM, Nelson K, Silver P, Alvestad R (2000) Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. *Landsc Ecol* 15:563–576
- Palomäki R, Hellsten S (1996) Littoral macrozoobenthos biomass in a continuous habitat series. *Hydrobiologia* 339:85–92
- Peres-Neto PR, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87:2614–2625
- Pip E (1989) Water temperature and freshwater macrophyte distribution. *Aquat Bot* 34:367–373
- R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org> (accessed January 2006)
- Riera JL, Magnuson JJ, Kratz TK, Webster KE (2000) A geomorphic template for the analysis of lake districts applied to the Northern Highland Lake District, Wisconsin, USA *Freshw Biol* 43:301–318
- Roberts DW (2006) labdsv: laboratory for dynamic synthetic vegetation phenology. R package version 1.2–2 <http://ecology.msu.montana.edu/labdsv/R>
- Rondeau B (1993) Qualité des eaux du fleuve Saint-Laurent/1985–1990/Tronçon Cornwall-Québec. Centre Saint-Laurent, Environnement Canada, Montréal, Québec
- Sand-Jensen K (2003) Drag and reconfiguration of freshwater macrophytes. *Freshw Biol* 48:271–283
- Sand-Jensen K (1989) Environmental variables and their effect on photosynthesis of aquatic plant communities. *Aquat Bot* 34:5–25
- Sylvestre A (1989) Pertes d'usage du milieu aquatique dans le lac Saint-François. Direction de la qualité du milieu aquatique, Ministère de l'Environnement du Québec
- Titus JE, Adams MS (1979) Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* and *Vallisneria spiralis*. *Michx Oecologia* 40:273–286
- ter Braak CJF, Šmilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide: software for Canonical Community Ordination (version 4.5). Micro-computer Power, Ithaca
- Turner MG (2005) Landscape ecology in North America: past, present, and future. *Ecology* 86(8):1967–1974
- Turner MG, Gardner RH, O'Neill RV (2001) Landscape ecology in theory and practice: pattern and processes. Springer-Verlag, New-York
- Van den Berg MS, Coops H, Simons J (2001) Propagule bank buildup of *Chara aspera* and its significance for colonization of a shallow lake. *Hydrobiologia* 462: 9–17
- Vestergaard O, Sand-Jensen K (2000) Alkalinity and trophic state regulate aquatic plant distribution in Danish lakes. *Aquat Bot* 67:85–107
- Wiens JA (2002) Riverine landscapes: taking landscape ecology into the water. *Freshw Biol* 47:501–515