HISTORICAL CHANGES IN HERBACEOUS WETLAND DISTRIBUTION AND BIOMASS : EFFECTS OF HYDROLOGY ON FAUNAL HABITATS IN LAKE ST. PIERRE (ST. LAWRENCE RIVER, QUEBEC, CANADA)

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Abstract: A model predicting the occurrence of nine herbaceous plant associations (HEPA) from hydrological conditions was elaborated for St. Lawrence River wetlands, using relative abundance index (height x percent cover) of wetland plants in 630 field quadrats sampled at 13 sites (1999-2002). Hydrological regime was linked to 9 classes of HEPA, ranging from high marsh (wet meadow, annual transition, barren transition), low marsh (scattered tall *Scirpus*, mixed narrow-leaved emergents, closed with aggressive emergents, dense with robust emergents) to more aquatic vegetation (open marsh with floating leaves and submerged aquatics), which constitute the wetland fringe most responsive to water level variations. The low marsh HEPA classes also corresponded to a gradient of riparian habitat heterogeneity (relative importance of emergent and submerged vegetation), shifting from completely closed, to dense, mixed, scattered and open marshes to mostly submerged vegetation.

The four hydrological variables best defining HEPA classes were (1) height with respect to average water level in July, (2) average water depth over the previous growing season, (3) number of days underwater over the previous growing season and (4) water depth variability (standard deviation) over the current growing season. Between 58 and 96% of the total area of wetlands in lake Saint-Pierre were properly classified when model predictions were compared to remote sensing images taken over different hydrological conditions (1984-2002). Concordance between taxa-based clusters and HEPA classes based on hydrology of showed that 71% (24-84% depending on HEPA classes) of quadrats were allocated to the right HEPA class.

Inferred historical variations (1961-2002) in HEPA distribution in Lake Saint-Pierre showed that total surface area of herbaceous wetlands ranged from 11 (in 1972) to 128 (in 2001) km^2 between periods of high (1970's) and low (1960's, late 1990's) river levels, respectively. Through vegetation changes, different hydrological regimes modify habitat availability and surface area overall production of HEPA; these changes in HEPA markedly alter the quantity and quality of habitats and food supply for a wide range of vertebrate faunal groups. Historical (1961-2002) changes in wetlands distribution inferred from hydrological modelling reveal that lake Saint-Pierre wetlands alternated between 2 major configurations in the past, with the recent (1996) occurrence of a third configuration. Low-level years (1961-1967) exhibited a high surface of high marsh assemblages, dominated by facultative wetland plants and an overall higher biomass. High-level years (1971-1977) coincided with the predominance of scattered, tall *Scipus* low marshes, characterized by obligatory emergent and submerged wetland plants and an overall lower biomass. In most recent years, hydrological conditions favoured a previously-unseen rise in the surface of closed marshes dominated by aggressive emergent taxa (1996, 2000 and 2002) alternating with the low-level (1999 and 2001) and high-level (1997 and 1998) configurations observed in the past. This unusual pattern indicates that lake Saint-Pierre wetlands have been subjected to a type of hydrological inter-annual variability which had not been experienced before. In addition, the occurrence of large surfaces of closed marshes dominated by aggressive emergent taxa is also alarming, since it could become the permanent wetland configuration in the future of the lake.

Nine relationships quantifying the linkages between hydrological variables (mean annual and mean growing season levels, flood and low-water levels) and wetlands characteristics (total surface area, surface and biomass or high marsh and low marsh, landscape diversity) were identified. These performance indicators can be translated into two regulation criteria for environmentally-sustainable water management: (1) maximize the water level range between spring (high) and late summer-fall (low) levels and (2) maintain discharge pattern closest to natural, unmanaged (pre-project) conditions.

Key words: river, wetlands, herbaceous plant associations, aboveground biomass, hydrology, water level, vertebrate habitat, St. Lawrence River, Lake Saint-Pierre, historical changes, CART model.

INTRODUCTION

Wetland plant assemblages are well-linked to hydrology; water level variations are dominant forces shaping the distribution, species composition and biomass of riparian wetlands (Keddy and Reznicek 1986, Hudon 1997, Wilcox et al. 2002). Modeling wetland assemblages has concentrated on broad categories ranging from swamps to emergent herbaceous vegetation (Hill et al. 1998, Painter and Keddy 1992, Toner and Keddy 1997). Owing to their individual species composition, each of these plant assemblages reacts to hydrology on different time scales: forested swamps, shrubby swamps and herbaceous vegetation were shown to establish themselves over decades, years and months, respectively. Modeling the entire range of wetlands plant assemblages as a function of hydrology is thus done at the expense of fine scale resolution of herbaceous plant assemblages (Williams 1995). Herbaceous plant assemblages (HEPA) encompass the complex transition between meadows, marshes, floating leaves and submerged vegetation, which range from temporarily (albeit for various duration) flooded to continuously submerged conditions (Buteau et al. 1994). Owing to their complete regeneration of aboveground structures every year, HEPA assemblages are notoriously diversified and adapt most quickly to changing water levels (Harris and Marshall 1963, Nilsson and Keddy 1988, Day et al. 1988, Jean and Bouchard 1991, Wilcox et al. 2002, Hudon 2004).

Maintenance of diversified, healthy wetlands lies at the heart of freshwater management objectives (Chambers et al. 1999). Wetlands HEPA represent key riparian habitats for numerous faunal groups (Herdendorf et al. 1981), which take advantage of the cover (plant architecture, height and density) and of the diversified food sources (bacteria, micro-algae and invertebrates) made available as macrophytes grow, mature and decay (Carpenter and Lodge 1986). Faunal species may use different habitats for different stages of their life history, which may also vary regionally and/or according to habitat availability. For example, in the St. Lawrence River, pike spawns in early spring, among the flooded remains of the tall grasses of the previous summer's meadow. If the timing or the magnitude of the flood is inadequate, pike may spawn on the remnants of submerged or robust emergent (*Typha, Scirpus*) plants, both of which are less optimal spawning and nursery habitats (Casselman and Lewis 1996). Favourable fry, juvenile and adult fish habitats are found in scattered emergent, floating leaves and submerged vegetation, with specific preferences for different combinations of water depths, plant composition and density (Herdendorf et al. 1981). Low marshes flooded to provide an optimal ratio of open water to shallow emergent vegetation represent important habitats for aquatic birds and waterfowl (Kaminsky and Prince 1981), providing a food supply of plants and invertebrates (Cyr and Downing 1988) as well as shelter from predators (Lemay 1989). Muskrats are among the few vertebrates to feed directly on robust emergent plants (*Typha, Butomus, Sparganium, Scirpus*) and whose feeding and house-building activities contribute to generate spatial heterogeneity (openings) in densely vegetated low marshes (van der Valk and Davis 1978).

We hypothesize that (1) variations in water level in the current and the previous growing season determine the distribution and composition of HEPA; (2) through these changes in vegetation, different hydrological regimes modify the overall production of HEPA: high-level years should correspond to a predominance of low marsh and submerged assemblages, characterized by emergent and submerged obligatory wetland plants and an overall low biomass, whereas low-level years should show an increase in the surface of high marsh assemblages, dominated by facultative wetland plants and an overall high biomass. These changes in HEPA are expected to alter the quantity and quality of habitats and food supply for a wide range of vertebrate faunal groups.

This study describes, validates and applies a model of HEPA in Lake St. Pierre, a large (312 km^2) fluvial lake formed by a broadening of the St. Lawrence River. The model was developed from 4 years (1999-2002) of sampling river wetlands under contrasting level conditions. Predictions of the model were validated using remote sensing data for 7 years of different hydrological conditions, allowing to infer the historical (1961-2002) variations in the surface area, distribution and biomass of high and low marshes in lake Saint-Pierre.

METHODS

Study area

The study area covers a 225-km-long section of the St. Lawrence River between the Lake Saint-François and the outlet of Lake Saint-Pierre (Figure 1). The wide (> 5 km), shallow (mean depth < 5 m) fluvial lakes are joined by narrow (< 4 km) corridors that flow through the greater Montreal area. The shores of the Lake Saint-Louis, La Prairie Basin and Montreal sectors are heavily urbanized (population of about 3 million) and have been considerably altered by human activities, such as dredging and channelling for ship traffic, creation of islands for Expo ‘67 and deepening of the Montreal harbour. The sector downstream of Montreal to Lake Saint-Pierre corresponds to a more rural setting, where agricultural activities and shoreline erosion are probably the main factors responsible for the loss of wetland habitats (Jean et al. 2002).

The region is located in the St. Lawrence Lowlands, a flat landscape of clay deposits intersected with moraine landforms. Bottom sediments generally consist of fine silt and sand, with a locally variable organic component, lying on glacial deposits of marine clay. Flow velocity is high (1-1.6 $m \bullet s^{-1}$) in the deep ($\geq$ 11.3 m) channel maintained for ship traffic, drops to < 0.7 $m \bullet s^{-1}$ outside of the main channel in the fluvial corridors, and < 0.1 $m \bullet s^{-1}$ in the fluvial lakes and riparian zones (< 2 m) . In the fluvial corridors, emergent marsh vegetation colonizes the shallow (< 2 m) shelf around islands and shoals, which drops sharply along a steep slope to deeper waters. Fluvial lake bottoms are characterized by a wide littoral margin, which deepens progressively over a gentle slope (Table 1). Thirteen wetlands from fluvial lakes and fluvial corridors were selected to represent the various combinations of hydrological variations, exposure to wind, predominant water mass and resulting water quality (Table 1).

St. Lawrence River discharge is currently regulated to optimize hydroelectric production, control flooding of riparian property, and maintain water levels for commercial ship traffic. The regulated outflow at the Moses-Saunders Dam averages 7000 $m^3 \bullet s^{-1}$ and represents the main source of inflow to Lake Saint-François, which is stabilized within $\pm$ 0.40 m. Water level variations in Lake des-Deux-Montagnes reflect the Ottawa River discharge regime, which is regulated through the operation of several upstream reservoirs. Most of the Ottawa River (mean annual discharge 1900 $m^3 \bullet s^{-1}$) empties into the St. Lawrence downstream of the Island of Montreal through the Mille-Îles and des Prairies rivers (Figure 1). Although the Ottawa River is partially regulated through the Carillon Dam, its influence, as well as that of other smaller tributaries, increase flow rate and vertical range to > 1 m. The influence of the Ottawa River and other tributaries in driving the seasonal variations in water levels in the St. Lawrence is increasingly evident at all gauging stations located downstream of Montreal. Annual range is maximal (> 2 m) at the outlet of Lake Saint-Pierre, owing to the influence of the Richelieu, Yamaska, Saint-François and Nicolet rivers, in addition to a small (< 0.3 m) tidal effect. In addition to their effects on seasonal discharge pattern, the inflow of the Ottawa River and other tributaries in the St. Lawrence subject wetlands to water masses of different transparency and nutrient contents (Table 1).

With its 11700 hectares of high and low marshes, lake Saint-Pierre represents over 70% of St. Lawrence River marshes (Jean et al. 2002). Lake Saint-Pierre supports the largest nesting blue heron population (over 1300 nests), a major resting area for migratory wildfowl (over 800 000 ducks and geese annually) and 167 species of nesting birds (DOE 1996). Permanently submerged areas and the spring floodplain host 13 amphibian and 79 fish species, many of which are exploited by sports and commercial fisheries alike. The ecological value of lake Saint-Pierre was recognized by its identification as a RAMSAR site (http://www.ramsar.org), a world Biosphere UNESCO (http://www.unesco.org/mab/) site and its protection status under the Eastern Habitat Joint Venture. Paradoxically, additional habitat protection is indirectly provided by its past (1952-2000) use as ballistic testing grounds for the Department of National Defence: access to the portion of the lake located south of the navigation channel (160 km^2) is restricted and activities involving a contact with the lake bottom are discouraged for safety reasons. The highly valuable character of lake Saint-Pierre thus results from the combination of its morphological features, the persistence of major surface area of marshlands, its use by a highly diversified and abundant fauna and its various protection status.

Sampling procedure: assessment of HEPA distribution and biomass

Sampling followed the method outlined in Hudon (1997) and Hudon et al. (2003). HEPA distribution and biomass were assessed in thirteen marsh sites (Figure 1), where sampling took place in late summer (end of July to early October) of 1999 to 2002. At each site, plants were sampled in 6 to 27 permanent quadrats (1 x 2 m) located along a transect line perpendicular to the shoreline, from a height of about 1 m above CD to a depth of about 1 m (Table 2). At each quadrat, DGPS position (±1-2 m), quadrat elevation (±1 cm), water depth (±1 cm), average height (±1 cm) and relative abundance of each plant species were measured. Sediment samples were taken at a subset of sampling locations in 2000 and 2001 (Table 2). Quadrat elevation was determined with respect to water level at the time of sampling using a Surveyor's level and corrected to Chart Datum level using daily (or hourly for lake Saint-Pierre) level value at the nearest gauging station (see next section). Species' relative abundance was determined as the product of average plant height (in cm) with the median percent cover (Table 5, Vincent and Bergeron 1983). This procedure provided an indication of plants' architecture; for example, the maximum cover (class 7, median 87.5%) of 1 cm germlings would yield an index of 87.5, whereas the same cover by 1 m-high plants would generate and index of 8750. The same quadrats were visited annually over the 1999-2002 period, yielding a total of 630 observations (Table 2).

Plant biomass was assessed at the same sites by collecting all plant matter (above and belowground structures) in 81 quadrats (25 cm x 25 cm) next to the one used to assess relative abundance in lake Saint-Pierre. Vegetation was collected by hand, using a knife or a shovel to section roots down to 25 cm. Aboveground parts were identified and processed separately for each species, while underground matter was pooled for each quadrat. Periphyton, loose detritus and sediment were carefully washed off plant matter, which was subsequently dried to a constant mass and weighed (±0.001 g). Biomass data was pooled on the basis of HEPA class: assignment of each quadrat of biomass to a HEPA class was done by from the distribution of predicted classes on each year of sampling. This allowed to compare measurements of biomass and species composition at known points with the HEPA class predicted at the same location and the same year.

The limits of closed - dense (> 50% surface cover) and scattered – open (< 50% cover) marshes were surveyed in the field (2000-2002) by following the inner and outer limit of scattered emergents in a hydrofoil, with a continuous (DGPS) position recording. The average water depth of the limits of each emergent plant density was assessed by superimposing the XY positions tracked on the bathymetric map of that day.

Physical data acquisition: Climatic, sedimentary and hydrological variables

Climatic variables were analysed to determine the relative importance of between-year differences in weather conditions on HEPA classes (Table 3). Daily air temperature (^{o}C), precipitation (mm) (1999-2002) and daily sunshine (h) (1999-2000) were obtained from St. Hubert airport weather station (DOE 2003a). Daily sunshine for 2001-2002 was obtained from Dorval weather station (26 km to the west, Figure 1). The onset of the growing season was determined as the time at which average air temperature > 5.0^{o}C ; in the St. Lawrence River valley, this threshold is usually reached in the first week of April. The period of April 1 to September 30 was used to define the plant growing season, over which period hydrological characteristics were deemed to exert their maximum influence on HEPA. An index of daily drought (Keetch-Byram Drought Index, KBDI, Keetch and Byram 1968) using maximum daily air temperature, cumulative rain and the number of consecutive days since the last rain was used to determine how much rain would be necessary to saturate the soil on each day of the growing season. The effect of exposure to wind and waves was assessed by including a variable quantifying the open-water fetch (m) from SW direction (Table 1), which is the predominant wind direction in the St. Lawrence River valley in spring-summer (Morin and Bouchard 2001).

Sedimentary variables were investigated to assess the relative magnitude of between-site effects, especially with respect to upstream-downstream differences in nutrient enrichment and fine sediment build-up from erosion and tributary inflow. Percent sand, loam and clay, mean, median and variance in particle diameter, percent of volatile organic contents, organic N, total P and pH were measured on surface sediment cores (10-cm) collected at the time of HEPA sampling in 2000 (122 cores) and 2001 (143 cores) (2001) (see Hudon et al. 2003 for additional information) (Table 2).

Hydrological conditions represented the main factor of our analysis, which tested the hypothesis that HEPA classes observed over a given year were the result of the hydrological conditions experienced during the current and previous growing season. The hydrological regime of each quadrat was characterized using daily water level measurements at the nearest gauging stations: Summerstown (lake Saint-François, station 14940, 02MC023), Sainte-Anne-de-Bellevue (lake des-Deux-Montagnes, station 16005, 02OA013), the Port of Montreal's Jetty No. 1 (station 15520, 02OA046), Varennes (station 15660, 02OA050), and Courbe No. 2 (lake Saint-Pierre station 15975, 02OC016) (DFO 2003). Between-site differences in elevation (referenced to the International Great Lakes Datum of 1985, IGLD85) were accounted for by adjusting level values to navigation charts (hereafter referred to as Chart Datum reference level, or CD). For this purpose, individual site elevation (m, IGLD85) was subtracted from daily level values of the nearest gauging station.

The hydrological conditions to which each quadrat was subjected were assessed using 54 hydrological variables (Table 4). Variables included the number of days spent underwater, the number of wet-dry (water-air-water) transitions, quadrat depth (mean and standard deviation) and quadrat elevation with respect to water level (mean and standard deviation). Different periods and time intervals were chosen to address different selective effects of hydrological regime on HEPA over the very short (weeks), short (month) and middle terms (current and past growing seasons). All hydrological variables were computed for the current growing season (ending on the day each quadrat was sampled); longer term variables (month, growing season) for the previous growing season (1 April – 30 September) were also computed. The choice of hydrological variables reflected their potential effects on HEPA processes such as seed germination of annuals, budding of underground structures of perennials, survival/death of obligatory and facultative taxa by flooding or drying out. This allowed us to test our first hypothesis that the occurrence of a given HEPA class at a given location and time should primarily result from favourable hydrological conditions, at the proper temporal scale or frequency. This further implied that propagules of taxa characteristic of all classes of HEPA were largely distributed in wetlands (or have dispersion mechanisms that operate over periods shorter than that of critical hydrological variability) and remained latent (unexpressed) when hydrological conditions were not favourable.

Identification of HEPA classes

Species nomenclature follows Marie-Victorin (1995), with the exception of species' whose morphology vary noticeably with water levels (*Scirpus lacustris, Sagittaria latifolia*), for which the nomenclature of Fleurbec (1987) was used. Each species was allocated to obligatory or facultative wetland taxa (Reed 1988, Gauthier 1997), obligate perennial (i.e. requiring more than one growing season to produce seeds) or annual life cycle (Marie-Victorin 1995) and to an ecological type (meadow, emergent, submerged, floating-leaved). Shannon (H') diversity index (Legendre and Legendre 2000) was calculated from the percent cover of all species sampled in each quadrat.

HEPA classes based on the relative abundance (height in cm x % median cover) of taxa were identified from the results of multivariate analyses carried out on different subsets of the 630 quadrats. In order to reduce the number of species occurring in < 1% of all quadrats (< 7 quadrats), some species were lumped at the genus level or in groups of similar ecological form (i.e. linear-leaved *Potamogeton* species). This procedure reduced the total number of taxa from 207 to 133, 76 of which occurred in sufficient frequency (> 1%) to be included in multivariate analyses. Groups of quadrats supporting homogeneous herbaceous plant assemblages were identified from cluster analyses using a Bray-Curtis dissimilarity coefficient (Legendre and

Legendre 2000) computed between all pairs of quadrats and the "Flexible-Beta" (Lance and Williams 1967) clustering method (SAS, PROC CLUSTER, beta=-0.25). These procedures were selected because they are well-suited for relative abundance data and also because the absence of a given taxon from two quadrats does not count as an element of similarity. Two identical cluster analyses carried out separately on years of low (1999 and 2001, N= 287 quadrats x 82 taxa) and average (2000 and 2002, N = 343 quadrats x 74 taxa) levels, allowing to highlight two HEPA classes (annual transition and barren transition) characteristic of low-level conditions. Five additional HEPA classes were common to all years, corresponding to meadow, mixed marshes with narrow-leaved emergents and other marshes, floating-leaved and submerged vegetation. Diagnostic taxa, top ranking in their excess relative to expected abundance, were identified for each HEPA class.

Hydrological model development and validation

The relative importance of climatic, sedimentary and hydrological variables on HEPA classes was assessed by running Canonical Correspondence Analyses (CCA, ter Braak and Smilauer 1998) on data subsets for which the information was complete. Separate analyses were carried out to determine the fraction of variance in HEPA classes explained by environmental variables (cumulative degree-days, precipitation and hours of sunshine, drought index, water mass and clarity, fetch from the NE and SW) and sediment characteristics (% sand, % clay, % loam, total P, organic N, % organic contents. pH and grain size distribution (mean, median and standard deviation)). CCA was used to identify the subset of most influent variables using forward selection of highly significant ($p < 0.01$) variables while avoiding co-linear variables.

The relative importance of hydrological variables (N= 54, Table 4) on HEPA classes was assessed in the same way, allowing to identify the subset of most influent hydrological variables to be included in predictive models. The combination of hydrological variables and the critical thresholds allowing the best separation of HEPA classes were identified using classification tree (CART, Breiman et al. 1984) analysis. This hierarchical model was used to predict the long-term variations (1961-2002) in the surface area and distribution of HEPA classes in lake St. Pierre, as a function of daily water levels (1961-2002). The expected HEPA class was predicted from the hydrological conditions experienced by each pixel of lake bottom at a know elevation using a 2-dimension hydrodynamic simulation model (see section below).

The validity of the output of the hydrological CART model was assessed by three methods. First, the surface area and distribution of each HEPA class predicted from the hydrological model was compared to wetland classes identified from remote sensing images. Late-summer wetlands distribution in lake Saint-Pierre could be assessed independently on eight remote sensing images from LANDSAT-TM (1984, 1986, 1987 and 1988 (2 dates); Lalonde and Létourneau 1996), MEIS-II (1990 and 2000; DOE 2004) and IKONOS (2002, DOE 2004) platforms (Table 7). For each pixel of lake bottom, we assessed the concordance between HEPA classes predicted from hydrology (9 classes) and the wetland category inferred from its remote-sensing spectral signature (55 categories). This exercise was based on a (9 x 55) matrix where roughly 46% of the hydrological and spectral HEPA class pairs were deemed concordant, based on the plant species typically associated with the classes. Second, the limits of continuous (> 50% surface cover, dense and closed marshes, HEPA classes 8, 9) and sparse (< 50% cover, scattered and open marshes, HEPA classes 4, 5) emergents surveyed in the field (2000-2002) were compared with the limits of equivalent classes derived from the hydrological model and from remote sensing for the same years. Third, the attribution of groups of quadrats derived from the hydrological model was verified against the HEPA classes previously identified by the cluster analyses, to determine the fraction of quadrats properly classified using hydrology alone.

Model application to Lake Saint-Pierre

The long term variations of HEPA classes in Lake Saint-Pierre were modeled using daily levels (1960-2002) at Lake Saint-Pierre Courbe No. 2 (15975, 02OC016) and Trois-Rivières (3360, 02NG010), respectively located at the inlet and outlet of the lake (DFO 2003). The level regime affecting the area of Lake Saint-Pierre supporting the belt of wetland HEPA (elevations between 2.94 m to + 4.45 m IGLD85, Hudon et al. 2003) was determined using a hydrodynamic simulation model (Morin and Bouchard 2001) combined to a numerical elevation model (m IGLD85) (DOE 2003b). These elevation thresholds coincided roughly with the 1-m depth isobath in the month of August (which marks the lower limit of emergent plant colonization) and with the 2-yr recurrent flood limit (beyond which HEPA tends to be replaced by shrubby and forested swamps if natural succession is allowed to take place). The slope of the water level of the Lake Saint-Pierre was assessed by interpolating the daily water levels from both stations (Courbe No.2 and Trois-Rivières) on 40000 polygons. This slope was then corrected on a daily basis by using a simulated slope from the MSC as a reference to calculate the slight variations caused by topometry, winds and tides. The simulated slope that was used to correct the interpolated slope was derived from a simulated scenario corresponding to a mean discharge of 9500 $m^3 s^{-1}$ in spring. Hydrological conditions experienced by each pixel of lake bottom at a know elevation were then used to predict the expected HEPA class at each point.

The distribution of predicted HEPA class for each year was mapped using a geographic information system (MapInfo version 6.5), which was then used to determine the surface area of each class reached at the end of the growing season for each year (1961-2002). Aboveground biomass of each class of HEPA was obtained by the sum of the products of the surface area (km^2) with average biomass (kg dry • m^{-2}) for each class. Annual biomass production was assessed for high marsh (HEPA classes 1+2+3), low marsh (HEPA classes 4+6+8+9) and aquatic vegetation (HEPA classes 5+7), coinciding with the predominance of terrestrial, emergent and submerged plants, respectively. Overall landscape diversity (Shannon H', Elkie et al. 1999) was computed using Patch Analyst (Rempel and Carr 2003).

Lake Saint-Pierre habitat dynamics implied by hydrological model

The 42-yr sequence of changes in HEPA class surface area was reduced from a 9-descriptor (surface of 9 classes) time series to a 2-dimensional state-space diagram. The new factors consisted of simple differences of HEPA class areas and were identified by inspection of the first two principal components of the covariance matrix between HEPA surface areas. This synthesized representation of Lake Saint-Pierre HEPA dynamics revealed the presence of a small number of recurrent patterns through time.

Linear relationships between hydrology and HEPA characteristics

Linkages between HEPA characteristics (surface, biomass, diversity) and hydrological variables at Sorel (1961-2002, DFO 2003) were assessed using non parametric (Spearman r) correlations (SAS, PROC CORR) and linear regressions (SAS, PROC AUTOREG). To obtain a small number of fairly general but robust relationships, surface area and biomass were grouped according to broad categories of high marsh (HEPA classes 1+2+3), low marsh (HEPA classes 4+6+8+9), aquatic vegetation (HEPA classes 5+7) and total wetlands (sum of HEPA classes 1-9). For each year, flood and low-water levels were determined from maximum and minimum values of the 7-day running average level values reached before and after July 1, respectively. The annual range was determined as the difference between flood and low-water levels. The date of flood and low-level were identified as the first day of the 7-day maximum and minimum-level period, respectively. Mean annual level and mean level during the growing season (April 1 - Sept. 30) were determined from daily level values.

RESULTS

Identification of key variables

Seven broad classes of HEPA were identified from the cluster analyses on taxonomic composition, corresponding to the gradient ranging from seasonally dry to constantly wet conditions: wet meadow, annual transition, barren transition, mixed marshes with narrow-leaved vegetation, open marshes with floating leaves vegetation, other marshes and submerged vegetation. The relative association of environmental (among-years), sedimentary (among-sites) and hydrological variables with HEPA classes was first assessed from separate canonical analyses of correspondence on subsets of quadrats.

In spite of the major differences in climatic conditions among years (Table 3), canonical correspondence analysis revealed that environmental and climatic conditions only explained 9.6% of total variance in the above HEPA classes. Expectedly, cumulative precipitations were negatively correlated to cumulated sunshine and degree-days, and explained together 57.2% of the variance of the first axis. Similarly, fetch from dominant wind directions was inversely correlated to water clarity and explained 29% of the variance of the second canonical axis. Open marshes with floating vegetation occurred in areas that were sheltered from dominant winds and of relatively good water clarity.

Sediment characteristics varied between sites (not shown), but explained only 11.5 % of the variance in HEPA classes. The first axis (65% of variance) was positively correlated to particle size and to the % sand and was negatively correlated to pH and organic N content. Submerged vegetation (HEPA class 7) and mixed marshes with narrow-leaved emergents (HEPA class 6) were found on sandy sediments, with a high median size and low organic contents, whereas other marshes (HEPA classes 4, 8, 9) and wet meadows (HEPA class 1) tended to grow on finer, more organic sediments.

Hydrological variables alone explained 25.0% of the variation in HEPA classes, allowing to identify a subset of 9 most significant hydrological variables. Once the effect of environmental and sedimentary conditions was removed from the analysis, hydrology still explained 24% of total variance. These 9 variables were used in the development of a predictive binary CART model based exclusively on combinations of hydrological variables; environmental and sedimentary variables were excluded since they represented only about 10% (each) of variability among HEPA classes.

Model development and concordance assessment

The hydrological model (CART) increased from 7 to 9 the total number of HEPA classes that could be predicted from hydrological conditions (Figure 3), as it yielded predictions for three subsets of marshes which were originally lumped together as "other marshes" in the taxa-based cluster analysis. For the sake of clarity, we present the correspondence between HEPA classes resulting from remote sensing categories, taxa-based clusters, hydrology-based CART classes and habitat categories (Table 6).

The hydrology-based CART model (Figure 3) first distinguished between quadrats that were above (dry) or below (wet) the average water level in July. That threshold distinguished between the areas which were dry for most of the growing season (high marshes = HEPA classes 1, 2, 3) from the ones subjected to water-logged or submerged conditions throughout the current growing season (HEPA classes 4 to 9). Incidentally, this criterion also corresponds with one of the defining characteristic of high and low marshes (Buteau et al. 1994). Three sub-classes of high marsh were distinguished from the average water depth over the previous growing season: water < 22.6 cm resulted in wet meadow vegetation (HEPA class 1), water depth between 22.6 and 94.9 cm during the previous growing season resulted in annual transition vegetation (HEPA class 2), water depth > 94.9 cm resulted in barren transition (HEPA class 3).

The six remaining classes were divided according to the number of days spent underwater over the preceding season. Areas always under water (> 180.5 days in the growing season) over the previous growing season yielded open marshes with floating-leaved vegetation (HEPA class 5) and scattered marshes with tall *Scirpus* (HEPA class 4), which were distinguished on the basis of small (class 5) and large (class 4) seasonal water depth variability. The four remaining classes were divided into those located in water deeper (HEPA classes 6, 9) or shallower (HEPA classes 7, 8) than 77 cm below the July level. The number of days underwater over the previous season allowed to distinguish mixed marshes with narrow-leaved vegetation (HEPA class 6, > 46 days underwater) from closed marshes with aggressive emergents (HEPA class 9, < 46 days underwater). Finally, dense marsh with robust emergents (HEPA class 8, > 100.5 days underwater) tended to be flooded for longer durations over the previous season than perturbed submerged vegetation (HEPA class 7, < 100.5 days underwater).

Comparison of HEPA class distribution predicted from the hydrology model with remote sensing images for 8 years (Table 7) revealed that the wetland assemblages coincided over 58 (1988) to 96% (1987) of the surface area. The relatively poor performance (58% and 64% accuracy) of the two 1988 images remained unexplained. The correspondence between high marsh HEPA classes (meadows, annual and barren transitions) with remote sensing was unequivocal. Closed, dense and mixed (HEPA classes 9, 8, 6) marshes were also adequately represented by both methods. Field survey of the limit of continuous (> 50%) cover of emergents coincided well with that of mixed marshes with narrow-leaved vegetation from remote sensing (Figure 4). However, the correspondence between scattered and open marshes towards the submerged vegetation was more delicate, particularly the correspondence between HEPA class 5 (open marsh with floating leaves) and remote sensing categories (deep marshes, floating leaves or submerged vegetation). Field surveys delineating the outer limit of open - scattered (< 50% cover) emergent vegetation in deep water (1-2 m) showed a good concordance with HEPA class 5 (open marsh with floating vegetation), which were however too scarce to be adequately discerned from remote sensing.

A 71% overall match was observed between HEPA class derived from taxa-based cluster analysis and allocation from hydrological CART model. Depending on HEPA class, the percentage of well-classified quadrats varied from 84% (open marsh with floating vegetation) to 24% (submerged vegetation) (Table 8). As observed in the previous two validation steps, attribution of quadrats to the 3 drier HEPA classes (meadows, annual and barren transition) was highly successful (70-79% concordance). The allocation of quadrats belonging to marsh categories reflected the difficulty of accurately describing the transition between terrestrial and aquatic environments (45-58% of quadrats properly classified). Again, the two most aquatic

HEPA classes tended to be lumped together, as most (N = 46 out of 65) quadrats classified as submerged vegetation (HEPA class 7, 24% well-classified) were attributed to HEPA class 5 (open marsh with floating vegetation, 84% well-classified). Specifically, all submerged vegetation quadrats originating from lake Saint-Pierre were classified into open marshes with floating vegetation.

Description of HEPA classes

The nine HEPA classes derived from the hydrological model (Figure 3) can be described from the hydrological (Table 8), biological (Table 9) and taxonomical (Table 10) standpoints, all important characteristics defining their properties as faunal habitats.

Wet meadow (HEPA class 1) – This class was the one located at the highest elevation (104 ± 41 cm IGLD85) of the HEPA gradient and was the first to be dried out as spring flood receded (Table 8). It formed a large sample (N= 120 quadrats) which was fairly well-represented in lake Saint-Pierre (N_{LSP} = 21) and was well-classified at 71% by the CART analyses. *Phalaris arundinacea*, *Lythrum salicaria*, and *Onoclea sensibilis* were diagnostic taxa of this group, which formed a dense, high biomass (564 g dry mass m^{-2}) cover of tall grasses (about 1m) (Table 10). Quadrats dominated by *Spartina pectinata* were also classified in meadows, although they only represented about 25% of quadrats. Obligatory emergent taxa (*Typha spp. and Bolboschoenus fluviatilis*) were also observed in this class, contributing to its diversity: of all HEPA classes, meadow comprised the highest number of recorded taxa (103), representing on average 9.8 taxa per quadrat (2 m^2). Most taxa in this class were perennials, with a roughly equal representation of obligatory and facultative wetland taxa (Table 9).

Annual transition (HEPA class 2) – Located at a lower elevation than the previous one (45 ± 29 cm), but still 37 cm above the average July water level (Table 8), this HEPA class appeared when low-level conditions resulted in the drying out of marsh vegetation over most of the growing period. The annual transition class was observed in the low-level years only (1999 and 2001) and was characteristic of 103 quadrats, 25 of which originated from lake Saint-Pierre (Table 8). This low representation results from the fact that the southern part of lake Saint-Pierre

(DND restricted area) could not be sampled by foot when dried out, for safety reasons. Periodic drying out of marshlands resulted in particularly high diversity (Shannon H' = 1.49), resulting from the co-occurrence of perennial (6.3 taxa per quadrat) with obligate annual (2.7 taxa per quadrat) taxa. This gave rise to the presence of *Polygonum* spp., *Urtica dioica* and tall (> 10 cm) *Cyperus* spp., which not commonly observed in other HEPA classes. These taxa, as well as other graminea (*Leersia oryzoides, Phalaris, Phragmites, Spartina*), *Lythrum salicaria*, *Populus* spp. and *Acer* spp. were observed germinating in the dried, open spaces between the stems of obligatory emergent taxa usually dominant under wetter conditions. Obligatory emergent taxa (*Bolboschoenus, Typha, Sparganium, Butomus*) persisted over the dry period owing to their complex underground structures. Combination of meadow (4.9 taxa per quadrat) and emergent (4.1 taxa per quadrat) taxa resulted in fairly high aboveground biomass (315 g dry mass m^{-2}) in this transitory class (Table 9). In contrast with the wet meadow class, the annual transition wetland class provided a rather heterogeneous ground cover for fauna, including tall grasses, scattered lumps of stunted emergent plants and a low cover of annuals germinating on the dried ground.

Barren transition (HEPA class 3) – As with the previous class, the barren transition was only observed on low-level years. A barren transition zone was observed when the water's edge receded to unprecedented low levels in July. For the same reasons outlined for the annual transition HEPA class, only 4 out of the 44 quadrats belonging to this class originated from lake Saint-Pierre, although such zones were frequently observed. The drying out of areas colonized by submerged vegetation over the previous year (average depth over the previous season = 119 ± 20 cm of water) generated the appearance of mud-flats, whose intensity of annual colonization depended on the duration of de-watering and short-term variability (standard deviation = 57) of water depth (Table 8). Since it was located near the edge of water in July (-3 ± 20 cm), quadrats belonging to this group were subjected to frequent wet-dry cycles (6 times per season on average), imposing a sharp selection pressure in favour of highly tolerant, quick-responding taxa. *Polygonum* spp., *Leersia oryzoides* and filamentous algae were diagnostic taxa of this group (Table 10), which comprised a mixture of small amounts of meadow (1.5 taxa per quadrat), emergents (2.3), submerged (1.5) and floating-leaved (0.2 taxa per quadrat) taxa. This class was also rich in taxa specifically adapted to sharp water-level drops (*Alisma plantago-aquatica*), able to germinate and flower on water-logged soils *(Heteranthera dubia)* and taking advantage of open substrate to germinate *(Polygonum* spp., *Populus deltoides, Lythrum salicaria, Lindernia dubia).*

Low marshes – Low marshes cover the areas that remain water-saturated or inundated year-round (Buteau et al. 1994), covering a depth range between 0 and about 1 m below the level in July (Table 8). In addition to the effects of hydrology, marsh assemblages also reflect, among other things, the effects of scouring by ice, exposure (wind-waves) and of nutrient enrichment. For these reasons, division of marshes into distinct, yet ecologically-meaningful HEPA classes was a challenge, since marshes represent a complex continuum of emergent and submerged plant assemblages grading into each other. The initial cluster analysis carried out on relative abundance of plant taxa led to the initial division of marshes into three groups: an open marsh with floating-leaves (HEPA class 5), a mixed marsh characterized by narrow-leaved emergents (HEPA class 6) and a single group of all other marshes (HEPA classes 4, 8 and 9) (Table 6). The "other marshes" group was subsequently resolved into three additional marsh classes through the hydrological CART model (Figure 3), which also succeeded in distinguishing the previously-defined marsh classes (open-floating leaves and mixed-narrow leaves marshes). We thus describe the five low marsh classes in the same order as that of the hydrological model output (Figure 3), without regard for any given sequence of water depth, taxonomic composition, emergent plant height, biomass or stem density. Owing to the various combinations of these characteristics, however, each of the low marsh class bears a distinct faunal habitat potential.

Open marsh with floating leaves vegetation (HEPA class 5) – As indicated by its name, this class is characterized by the occurrence of diagnostic taxa such as *Nuphar variegata* and *Nymphaea odorata*, accompanied by emergents (*Scirpus lacustris*), submerged (*Vallisneria americana, Elodea* spp.) and algae (*Chara* spp. and filamentous algae) (Table 10). This large group (N = 162 quadrats) was the least diversified (H' = 0.84) and supported only an average 4.3 taxa per quadrat (Table 9). Open marsh with floating vegetation was the HEPA class most characteristic of the offshore belt of southern lake Saint-Pierre (N=27 quadrat) deep-water (53 ± 28 cm) marshes, well below (73 ± 31 cm) the average level in July. This type of marsh covered large areas in which small patches (< 5 m across) of *Scirpus lacustris* emerge among submerged and floating vegetation. Although the maximum depth limit of this assemblage was fixed at 1 m below the late summer level, field surveys revealed the occurrence of *S. lacustris* to a depth of 1.5 m (s.d. 0.5 m) (Figure 4).

Scattered tall Scirpus. marsh (HEPA class 4) – Sheltered areas of lake Saint-Pierre were typically colonized by scattered marshes, to which all quadrats (N = 18) of this class belonged. Similarly to HEPA classes 8 and 9, scattered *Scirpus* marsh lied in fairly deep (46 ± 10 cm), but highly variable (Zsd = 70 cm) water depth, although seldom dewatered (Table 8). These hydrological conditions resulted in a moderate diversity (H' = 1.16), the exclusive presence of obligatory wetland taxa (4.3 taxa per quadrat), most of which (4.2) were perennial. This class was characterized by a fairly high biomass (343 ± 326 g dry mass m^{-2}) for marshes, which reflected the presence of robust emergent plants and canopy-forming submerged plants. *Scirpus lacustris, Bolboschoenus fluviatilis* were the dominant emergent taxa, accompanied by *Myriophyllum* spp., *Potamogeton richardsonii* and *Heteranthera dubia.* This resulted in a complex arrangement of patches of tall (> 1m) emergent plants interspersed with pools of fairly dense submerged vegetation.

Mixed marsh with narrow-leaved emergents (HEPA class 6) – This class of marsh was also well-represented in lake Saint-Pierre (59 out of 87 quadrats), where it often colonized the inner fringe between high and low marshes, between the continuous (> 50% cover) and sparse (< 50% cover) emergents (Figure 4). Mixed marshes with narrow-leaved emergents were found in shallow areas (29 ± 26 cm) periodically dewatered (on average 99 ± 30 out of 183 days) over the previous growing season. These moderately variable hydrological conditions yielded the highest diversity of all marsh classes (H' = 1.24), with an average 7.7 taxa per quadrat. Distinctive taxa of the narrow-leaved emergent marsh class included *Schoenoplectus pungens*, *Eleocharis palustris, E. acicularis* and *Pontederia cordata*, which formed a medium height (0.5 – 1.0 m), medium biomass (224 ± 183 g dry mass m^{-2}) emergent assemblage nearly devoid of submerged plants (1 taxon per quadrat) (Table 9).

Closed marsh with aggressive emergents (HEPA class 9) – Similarly to the previous two HEPA classes, closed marshes were also found in shallow (10 ± 26 cm) variable (Zsd = 43 ± 9) water depth. However, the hydrological regime of this class differed in the extended dewatering period to which this class was subjected, as it spent only 34 (± 5) out of 183 days underwater during the previous growing season (Table 8). This resulted in a low diversity (H' = 1.1) and a small number of taxa (5.6) per quadrat, with a strong dominance of aggressive, clonal obligatory wetland taxa. *Phragmites australis, Typha* spp., *Sparganium eurycarpum* and *Butomus umbellatus* were most abundant in this class, which represented an assemblage of tall (1.5 to 2.5 m-high), closed cover of robust emergent plants. Lake Saint-Pierre hosted only one out of the 34 quadrats belonging to this low marsh class, which occurred mostly in the perturbated wetlands of the fluvial corridor. This small sample size in lake Saint-Pierre could result from the fact that closed marshes are, by their very nature, difficult of access, especially under low-water level conditions.

Dense marsh with robust emergents (HEPA class 8) – The last of the five low marsh class was found in deep waters (73 ± 19 cm) waters, over 1 meter below average level in July, spending most (155 ± 22 out of 183 days) of the previous growing season underwater. Dense, robust emergent taxa (*Bolboschoenus fluviatilis*, *Butomus umbellatus, Typha spp.* and *Sparganium eurycarpum*) coexisted with floating leaved (*Nuphar variegata*) and a variety of submerged taxa (*Alisma plantago aquatica, Potamogeton* spp). This marsh class was characterized by the coexistence of various robust emergents (2.7 taxa per quadrats) and abundant submerged (2.6 taxa per quadrat) taxa. In contrast with the previous marsh assemblage, intermediate emergent cover and deep water allowed dense submerged vegetation to grow among emergent plants, whereas submerged plants were most likely restricted by shallow water, low light and dense emergent cover in the closed marsh. In lake Saint-Pierre, this assemblage was represented in 29 out of the 42 quadrats.

Submerged aquatic vegetation (HEPA class 7)- This final class of HEPA comprised only a small number of quadrats (N=20), none of which originated from lake Saint-Pierre. This assemblage likely reflected shallow-water (57 ± 26 cm), submerged aquatic vegetation which was perturbated since it was underwater for only 76 days over the previous 183 days growing-season. Seventeen submerged taxa were recorded (5.4 taxa per quadrat), with an overall low biomass (64 ± 77 g DRY MASS m^{-2}) dominated by *Elodea canadensis*, *Myriophyllum* spp., *Potamogeton* spp., *Vallisneria americana, Chara* and filamentous algae. The presence of small amounts of *Lythrum salicaria, Eleocharis palustris, Schoenoplectus pungens* and *Typha* spp. (Table 10) was indicative of the periodic disturbance caused by drying out of this normally aquatic assemblage. This situation was mostly observed at sites located in the fluvial corridor.

Temporal variations of HEPA in lake Saint-Pierre (1961-2002)

Application of the hydrological model using historical water level and bathymetric data for lake Saint-Pierre allowed to reproduce the long-term (1961-2002) variations of the surface area of the 9 HEPA classes (Figure 5). Wet meadow (0-26 km^2), annual transition (0-48 km^2), barren transition (0-26 km^2), scattered tall *Scirpus* marsh (0-69 km^2), mixed marsh with narrow-leaved emergents (0-29 km^2) and open marsh with floating-leaves vegetation (0-75 km^2) appeared and disappeared periodically during the 42-yr interval. HEPA class 9, closed marsh with aggressive emergents, was absent for most of the series but occupied a large (> 25 km^2) surface area for the first time in 1996. Two classes of HEPA (classes 7, 8) were virtually absent from lake Saint-Pierre, corresponding closed marsh with robust emergents and perturbed submerged vegetation, which coincided with their small frequency from our field observations in lake Saint-Pierre.

Aboveground biomass produced annually in lake Saint-Pierre wetlands (0-1 m depth range; Figure 6) was assessed by the product of surface area (Figure 5) with average biomass (Table 9) for each class. HEPA classes were grouped according to high marsh “terrestrial” (Classes 1, 2, 3), low marsh “emergent” (Classes 4, 6, 8, 9) and “submerged” (Classes 5, 7) vegetation (Figure 6). Temporal changes covered a 20-fold biomass range, from 1,500 (in 1973) to nearly 30,000 tons (in 1965) of dry plant matter, depending on water level conditions during the current and previous year. Low-level periods (for example, 1962-1965) tended to have highest total biomass values, dominated by terrestrial vegetation, whereas high-level periods (1973-1986) showed lowest total biomass values, dominated by submerged vegetation. Inter-annual variations in water level as experienced since 1994 tended to generate variable biomass (6,500 – 25,000 tons annually) alternating between mostly emergent or submerged/terrestrial plants (Figure 6).

Long-term (1961-2002) shifts of Habitats and Landscapes in Lake Saint-Pierre

The realisation that the first two components of a principal component analysis captured 82% of the overall variation in HEPA class surface area history led to a useful representation of our model's predictions. Two simple axes, inspired by principal components, were defined to represent the global changes in surface area of all HEPA classes in lake Saint-Pierre (Figure 7). The resulting V-shaped diagram showed that the lake alternated between three broad-scale wetland configurations, dominated by open marsh with floating-leaves (upper left), scattered tall *Scirpus* marshes (upper right) and closed marsh with aggressive emergents (bottom).

Lowest lake level conditions experienced in the 1960-1967 period, 1999 and 2001 coincided with assemblages found in the upper left arm of the V-shaped diagram. In those years, lake Saint-Pierre wetlands were characterized by large expanses of wet meadows (HEPA class 1, mostly in the 1960's), annual transition (HEPA class 2) and open marsh with floating-leaf vegetation (HEPA class 5). This configuration resulted in a sharp dry-wet boundary, mostly devoid of transitional marsh assemblages and coincided with high total biomass values, dominated by terrestrial plant biomass (Figure 6). Years over which a sharp drop in level occurred exhibited the additional appearance of an intermediate barren transition zone (HEPA class 3) between dry vegetated and wet areas. This particular configuration was observed in 1962, 1975 and 1977, with barren areas totalling 8, 12 and 22 km^2 respectively. In recent years (1995, 1999 and 2001), the same configuration was also observed, albeit more frequently and covering larger areas (20 km^2 and more). The 1960-1969 period also coincided with fairly high and stable values of landscape diversity (Figure 8).

During the years appearing on the lower left arm of the V-shaped diagram (Figure 7), the barren transition zone tended to be replaced by mixed marshes with narrow-leaved emergents (HEPA class 6), which provided a more gradual passage from dry, high marsh (HEPA classes 1, 2, 3) to submerged open-marsh areas (HEPA class 5). This configuration was observed in 1964-1969, 1989-1990 and 1992-1994, all years over which narrow-leaved marsh covered ≥ 8 km^2 (> 25 km^2 in 1966 and 1989) of lake Saint-Pierre wetlands (Figure 5).

The period of high average water levels observed in the 1970's coincided with a different wetland configuration, which correspond to the right arm of the V-shaped diagram (Figure 7). The years 1971 and 1991 (Figure 7) show the replacement of open marshes by floating-leaves aquatic vegetation (HEPA class 5) by scattered *Scirpus* marsh (HEPA class 4). Scattered *Scirpus* marshes dominated lake Saint-Pierre wetlands in 1971, 1974-1975, 1977-1979, 1983, 1991 and 1993, over which periods they covered 20-69 km^2. Over these years, total wetland biomass also tended to be high (> 20,000 tons), but was dominated by the emergent plant component (Figure 6). Depending on year-to-year level conditions, scattered *Scirpus* marshes were accompanied by annual transition (up to 22 km^2) and narrow-leaved marshes (up to 11 km^2).

The group of years clustered at the basis of the diagram (Figure 7) revealed a third wetland configuration. Years of highest water levels (1972-1974, 1976) coincided with the lowest total (< 20 km^2) overall surface area of wetlands in lake Saint-Pierre. Over these years, wetlands were divided between scattered *Scirpus* marshes (HEPA class 4) and marshes with narrow-leaved emergents (HEPA class 6), with the first occurrence of small surfaces (< 5 km^2) of closed marsh with aggressive emergents (HEPA class 9). The 1973-1975 period also marked a dramatic decline of landscape diversity (Figure 8).

The years 1996, 2000 and 2002 are found in the lowest part of the V-shaped diagram. Over these years, total wetlands surface was near-average (50-90 km^2), but was mostly covered with closed marsh with aggressive emergents (HEPA class 9, > 25 km^2), with minor surfaces (< 15 km^2) of previously observed HEPA classes (1, 3, 5, 6). Possibly as a result of the high patchiness and owing to the simultaneous presence of other wetlands HEPA classes, landscape diversity showed a tendency to rise in the 1997-2002 period.

In addition to the shifts between 3 wetland configurations of lake Saint-Pierre, the distribution of years in the V-shaped diagram also provided indications on the decadal-scale level of variability. It is noticeable that all years of the 1961-1967 period were located in the left arm of the diagram (Figure 7; circles), whereas the years 1971-1977 (Figure 7; squares) shifted to the right arm of the diagram. In contrast, over the most recent years (1997-2002) (Figure 7; pentagons) wetlands switched rapidly between the three configurations, from the scattered *Scirpus* marsh (right side) to the open marsh (left side), with the unprecedented occurrence of closed marshes with aggressive emergents (bottom) in the most recent years. Over the last 7-yr period, lake Saint-Pierre wetlands have been subjected to (by far) the largest hydrologically-induced, year-to-year variability observed since 1961.

Linear relationships between hydrology and HEPA characteristics

Operational tools for inclusion of lake Saint-Pierre wetlands into water level management were derived from the above results, by identifying the strongest, yet ecologically-meaningful linear relationships between hydrological components and wetlands characteristics. Many significant relations between pairs of hydrological and biological variables were thus identified (Table 11), leading to the selection of 9 performance indicators for which linear regression coefficients were computed (Table 12).

Mean annual water level and mean level during the growing season (April 1-Sept 30) yielded very similar relationships, because these two hydrological variables are highly correlated with each other ($r = 0.91$, Table 11). Both variables were also strongly positively correlated to maximum spring and minimum fall level. Mean level during the growing season was selected because of its ecological significance. Strong, negative relationships were observed between mean level during growing season and the total surface area and total biomass of lake Saint-Pierre wetlands. This relationship stems primarily from the simple hydrological link between level and the surface lying under < 1m of water at the end of the summer. Given the shallow sloping shores of lake Saint-Pierre (Table 1), a small change in water level generates large changes in the surface area sufficiently shallow (0-1.5 m) to be to be colonized by emergent plants. In addition, this confirms and refines the previously described relationship between water level during the growing season and the percent cover of emergent wetlands derived from analyses of aerial photographs and remote sensing images (Hudon 1997).

Average levels during the growing season were also strongly, negatively related to the surface and biomass of the three high marsh HEPA classes: wet meadows, annual and barren transition (1+2+3). Low levels resulted in large areas of dried lake bottom, allowing the colonization and growing of tall grasses and facultative annual plant taxa. Owing to their terrestrial life-forms, these plants must produce structural elements to maintain their vertical bearing on land, which result in a higher amount of dry plant mass and a higher fraction of cellulose. The relationship with biomass is not altogether unexpected, as it stems from the product of biomass estimates (per m^2) with the total surface. This relationship is most representative of the temporal changes in the importance of the annual transition wetland class, since it was the most commonly observed (35 years out of 42) and also represented a fairly high areal biomass (315 g dry mass m^{-2}) value.

Strong, negative correlations were observed between growing season level (r = - 0.68***), spring flood level (r = - 0.69***) and the total biomass of low marshes (HEPA classes 4+6+8+9) (Tables 11-12). In contrast with biomass, the surface area of low marshes responded more weakly to hydrological conditions (highest r value = 0.38 with growing season level, Table 11), in part owing to our use of cumulative surface areas for the sake of robustness. The lumping of different low marsh classes was justified by the fact that each class responded to a complex combination of hydrological variables, distributed over the current and previous growing season. Finer linkages between low marsh features and hydrology will require additional studies.

Spring flood level was also negatively correlated to landscape diversity (r = -0.55**) indicating that springs of high levels resulted in more homogeneous wetland landscape (a smaller number of classes and a smaller surface area) than years of low floods (see also year 1974 on Figure 7).

Late summer and fall low-water level was negatively correlated to the total wetlands surface area and to the surface and biomass of high marshes (HEPA classes 1+2+3). In this case, low levels in late summer and fall resulted in a high surface area of all cumulated classes of wetlands (r = -0.92***); high marshes' surface (r = -0.79***) and biomass (r = -0.85***) responded particularly strongly to low-water levels (Table 11).

Dates of spring flood and late summer-fall low-water levels (Table 11) were not used in regressions, because they showed generally weak relationships with biological variables and were thought to have little use in terms of water-level management. Surprisingly, the overall amplitude (flood level – low-water level) did not show strong correlations with biological variables. This probably stems from the fact that wetlands assemblages respond more specifically to the flood or the low-water level (to which amplitude was highly correlated, Table 11) rather than to their combined effects.

Whereas for the regulated (1961-2002) period a strong, positive correlation was observed between spring flood level and late-summer and fall low-water levels ($r = 0.66^{***}$), the same relationship was not significant for the pre-regulation (1912-1959) period ($r = 0.2$). This difference could stem from the combination of two phenomena. First, the lack of correlation in the pre-regulation period could result from the past impact of ice-jams on flooding, which has been largely controlled since the 1960's. Second, the strong correlation in the regulated period could stem from the tendency to store more water on Lake Ontario in the spring when supply is abundant and to release it in late summer and fall, thus artificially tying the magnitude of the two events.

DISCUSSION

Our results confirm our first hypothesis, that variations in water level in the current and the previous growing season determine the distribution and composition of HEPA. Herbaceous wetland plant assemblages form a continuum of mosaic grading into each other. Many taxa occurred in several HEPA classes, albeit in different abundance – emergent plants were shown to be found (seeds, propagules, underground structures, rhizomes, stolons) over a wide range of elevation to take advantage of current water level conditions. Given the wide variations of water levels in the St. Lawrence River, all taxa are not necessarily at their optimum elevation each year but this strategy allows them to respond very fast to fluctuating water levels (Hudon 1997).

Over the 4 years of sampling leading to the development of the hydrologic model, St. Lawrence River water levels followed the pattern of alternating low (1999 and 2001) and nearly average (2000 and 2002) conditions. These broad differences in water levels from year to year allowed us to document the considerable plasticity of herbaceous plant assemblages (HEPA) to hydrology. For example, shifts were observed between a tall grass meadow dominated by *Phalaris arundinacea* and diverse annual species under low water conditions, to a marsh dominated by *Butomus umbellatus*, *Sparganium eurycarpum* and *Typha angustifolia* when water levels returned to average values over alternating years (Hudon 2004). Similar shifts were observed following the low-level conditions during the summer of 1931 (Marie-Victorin 1943).

Conversely, high inter-annual variability in level and climate over the sampling period imposed a strong, yet previously unseen pattern of alternating environmental conditions, which likely strengthened the effect of hydrological variables over the previous year. The sequence of water level fluctuations over the 1999-2002 sampling period was such that Year 0 levels were always either higher (1999 and 2001 were preceded by years of nearly average levels) or lower (2000 and 2002 were preceded by years of low levels) than in Year 1. However, some limitations may also stem from this pattern. For example, low marsh communities observed in Year 1 may still have been observed if water levels had remained stable (rather than dropping) in comparison with the previous year (Year 0).

Our second hypothesis, that changes in vegetation induced by different hydrological conditions would modify the overall production of HEPA, was also partly confirmed. Although total wetland biomass was not strongly correlated to mean annual ($r = -0.40^*$) and growing season ($r = 0.-0.37$, Table 11) levels, biomass of high marsh ($r = -0.87^{***}$) and low marsh ($r = -0.68^{***}$) were strongly correlated to both. This pattern can be explained by the inter-annual shifts in the relative importance of high marsh "terrestrial" and low marsh "emergent" sources of biomass (see also figure 7), which likely resulted in changes in food quality supporting broadly different types of food-chain.

In addition to the effects of physical forcing emphasized in this study, biological interactions such as competitive exclusion, exotic species introduction also affect the heterogeneity and diversity of herbaceous wetland assemblages, for better or for worse. For example, the water chestnut (*Trapa natans*) is a potential invader of lake Saint-Pierre wetlands, as it infests the upper reaches of Richelieu river (< 100 km upstream) and has been recently reported in Chambly Basin (< 65 km upstream). Proliferation of this species in lake Saint-Pierre could be facilitated by nutrient enrichment and altered hydrology, resulting in a dramatic alteration of habitat diversity. *Trapa* forms a thick floating leaf canopy on the surface of water, below which dark, anoxic conditions exclude other plant and animal species.

Managing biodiversity and disturbance at different spatial and temporal scales

There is increasing evidence that biological diversity follows a dome-shaped relationship with disturbance gradients: diversity is maximal under moderate disturbance and decreases when disturbances are minimized or overly amplified (Huston 1979, 1994, Hill et al. 1998, Day et al. 1988, Ward et al. 1999). Factors responsible for wetland “disturbance” are numerous (altered hydrology, reduced connectivity, lowered water quality, physical alteration, biotic interactions and other factors) and involve complex interactions with ecosystem components and functions (Nilsson and Svedmark 2002, Detenbeck et al. 1999). Wetlands diversity can be quantified at different spatial scales, ranging from the landscape level, the community/ecosystem level, the population/species levels and genetic level, not all of which were addressed in this study. In hydrological terms, distinguishing between what constitutes a desirable (moderate) or undesirable (too low, too high or too unpredictable) degree of hydrological alteration becomes a crucial issue for environmentally-sustainable level management.

In river systems, physical “disturbance” induced by water-level regime is also compounded by its effects on overall productivity of the system. Accumulation of sediment and organic matter in shallow areas increases overall productivity, which was shown to set in place complex relations with wetlands plant diversity (Nilsson et al. 1999, Auclair et al. 1976a). Moderate enrichment will increase diversity up to a maximum beyond which enhanced biomass production leads to a decline in species richness and diversity (Grime 1973, Auclair et al. 1976a, 1976b, Tessier et al. 1984, Riis and Sand-Jensen 2001).

In the past, lake Saint-Pierre wetlands, high temporal (inter-annual) and spatial (patchiness) heterogeneity in herbaceous plant assemblages have resulted from intense physical disturbances such as intense flood events, erosion by waves generated by wind or shipping traffic, freeze-over and lift-off of ice pack, ice scouring (Marie-Victorin 1934, Cléonique-Joseph 1936). These intense, albeit periodic physical disturbances have selected taxa and wetland assemblages that were tolerant to the broad range of variations experienced in the St. Lawrence River (Dansereau 1959). Control of ice jams and associated winter floods, channel excavation and discharge control have all played a role in the reduction of the surface area and water circulation in shallow areas of lake Saint-Pierre. In conjunction with increased nutrient and suspended sediment outflow from the tributaries, the relief of physical constraints previously imposed by hydrological conditions have changed plant growing conditions in wetlands. Such changes likely affect not only wetlands but all aquatic ecosystem components – this justifies the need to adopt a management strategy that will maintain global wetlands and aquatic ecosystems functions rather than focus on individual groups or species (Tockner et al. 1999).

Maximum spring levels were negatively related to biomass of low marshes (HEPA classes 4+6+8+9). This relationship can be interpreted in different ways. First, high spring level may favour the flushing of organic matter and recently accumulated sediments thus maintaining nutrient-poor substrate. The re-setting and flushing of wetlands by massive spring flooding could provide a strong signal to maintain low biomass of emergent and submerged plants alike (Day et al. 1988). Second, high spring levels may be correlated to annual levels during the growing season, both of which would lead to a reduction of robust emergent plant biomass when they are submerged in deep water (van der Valk 1994). An example of this mechanism is in the practice of rising pond level to control or eliminate dense *Typha* stands (van der Valk et al. 1994).

In that sense, the apparition of large surface areas of dense marshes with robust emergents in lake Saint-Pierre could be the result of the lack of important floods in recent years. Our observations (CCA results) showing that scattered, dense and closed marshes (HEPA classes 4, 8, 9) tended to grow on fine, organic sediments supports the linkage between flood, sediment and vegetation types. Although the cause-effect mechanism remains uncertain, our results indicate that maintenance of healthy, diversified marshes relies on strong spring floods. However, the minimum flood recurrence period required to maintain healthy wetlands remains unknown: in any case, their generation is most likely to remain under climatic control.

Fall minimum water level was negatively correlated to the surface area and biomass of the three high marh wetland classes (HEPA classes 1+2+3), providing a strong indication of the effect of hydrological cycle on lake Saint-Pierre wetlands structure. The annual transition class is formed when low marshes are dried out, allowing to reduce temporarily the importance of emergent vegetation and to benefit annual, more terrestrial species which regenerate the seed-bank. At the small-scale level of taxonomic composition, our observation of high taxa diversity in periodically dried out marshes (HEPA class 2, annual transition) confirm that (1) wetlands species diversity is maximal just above the water line (Keddy 2002), (2) episodic low-level period favour wetlands species diversity, through the flowering of obligate annual species, which replenish wetlands' seed-bank (Keddy and Reznicek 1986). In the barren transition zone, extreme drops in water levels dry out shallow areas clogged by submerged vegetation, thus reducing their biomass and maintaining diversified shallow-water habitats when higher levels return. However, episodes of low levels were also shown to increase the rate of spreading of exotic, aggressive species (Jetté et al. in prep, Décamps et al. 1995). *Phragmites australis* monopolizes large areas of the more perturbed wetlands of the St. Lawrence River fluvial corridor (Lavoie et al. 2003); small patches of this highly aggressive species were observed for the first time in lake Saint-Pierre in the spring of 2003, following the low-level years of 1999 and 2001. *Phragmites* produces a closed, 2-4-m-high cover that excludes other plant species. In the long term, management of minimum fall levels may thus exert positive as well as negative effects on wetlands diversity.

At the other extreme of the disturbance scale, repeated, alternating years of high and low levels may impose excessive stress on wetlands ecosystems. This would result in the selection of only those species that are tolerant to extreme disturbance and thus also result in the reduction of diversity. In this respect, predictability of level variations could be as important as their overall magnitude. For example, highest diversity (Table 9) of all low marshes was found in mixed marshes with narrow-leaved emergent vegetation (HEPA class 6), which were subjected to moderate, highly predictable water-level variations (Table 8) – this class also predominates in the tidal river reaches. Given the highly variable water supply to the Great Lakes over the past decade, stabilisation of Lake Ontario level necessarily results in an increase in river discharge during periods of high supply and in the reduction of river discharge in periods of low supply (Carpentier 2003). This management practice could increase year to year variability in a way that is detrimental to wetlands in both Lake Ontario (stabilized levels) and St. Lawrence River (overly variable regime). As shown by our results, past periods of low (1960's) and high (mid 1970's) supply resulted in a sequence of many years of similarly high or low conditions, thus allowing wetlands to adjust over a period of several consecutive years. In contrast, between 1996 and 2002, lake Saint-Pierre wetlands shifted rapidly between the two previously observed and an additional (previously unseen) configuration. This unusual pattern indicates that river wetlands have been exposed to a type of inter-annual hydrological variability which had never been experienced before. In addition, the recent apparition of large surfaces of closed marshes characterized by aggressive emergent taxa is also alarming, in that it could become the permanent wetland configuration in the lake. Under chronically reduced water levels resulting from climate change, reduced flooding will likely accelerate the accumulation of organic matter and sediment in wetlands, further pushing lake Saint-Pierre wetlands towards closed marshes dominated by a small number of aggressive species.

Implications for faunal habitat potential

Wetland heterogeneity and diversity are not only desirable for their own sake, but also because they help maintain faunal habitat diversity, at the species, population and community levels – the availability of different types of habitats over time and space should ensure that the requirements of all faunal species are fulfilled at one time (location) or another. Such variability should maintain faunal species richness, through alternating good and poor years for recruitment and cohort growth. The rate of recurrence of given habitat combinations then becomes a critical element for faunal species of different longevity. In order to maintain a healthy faunal population, temporal recurrence of its critical habitats should be smaller than the effective duration of that species' breeding time, to ensure that mature individuals can generate a strong year class at least once during their lifetime. Once a cohort has been produced, critical reproductive habitat must recur at least once in its fecund lifetime. In the most extreme cases, however, habitat requirement may be so stringent that even the temporary disappearance of suitable habitat (water) signals that of the entire faunal group (fish).

Plant height, abundance and biomass reflect whether each taxon is growing under optimal or sub-optimal water level conditions – these factors also shape the architecture of each herbaceous wetland plant assemblage and determine its suitability for different faunal groups. For example, the large-scale habitat shift we observed in lake Saint-Pierre (Figure 7) could have a major impact on nesting and juvenile rearing wildfowl habitats. (1) Under its open-marsh configuration, abundant nesting ground should be available in the tall grassy, heterogeneous cover provided by annual transition (HEPA class 2) vegetation. However, abruptness of the land-water transition and the scarce cover of emergent plants in the open water marsh could provide insufficient shelter for young duckling. The appearance of large areas devoid of vegetation (barren transition, HEPA class 3) following massive level drop may also increase duckling vulnerability to predators (Lemay 1989, Keith 1961). (2) Under its scattered *Scirpus* configuration, optimal nesting and rearing conditions could be provided by the simultaneous presence of annual transition high marshes and rarely de-watered scattered low marshes. (3) The recently observed configuration in which closed marshes are dominated by aggressive emergents (HEPA class 9) could signal a decline in duck recruitment in lake Saint-Pierre, as closed marshes populated by tall, dense, uniform cover of *Typha* or *Phragmites* are not suitable for wildlife – the increased efforts of Ducks Unlimited to create open, managed marshes in lake Saint-Pierre is perhaps an additional indication of the progressive closing of its littoral marshes.

Translating wetlands performance indicators into criteria

Results of this study could be translated into regulation criteria of the type described in the following two examples:

Maximize the water- level range between spring (high) and late-summer and fall (low). At Sorel, the water level range during the growing period declined significantly from 1912 to 1994 (Hudon 1997). The vertical range is likely to decline further under the chronically low water supply to the basin, which will accentuate the tendency for management to store water in Lake Ontario in the spring (thus reducing spring flood levels) for release in the fall (thus raising low levels in late summer and fall). Such reduction in vertical amplitude is harmful to wetlands, which require a broad seasonal range of water levels to remain healthy. It is well documented that increased spring discharge flushes out organic matter and fine sediments, thus resetting the river system each year at the onset of the growing season. High spring levels are of major importance since they flood the upper margin of swamps and flush out sediments and organic matter accumulated in the previous seasons, thus maintain the equilibrium of ecosystems by preventing accumulation in the shallow littoral areas. Conversely, the occurrence of low levels in late summer and fall and periodic drying out of shallow areas allow the germination of annual plant species, thereby maintaining species diversity and ensuring the regeneration of seed banks.

Maintain natural discharge patterns. Given the uncertainties of future water supply under climate change scenarios, which may also affect the timing of freezing and thawing events, an environmentally-sound management option would be to maintain discharge patterns harmonised with natural supply patterns. Climate change will likely increase the frequency of winter thawing episodes, increase evaporation through reduced lake ice-cover, delay or eliminate ice formation in the river and change the relative magnitude and timing of the flow of the Ottawa River and other tributaries. These changes will bring additional (and unpredictable) changes to Lake Ontario – St. Lawrence River water supply, altering the magnitude and timing of seasonal episodes of high and low waters.

Understanding the linkages between water levels and the environment is of a particular importance if changing water supplies bring the Great Lakes water levels outside of the range experienced since the turn of the century; this very same situation prompted the frequent ad-hoc deviations from plan 1958-D and could still happen under future changes in climate. Whereas exceedingly high supplies were the problem in the 1970's and 1980's, the 2000's may bring extended periods of extreme low supplies. Although managing extremes is always a challenge, managing drought conditions may prove to be the biggest challenge of all, since drought exacerbates human pressures, thus imposing the need to weight economic against other interests. For the environment, in the mean time, the closest approximation to natural (unaltered) discharge and flow regimes remains the most environmentally-sound management measure.

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FIGURE 1. Map of the St. Lawrence River, between Cornwall and the outlet of lake Saint-Pierre, showing the location of the 13 field sites from which the hydrological model was developed. The model was used to predict wetlands distribution (classes of HEPA) in lake Saint-Pierre.

FIGURE 2. Spring flood, average growing-season (April 1 to Sept 30) and late-summer fall low-water levels at Sorel (1961-2002).

FIGURE 3. Classification and regression tree model (CART) allowing to predict the occurrence of 9 HEPA classes from the hydrological conditions of the current and previous years. The model predicts the occurrence of 3 high marsh classes (HEPA classes 1, 2, 3), 5 low marsh classes (HEPA classes 5, 4, 6, 9, 8) and perturbed submerged aquatic vegetation (HEPA class 7).

FIGURE 4. Comparison of the distribution of HEPA wetlands classes derived from remote sensing (top) and CART model predictions (bottom) under high (1986) and low (2000) water levels. The outline of continuous (red line, > 50% cover) and sparse (yellow line, < 50%) emergent plants obtained from the 2000 hydrofoil field survey is shown for reference for both right panels.

FIGURE 5. Historical variations (1961-2002) of the surface area of the 9 HEPA wetland classes predicted from the hydrological conditions of the current and the previous year. Average water level during the growing season (dotted line) is indicated as a reference on each graph.

FIGURE 6. Historical variations (1961-2002) of wetland biomass (tons dry mass) produced annually in Lake Saint-Pierre wetlands (0-1 m). HEPA classes were grouped to distinguish between high marsh “terrestrial” (HEPA classes 1+2+3), low marsh “emergent” (HEPA classes 4+6+8+9) and “submerged” (5+7) vegetation. Average water level during the growing season (line) is indicated as a reference.

FIGURE 7. State-space diagram derived from principal component analysis of the surface areas of the 9 HEPA describing the long-term (1961-2002) shifts in Lake Saint-Pierre wetlands. The horizontal axis is the difference in surface area of wetlands with large expanses of open marshes with floating leaves (HEPA class 5, 1963 and 2001 maps to the upper left) and those covered by scattered *Scirpus* emergent marshes (HEPA class 4, 1971 and 1991 maps to the upper right). The vertical axis distinguishes between wetlands dominated by open or scattered marshes or annual transition areas (HEPA classes 5, 4 or 2, near the top) from wetlands with large surfaces of mixed marshes with narrow-leaved emergents (HEPA class 6, 1966 map to the bottom left corner) or closed marshes with aggressive emergents (HEPA class 9, 2002 and 1996 maps to the lower middle). High-level years with low areas of wetlands are located near the center of the diagram (see 1974 map to the lower right corner). Seven-year periods corresponding to different patterns of temporal shifts in wetlands are identified: 1961-1967 (circles), 1971-1977 (squares), 1996-2002 (pentagons).

FIGURE 8. Historical variations (1961-2002) of landscape-scale diversity of lake Saint-Pierre wetlands, derived from changes in the surface area of the 9 HEPA classes.

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TABLE 10. Average height (cm) and relative abundance (height x median % cover) of the 30 major plant taxa (OBL > 56 occurrences, FAC > 31 occurrences) observed in the 9 HEPA classes identified from the hydrological model. Life history (LH) identifies perennial (P) and annual (A) taxa. Average plant height (cm) is specified for each taxon. Taxa whose abundance is diagnostic of a given HEPA class are indicated in bold. Average relative abundance was computed for all quadrats classified in each CART class, including null values (absence from a given quadrat).

TABLE 11. Spearman correlation coefficients among hydrological variables (at Sorel) and wetlands characteristics derived from hydrological model of HEPA in Lake Saint-Pierre (1961-2002). Prob. < 0.01*, < 0.001**, < 0.0001***.

TABLE 12. Linear regression equations between selected pairs of hydrological variables (at Sorel) and Lake Saint-Pierre wetland characteristics. All parameter estimates Prob. < 0.0001***.

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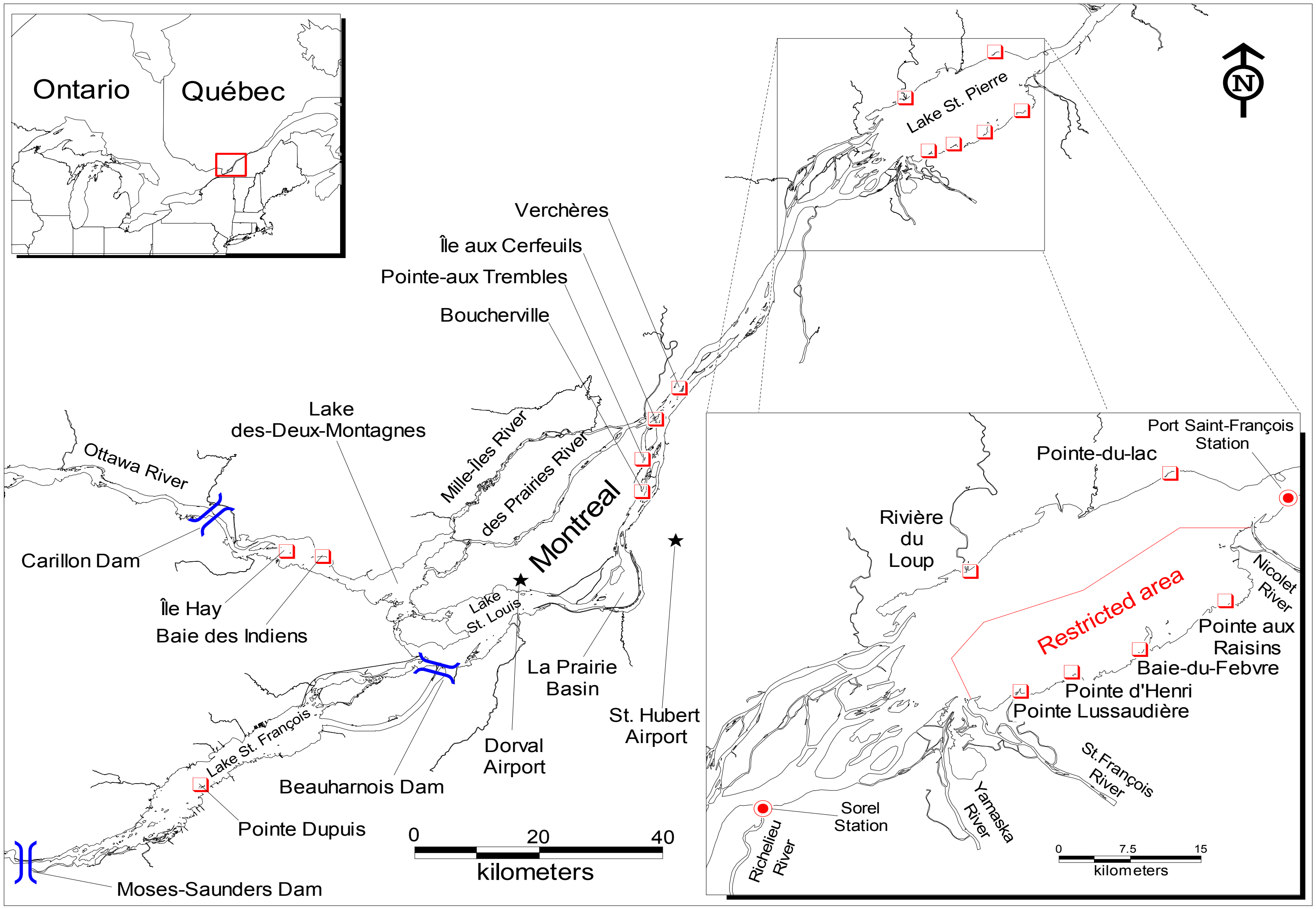

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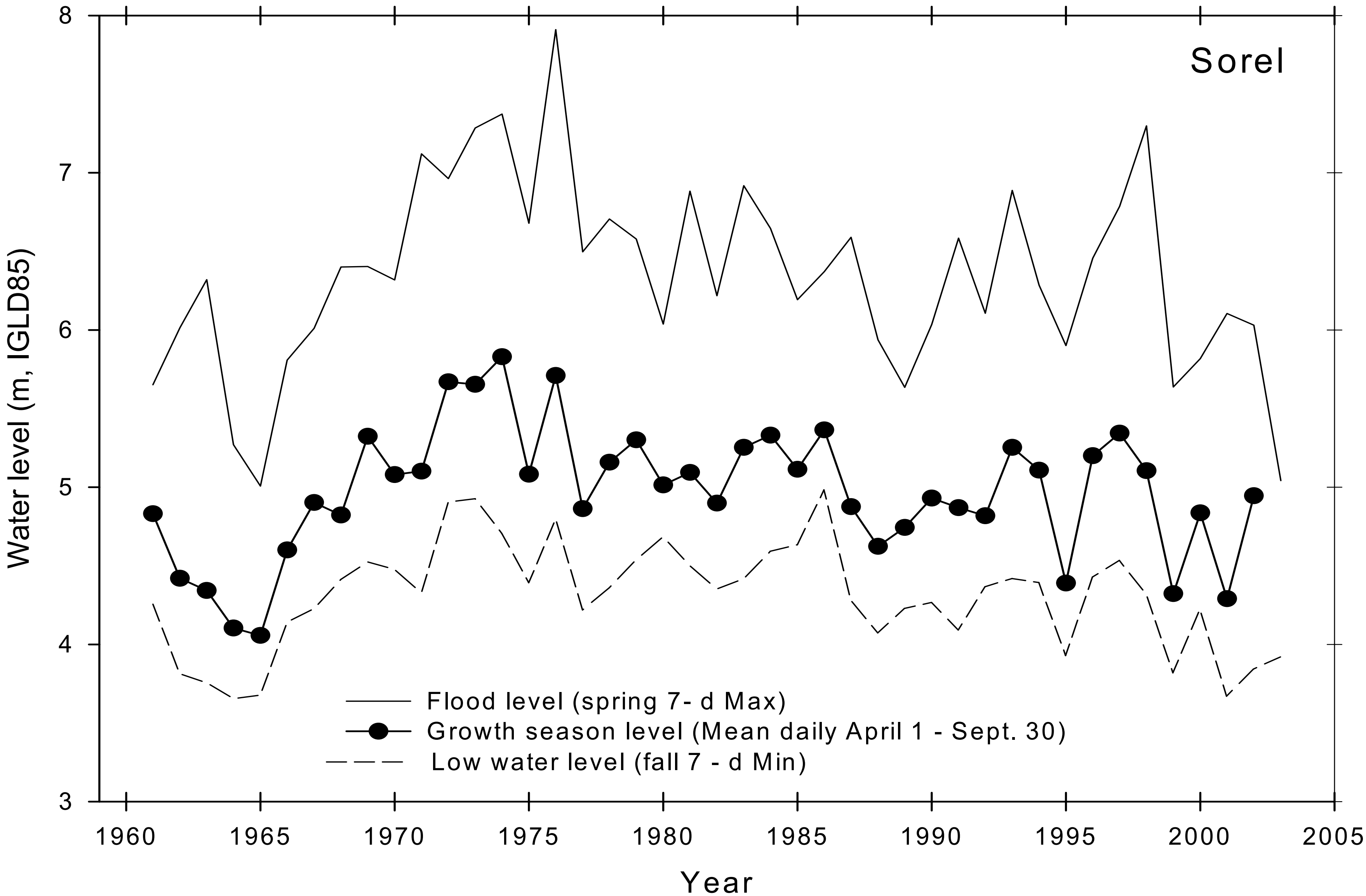


Figure 2 Spring flood, average growing-season (April 1 to Sept 30) and late-summer fall low-water levels at Sorel (1961-2002)

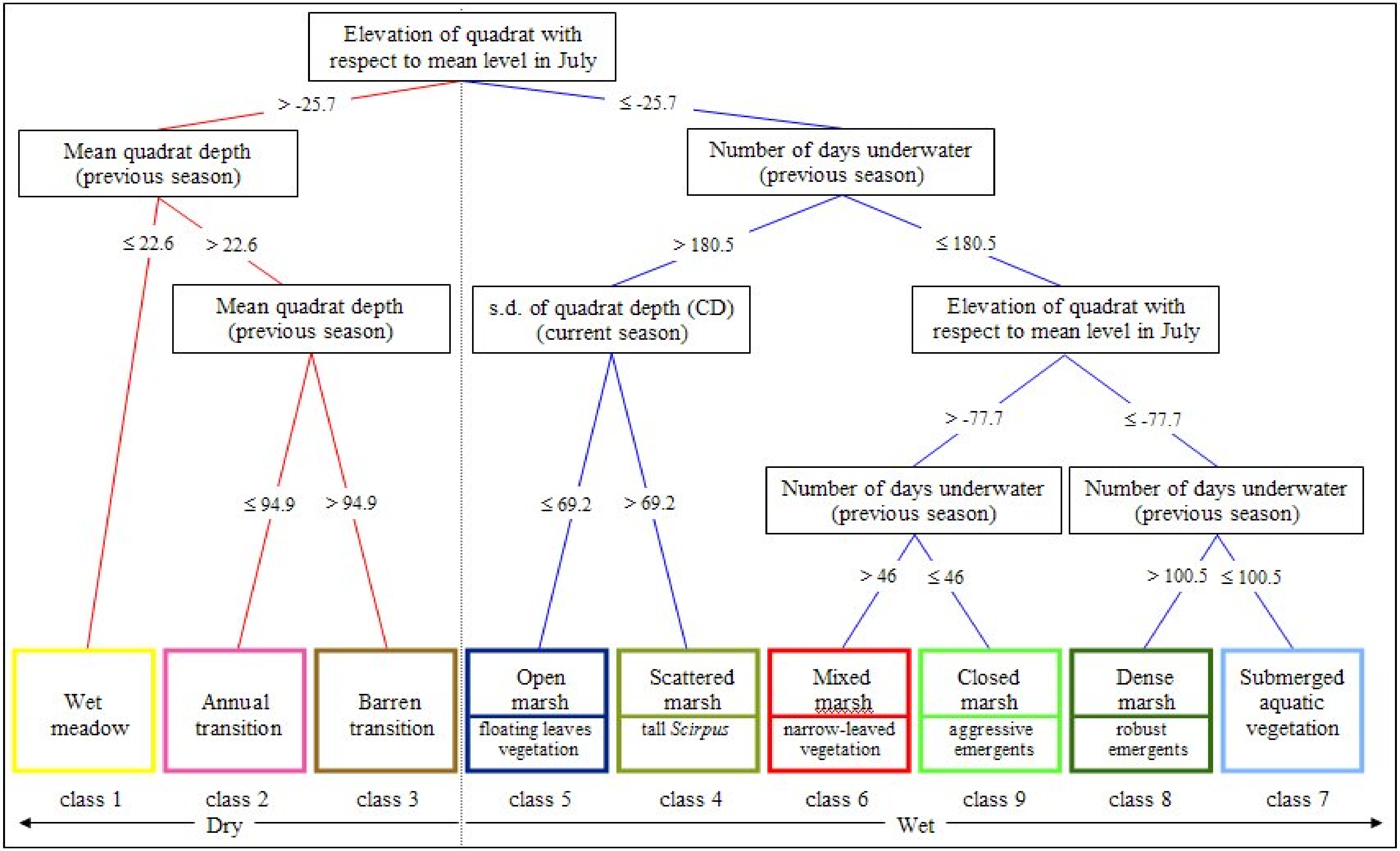
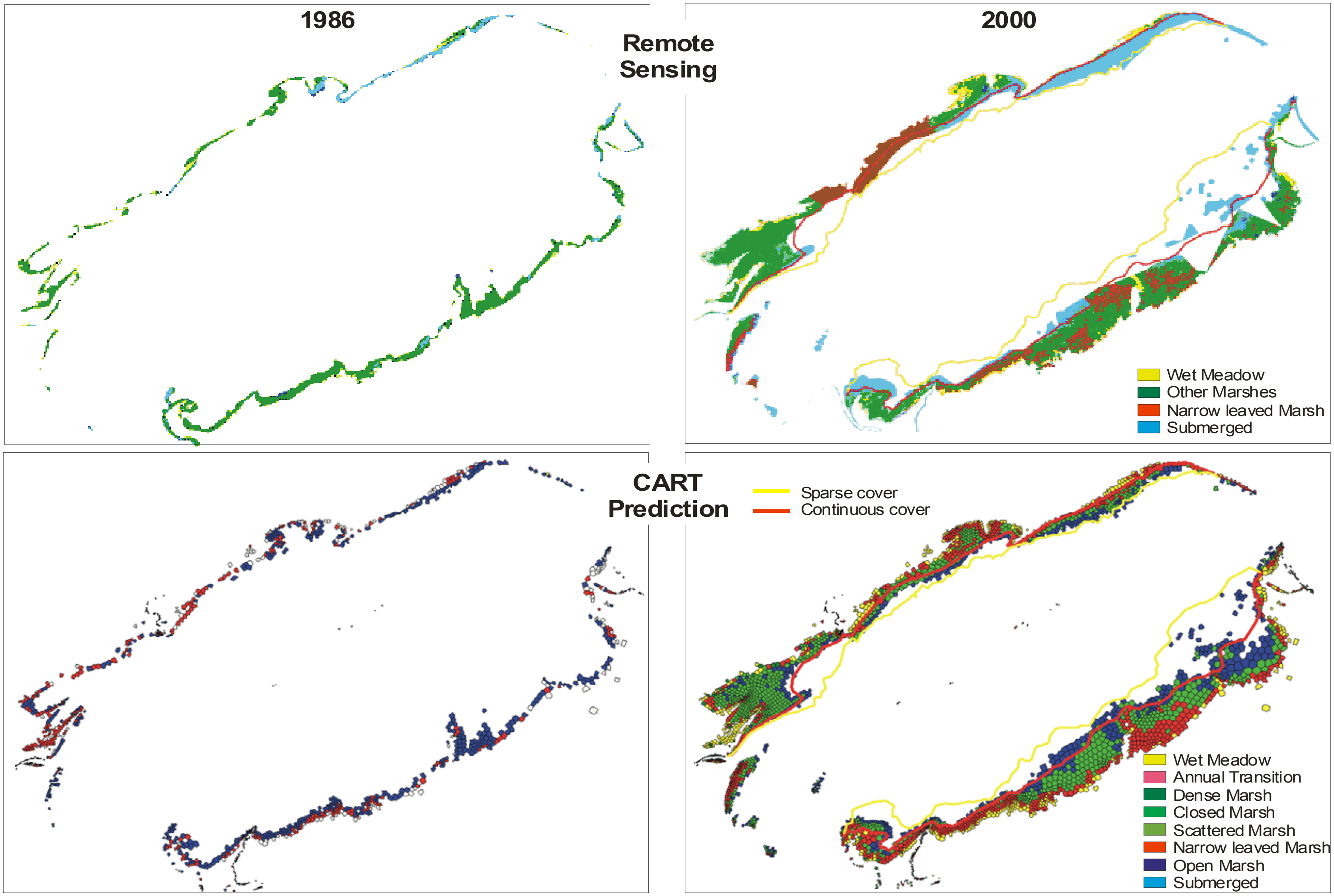


Figure 3 Classification and regression tree model (CART) allowing to predict the occurrence of 9 HEPA classes from the hydrological conditions of the current and previous years. The model predicts the occurrence of 3 high marsh classes (HEPA classes 1, 2, 3), 5 low marsh classes (HEPA classes 5, 4, 6, 9, 8) and perturbed submerged aquatic vegetation (HEPA class 7)



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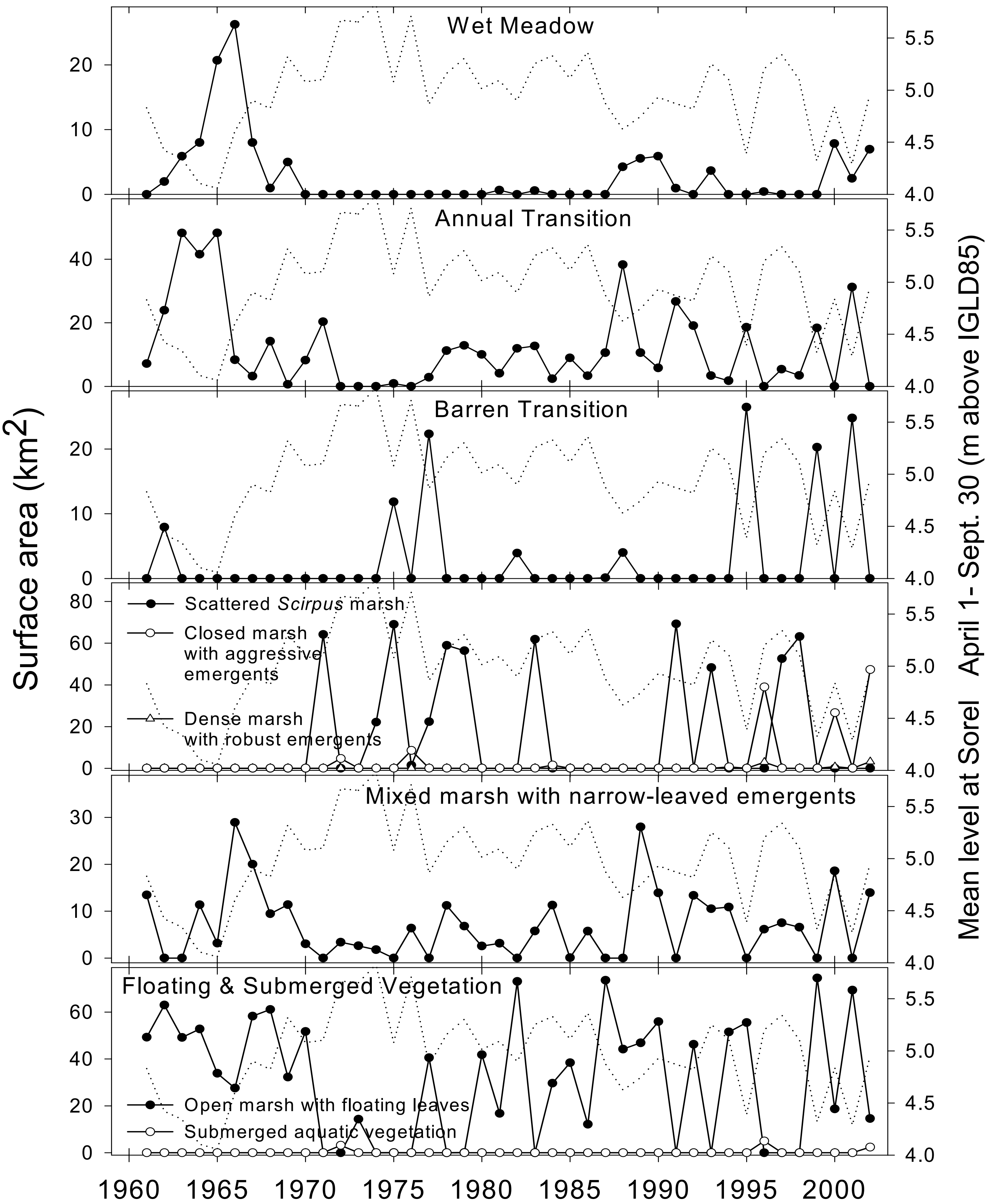

Figure 5 Historical variations (1961-2002) of the surface area of the 9 HEPA wetland classes predicted from the hydrological conditions of the current and the previous year. Average water level during the growing season (dotted line) is indicated as a reference on each graph

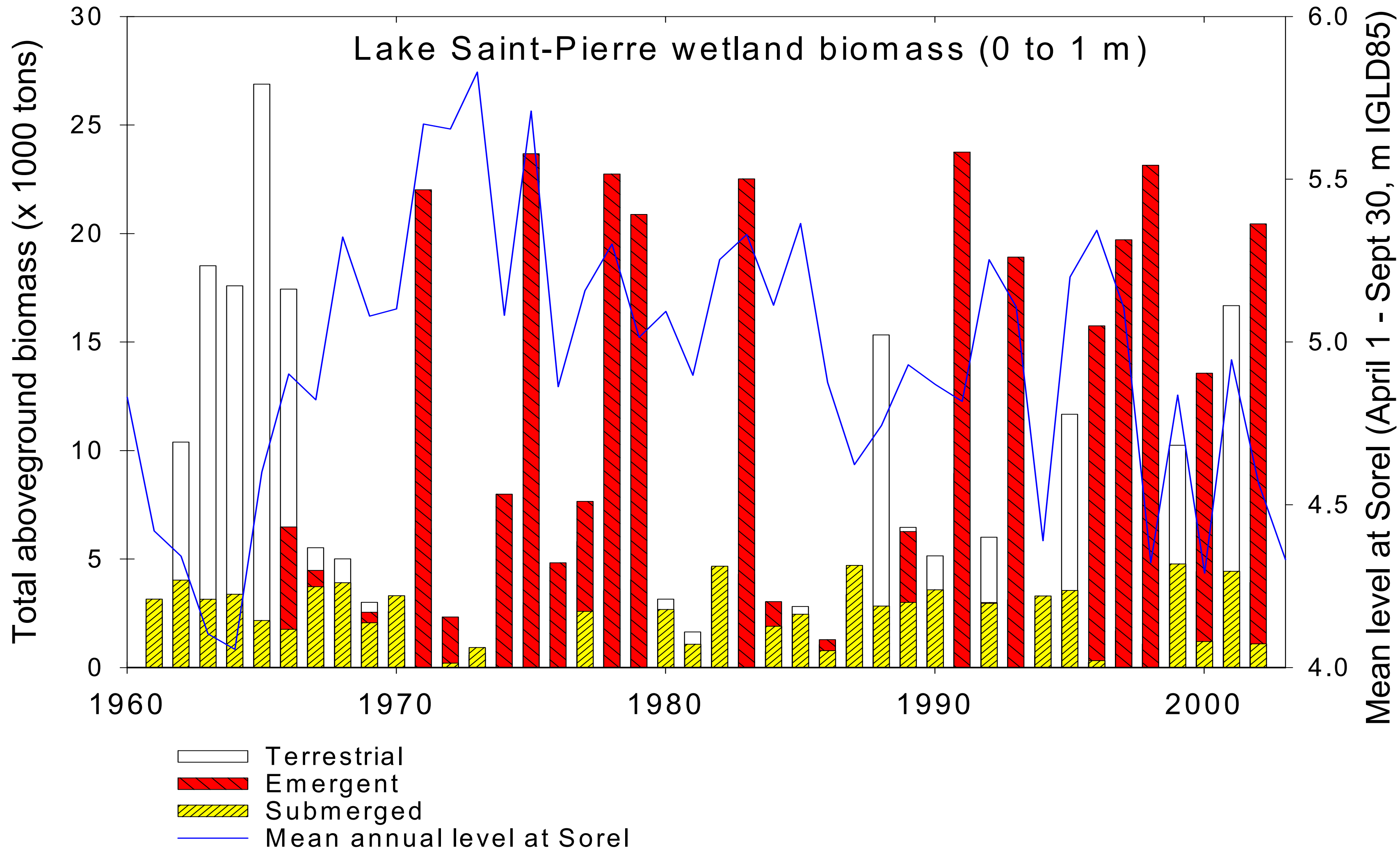

Figure 6 Historical variations (1961-2002) of wetland biomass (tons dry mass) produced annually in lake Saint-Pierre wetlands (0-1 m). HEPA classes were grouped to distinguish between high marsh "terrestrial" (HEPA classes 1, 2, 3), low marsh "emergent" (HEPA classes 4, 6, 8, 9) and "submerged" (5, 7) vegetation. Average water level during the growing season (line) is indicated as a reference

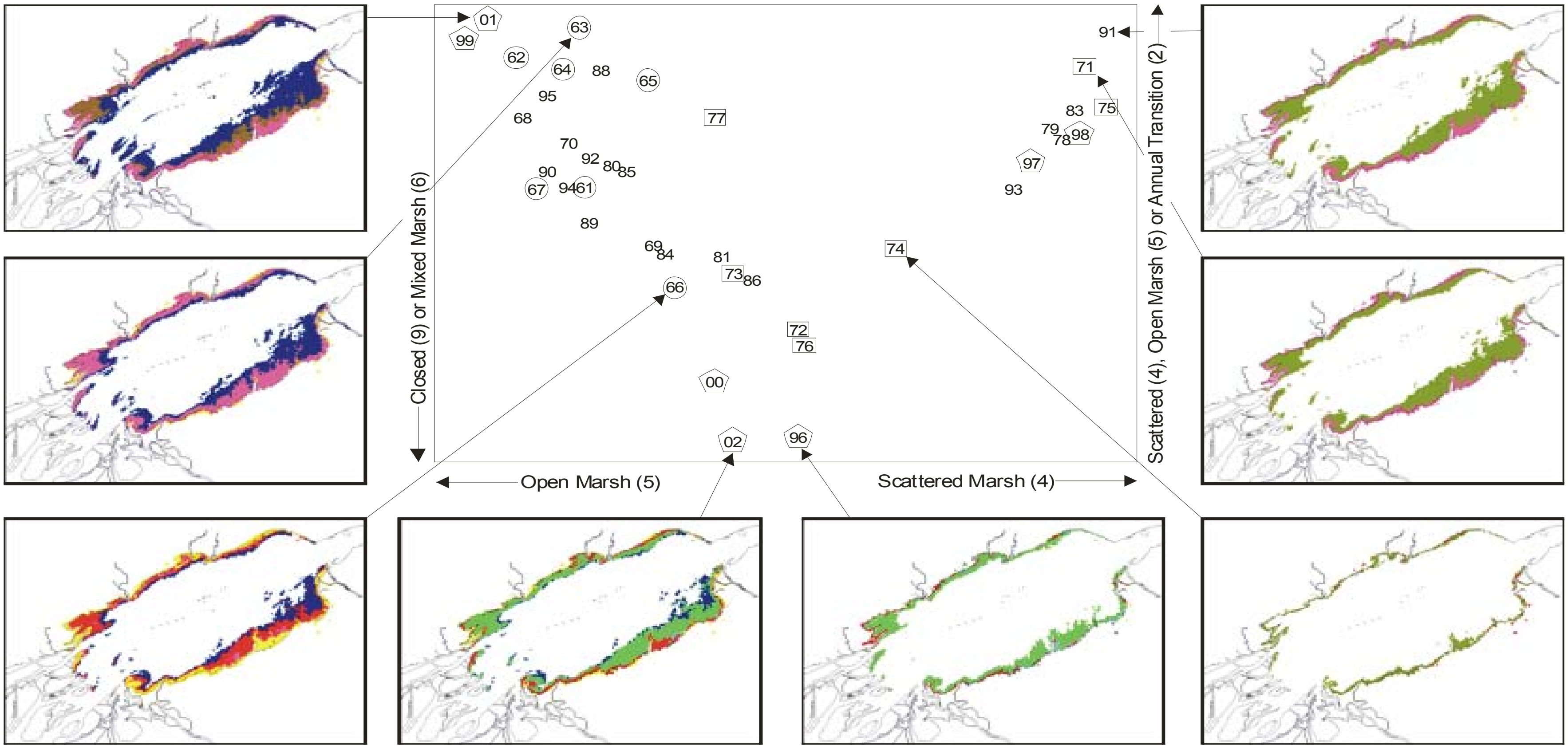

Figure 7 State-space diagram derived from principal component analysis of the surface areas of the 9 HEPA describing the long-term (1961-2002) shifts in Lake Saint-Pierre wetlands. The horizontal axis is the difference in surface area of wetlands with large expanses of open marshes with floating leaves (HEPA class 5, 1963 and 2001 maps to the upper left) and those covered by scattered *Scirpus* emergent marshes (HEPA class 4, 1971 and 1991 maps to the upper right). The vertical axis distinguishes between wetlands dominated by open or scattered marshes or annual transition areas (HEPA classes 5, 4 or 2, near the top) from wetlands with large surfaces of mixed marshes with narrow-leaved emergents (HEPA class 6, 1966 map to the bottom left corner) or closed marshes with aggressive emergents (HEPA class 9, 2002 and 1996 maps to the lower middle). High-level years with low areas of wetlands are located near the center of the diagram (see 1974 map to the lower right corner). Seven-year periods corresponding to different patterns of temporal shifts in wetlands are identified: 1961-1967 (circles), 1971-1977 (squares), 1996-2002 (pentagons)

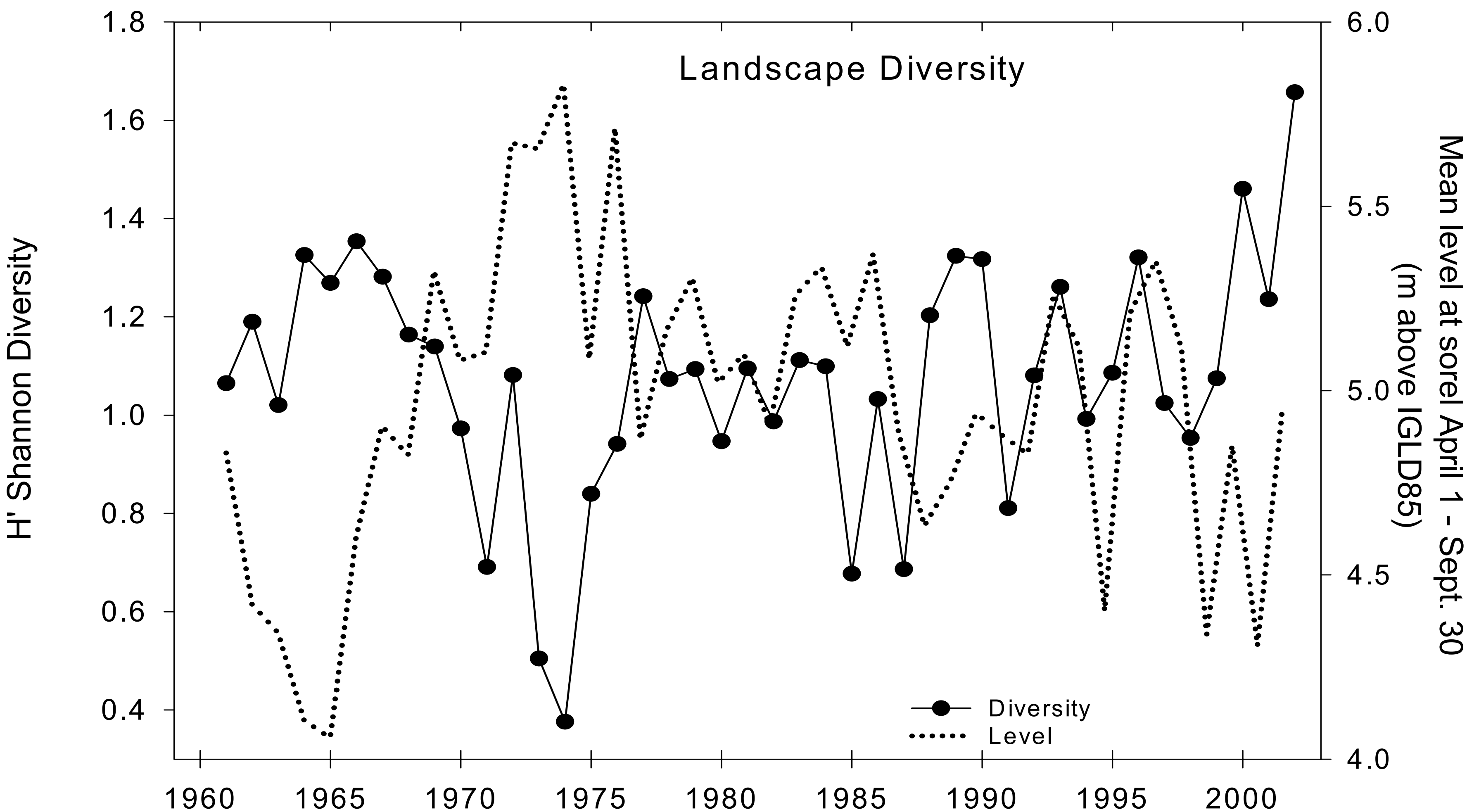

Figure 8 Historical variations (1961-2002) of landscape-scale diversity of lake Saint-Pierre wetlands, derived from changes in the surface area of the 9 HEPA classes

TABLE 1. Summary of physical and chemical characteristics of wetlands under study. Wetlands from fluvial lakes and corridors are presented in upstream-downstream order (Fig. 1). Littoral wetlands were facing open water whereas channel wetlands were in channels between neighbouring islands. Exposure to the predominant SW winds is assessed using the open-water fetch to the nearest shore (m). The range of values recorded over different seasons and years for light extinction coefficient, (K), conductivity and total phosphorus (Hudon, unpublished data) is provided as an indication of water quality, which largely depends upon the predominant water mass (SL, St. Lawrence River, OTT, Ottawa River, Trib., tributaries, Mixed).

Sites	Reference Gauging Station No.	Wetland type	Slope (cm m^{-1})	SW Fetch (m)	Water mass	K (m^{-1})	Conductivity ($\mu S\ cm^{-1}$)	Total P ($\mu g\ l^{-1}$)
Lake Saint-François								
– Pointe Dupuis	14940	Littoral	0.99	650	SL	0.3 – 0.4	226–305	8–14
Lake des Deux Montagnes								
– Île Hay	16005	Littoral	0.78	2 410	OTT	1.3 – 2.4	64–67	31–64
– Baie des Indiens	16005	Littoral	0.66	3 400	OTT	1.3 – 2.4	67–69	31–64
Fluvial corridor								
– Boucherville - Protected	15520	Channel	1.12	510	SL	0.5 – 0.7	230–290	10–38
– Pointe-aux-Trembles	15520	Littoral	3.30	320	Mixed	04 – 1.0	212–290	14–50
– Île aux Cerfeuils	15520	Littoral	2.95	0	Mixed	0.6 – 2.4	93–290	25–75
– Verchères	15660	Channel	1.64	4 040	SL	0.5 – 1.6	230–290	10–33
Lake Saint-Pierre								
North shore								
– Rivière du Loup	15975	Littoral	0.29	8 560	OTT-Trib	1.9 – 3.2	80–130	23–84
– Pointe-du-Lac	15975	Littoral	0.15	38 320	OTT	1.5 – 3.0	80–160	20–30
South shore								
– Pointe Lussaudière	15975	Littoral	0.15	470	Trib	2.5 – 3.5	130–256	25–210
– Pointe d'Henri	15975	Littoral	0.14	1 790	Trib	2.0–3.0	140–250	30–40
– Baie-du-Febvre	15975	Littoral	0.03	5 240	Trib	2.0–3.0	140–235	23–56
– Pointe aux Raisins	15975	Littoral	0.007	1 980	Trib	2.0–3.0	140–235	24–32

TABLE 2. Summary of HEPA distribution data set. Years and sites over which sediment samples were also taken are indicated in bold. *National Defence restricted area – access by foot, plant biomass and sediment sampling were forbidden.

Sites	**Number of quadrat per year (Elevation range, m CD, min-max)**			
	1999	2000	2001	2002
Lake Saint-François				
– Pointe Dupuis	11	**12**	**12**	12
	(-0.19 – 0.66)	**(-0.13 – 0.64)**	**(-0.13 – 0.61)**	(0.07 – 0.77)
Lake des Deux Montagnes				
– Île Hay	17	**16**	**17**	17
	(-0.28 – 0.50)	**(-0.45 – 0.41)**	**(-0.28 – 0.40)**	(-0.32 – 0.33)
– Baie des Indiens	16	**16**	**14**	15
	(-0.63 – 0.83)	**(-0.55 – 0.82)**	**(-0.39 – 0.83)**	(-0.57 – 0.82)
Fluvial corridor				
– Boucherville	24	**15**	**24**	27
	(-0.82 – 0.91)	**(-0.12 – 1.05)**	**(-0.46 – 1.15)**	(-0.36 – 1.11)
– Pointe-aux-Trembles	15	**13**	**15**	14
	(-1.16 – 1.56)	**(0.06 – 1.64)**	**(-1.27 -1.57)**	(-0.59 – 1.67)
– Île aux Cerfeuils	19	**11**	**19**	18
	(-0.95 – 2.39)	**(-0.10 – 2.39)**	**(-1.01 – 2.38)**	(-0.82 – 2.16)
– Verchères	13	**13**	**14**	14
	(-0.18 – 0.76)	**(-0.09 – 0.85)**	**(-0.13 – 1.02)**	-0.21 – 0.98)
Lake Saint-Pierre				
North shore				
– Rivière du Loup	-	**13**	**9**	9
		(0.29 – 1.21)	**(0.30 – 1.09)**	(0.37 – 1.17)
– Pointe-du-Lac	-	**13**	**19**	15
		(0.29 – 1.37)	**(-0.03 – 1.40)**	(0.20 – 1.37)
South shore				
– Pointe Lussaudière*	-	7	-	6
		(0.25 – 0.87)		(0.25 – 0.45)
– Pointe d'Henri*	-	7	7	7
		(-0.30 – 0.54)	(-0.32 – 0.17)	(-0.23 – 0.44)
– Baie-du-Febvre*	10	15	-	15
	(-0.03 – 0.88)	(-0.22 – 0.88)		(-0.17 – 0.88)
– Pointe aux Raisins*	-	12	12	11
		(-0.37 – 0.98)	(-0.35 – -0.03)	(-0.39 – 0.14)
Number of plant quadrats	**125**	**163**	**162**	**180**
Number of sediment samples	**0**	**122**	**143**	**0**

TABLE 3. Summary of climatic (St-Hubert) and hydrological (Lake Saint-Pierre gauging station no. 15975) conditions during the growing seasons (April 1 – Sept. 30) of the fours years of sampling (1999-2002) in comparison with long-term (1960-2002) average conditions.

Variable	**Year**				
	1999	**2000**	**2001**	**2002**	**(1960-2002)**
	average (min., max.)	average (min., max.)	average (min., max.)	average (min., max.)	average (min., max.)
Daily air temperature (^{o}C)	16.8	14.5	16.1	15.7	15.1
	(-5.2, 33.7)	(-6.4, 30.6)	(-5.5, 35.5)	(-8.4, 34.6)	(-14.6, 35.6)
Daily sunshine (h)	8.1	6.7	8.2	7.7	7.2
	(0, 15)	(0, 14.7)	(0, 14.6)	(0, 14.3)	(0, 16)
Daily precipitation (mm)	2.8	3.0	2.3	2.9	2.9
	(0, 53)	(0, 36)	(0, 43)	(0, 35)	(0, 92)
Drought Index (KBDI, mm)	55.9	33.3	47.2	39.8	n.a.
	(0.2, 115.8)	(0.2, 86.9)	(0.2, 114.0)	(0.2, 117.3)	
Daily water level	3.95	4.48	3.91	4.56	4.48
(m IGLD85)	(3.36, 5.39)	(3.68, 5.73)	(3.15, 6.04)	(3.38, 5.78)	(2.94, 7.34)

TABLE 4. Summary of hydrological variables.

Annual Lag	Period	Time interval (t)	Hydrological variable	Anticipated effect on HEPA	Abbreviation	N Variables
Current season	Days prior to sampling	*7, 14, 21, 28, 35, 42, 49, 56*	- Number of days underwater	Duration of wet conditions	js_j_j_*t*	8
			- Mean quadrat elevation with respect to water level (CD)	Height (and short-term variability) above or below the water table in the days-weeks preceding sampling may favour seed germination of annuals or budding of underground structures of perennials. *Ex. The time of dewatering at a given elevation (access to the water table) will determine the germination success of annuals' seeds and of perennials' underground structures.*	Em_j_*t*	8
			- Standard deviation of quadrat elevation with respect to water level (CD)		Esd_j_*t*	8
Current and previous season	Monthly value	*April* *May* *June* *July* *August* (of previous season only)	- Mean quadrat elevation with respect to water level (CD)	Height (and variability) above or below the water table over certain months during HEPA seasonal growth may be critical to the establishment and/or relative importance of taxa with different water requirements (facultative or obligatory), thus defining different classes of wetland HEPA. *Ex. Early drying out of substrate will result in one of the three HEPA high marsh class*	Emonth_*t* E_p_*t*	4 5
			- Standard deviation of quadrat elevation with respect to water level (CD)	Previous season – Hydrological conditions critical for a given growth stage (month) will exert effects over the following growing season. *Ex. Dewatering of an area of submerged HEPA for extended periods (month) at any time of the growing season will lead to barren transition class the following season*	Esd_*t* Esd_p_*t*	4 5
Current And previous season	Growth period	April 1 to sampling day	- Number of days underwater	Average (and variability) in hydrological conditions taking place over the current and the previous growing season (>150 days) determine HEPA classes *Ex. High number of air-water-air transitions and short-term changes in levels will lead to barren transition HEPA*	js_*t*	2
			- Mean quadrat elevation with respect to water level (CD)		Em_*t*	2
			- Standard deviation of quadrat elevation with respect to water level (CD)		Esd_*t*	2
			- Mean quadrat depth	Previous season – The occurrence of favourable level conditions for a given HEPA class in the previous season will allow it to occur over the following (once established, each HEPA class tends to maintain itself). *Ex. Open marsh with floating vegetation and submerged aquatic HEPA will remain in place from one season to the next even if average seasonal water depth varies, as long as no de-watering occurs*	Zm_*t*	2
			Standard deviation of quadrat depth		Zsd_*t*	2
			- Number of transitions air-water and water-air		tr_*t*	2
Total						**54**

TABLE 5. Values of the index (class, interval of % cover, median %) of herbaceous plant cover (Vincent and Bergeron 1983).

Class	Interval of % cover	Median % cover
1	< 1 %	0.5
2	1 - 5 %	3
3	6 - 10 %	8
4	11 - 25 %	18
5	26 - 50 %	37.5
6	51 - 75 %	63
7	> 75 %	87.5

TABLE 6. Correspondence between HEPA classes resulting from Quebec wetland nomenclature (1, Buteau et al. 1994), broad remote sensing categories (2, Lalonde and Létourneau 1996), taxa-based clusters (3), hydrology-based CART model classes (4), diagnostic taxa (5) and aquatic vertebrate habitats (6) – map colour-code is specified. Deep marsh (DM) and shallow marsh (SM) are identified.

QC Wetland Classes (1)	**Remote sensing categories (2)**	**Taxa-based clusters (3)**	**Hydrology-based CART model classes (4)**	**Diagnostic Taxa (5)**	**Aquatic Habitats (6)**
High marsh (dry)	Tall grasses, wet meadow	Wet meadow	1	*Phalaris, Lythrum, Onoclea*	Wet meadow
	Tall grasses, wet meadow, mixed marsh	Annual transition	2	*Polygonum, Urtica, Cyperus >10 cm*	Annual Transition
	Barren	Barren transition	3	*Polygonum, Leersia, Filamentous algae*	Barren transition
Low marsh (wet)	DM Floating leaves	Marsh with floating leaves vegetation	5	*Nymphaea, Nuphar, Vallisneria, Chara (Scirpus lacustris)*	Open marsh (floating leaves vegetation)
	SM Other Marshes	Other Marshes	4	*Scirpus lacustris, Myriophyllum, Potamogeton richardsonii, Heteranthera*	Scattered marsh (tall *Scirpus*)
	SM Narrow-leaved emergent vegetation	Narrow-leaved emergent vegetation	6	*Schoenoplectus pungens, Eleocharis palustris, E. acicularis, Pontederia cordata*	Mixed marsh (narrow-leaved vegetation)
	SM Robust emergent vegetation	Other Marshes	9	*Sparganium, Typha, Phragmites, Sagittaria, Butomus*	Closed marsh (aggressive emergents)
	SM Other Marshes Robust emergent vegetation	Other Marshes	8	*Bolboschoenus, Alisma, Potamogeton richardsonii,* linear-leaved *Potamogeton*	Dense marsh (robust emergent)
Submer-ged	Submerged aquatic vegetation	Submerged aquatic vegetation	7	*Myriophyllum, linear-leaved Potamogeton*	Submerged aquatic vegetation

TABLE 7. Summary of remote sensing images used for validation of model predictions in lake Saint-Pierre, with correspondent daily water level values at the Sorel gauging station (m, IGLD85).

Date	**Water level (m)**	**Accurate (km^2) (%)**	**Inaccurate (km^2) (%)**	**Type**	**Pixel size**	**Source**
1984-09-21	4.64	26.7 (93)	2.0 (7)	Landsat TM	25 m	Lalonde and Létourneau 1996
1986-08-26	5.20	14.4 (91)	1.5 (9)			
1987-08-13	4.70	68.8 (96)	2.8 (4)			
1988-07-30	4.23	32.5 (58)	23.2 (42)			
1988-09-16	4.38	26.5 (64)	14.6 (36)			
1990-07-26 1990-08-21 (composite)	4.89 4.69	28.6 (81)	6.7 (19)	MEIS II	7 m aggregated to 10 m)	DOE 2004
2000-09-18 2000-09-19 2000-09-20 (composite)	4.41 4.43 4.44	34.6 (92)	3.1 (8)	MEIS II	3.5 m (aggregated to 10 m)	DOE 2004
2002-07-22 2002-08-13 (composite)	4.61 4.52	37.2 (88)	5.3 (12)	IKONOS	4 m (aggregated to 10 m)	DOE 2004
Overall		83 (58-96)				

TABLE 8. Summary of hydrological (see abbreviations in Table 5) (cm, mean, standard deviation, minimum - maximum) characteristics of the 9 HEPA classes identified from the hydrological model. For each class, the total number of quadrats per class (N), the number of quadrats from Lake Saint-Pierre (N_{LSP}) and the proportion of well classified quadrats (% well classified) are indicated.

CART leaf no.	**1**	**2**	**3**	**5**	**4**	**6**	**9**	**8**	**7**
Name	Wet meadow	Annual transition	Barren meadow	Open marsh (floating leaves vegetation)	Scattered marsh (tall *Scirpus*)	Mixed marsh (narrow-leaved vegetation)	Closed marsh (aggressive vegetation)	Dense marsh (robust emergents)	Submerged aquatic vegetation
N	120	103	44	162	18	87	34	42	20
N_{LSP}	21	25	4	27	18	59	1	29	0
% well classified	71	70	79	84	45	58	45	45	24
Elevation CD (mean ± s.d.)	104 ± 41	45 ± 29	-3 ± 19	-21 ± 25	- 18 ± 9	32 ± 15	49 ± 12	- 3 ± 17	-0.3 ± 10
Height (+) – Depth (-) (mean ± s.d.)	+69 ± 64	+ 56 ± 38	+ 16 ± 20	- 53 ± 28	- 46 ± 10	- 29 ± 26	- 10 ± 26	- 73 ± 19	- 57 ± 26
E_July (cm)	44 (63)	37 (36)	-2 (19)	-73 (31)	-41 (9)	-59 (14)	-46 (11)	-103 (15)	-99 (11)
Zsd	27 (15)	46 (15)	57 (8)	38 (21)	70 (0)	48 (10)	43 (9)	46 (5)	48 (7)
Zm_pre (cm)	9 (6)	59 (21)	119 (20)	84 (40)	127 (9)	28 (7)	15 (3)	49 (10)	30 (5)
Js_pre (d)	34 (25)	161 (32)	183 (0)	183 (0)	183 (0)	99 (30)	34 (5)	155 (22)	76 (14)

TABLE 9. Summary of biological characteristics of the 9 HEPA classes identified from the hydrological model. The average per quadrat is indicated for each class, including total number of taxa, Shannon-Weaver diversity index H', number of diagnostic species and average biomass (kg dry mass m^{-2}). Life history categories (obligate annuals, perennials), wetland association (obligatory, facultative wetland taxa) and ecological type (meadow, emergents, submerged, floating).

CART leaf no.	**1**	**2**	**3**	**5**	**4**	**6**	**9**	**8**	**7**
Name	Wet meadow	Annual transition	Barren meadow	Open marsh (floating leaves vegetation)	Scattered marsh (tall *Scirpus*)	Mixed marsh (narrow-leaved vegetation)	Closed marsh (aggressive vegetation)	Dense marsh (robust emergents)	Submerged aquatic vegetation
N (quadrats)	120	103	44	162	18	87	34	42	20
Taxa recorded	103	91	48	30	19	59	36	31	17
Taxa / quadrat	9.8	9.3	5.6	4.3	5.3	7.7	5.6	5.9	5.4
H'	1.37	1.49	0.94	0.84	1.16	1.24	1.10	1.17	1.14
Diagnostic Taxa	3	3	3	4	4	4	5	5	2
Biomass (g DRY MASS m^{-2}) mean / (s.d., N)	564 (258, 8)	315 (310, 17)	220 (155, 3)	64 (77, 39)	343 (326, 5)	224 (183, 9)	343 (326, 5)	343 (326, 5)	64 (77, 39)
Life history									
Obligate annuals	1.4	2.7	1.9	0.9	1.1	0.7	0.3	0.7	1.9
Perennials	7.4	6.3	3.6	3.4	4.2	6.8	5.3	5.1	3.4
Wetland association									
Obligatory	4.4	5.8	4.4	4.3	5.3	6.7	4.6	5.8	5.3
Facultative	4.2	3.2	1.1	0	0	0.8	0.9	0.7	0.1
Upland	0.15	0.03	0.02	0	0	0.01	0	0	0
Ecological type									
Meadow	6.4	4.9	1.5	0.04	0	1.8	1.3	0.2	0.1
Emergents	2.6	4.1	2.3	1.0	1.9	4.6	3.1	2.7	0.6
Submerged	0.03	0.1	1.5	2.4	3.2	1.0	0.7	2.6	4.5
Floating	0.08	0.08	0.2	0.8	0.2	0.4	0.4	0.3	0.1

TABLE 10. Average height (cm) and relative abundance (height x median % cover) of the 30 major plant taxa (OBL > 56 occurrences, FAC > 31 occurrences) observed in the 9 HEPA classes identified from the hydrological model. Life history (LH) identifies perennial (P) and annual (A) taxa. Average plant height (cm) is specified for each taxon. Taxa whose abundance is diagnostic of a given HEPA class are indicated in bold. Average relative abundance was computed for all quadrats classified in each CART class, including null values (absence from a given quadrat).

				Relative abundance of major taxa forming each HEPA class defined by CART groups								
Taxa	**Type**	**LH**	**Height (cm)**	**1**	**2**	**3**	**5**	**4**	**6**	**9**	**8**	**7**
				Wet meadow	Annual transition	Barren meadow	Open marsh	Scattered marsh	Mixed marsh	Closed marsh	Dense marsh	Submerged
Phalaris arundinacea	FAC	P	90	**4550**	1193				94	6	1	
Lythrum mature	FAC	P	89	1356	995	11			384	1198	4	11
Phragmites australis	FAC	P	230	1277	814	15				**3478**		
Spartina pectinata	OBL	P	134	**1062**	188				210	98	2	
Onoclea sensibilis	FAC	P	36	**328**	3				1			
Polygonum spp	FAC	A	63	27	**1150**	**566**			1			
Leersia oryzoides	OBL	P	56	150	496	**531**			100	14		
Urtica dioica	FAC	P	53	114	**493**							
Cyperus spp > 10 cm	FAC	P	36	19	**119**	4						
Eleocharis palustris	OBL	P	63	49	570	29	233		**1317**	134	150	9
Schoeneplectus pungens	OBL	P	102	81	551		65	3	**3020**	263	611	44
Bolboschoenus fluviatilis	OBL	P	140	2192	1196	858	321	1397	706	3396	**3298**	
Sparganium eurycarpum	OBL	P	131	487	806	53	2	14	512	**4016**	1130	
Typha spp	OBL	P	200	1212	948	1322	134	406	161	**3949**	1366	693
Butomus umbellatus	OBL	P	82	271	230	47	7	66	52	**1345**	243	0
Scirpus lacustris	OBL	P	158	54	221	260	606	**2798**	512	2189	1399	0
Sagittaria latifolia	OBL	P	61	144	252	65	8	11	633	**2290**	509	32
Pontederia cordata	OBL	P	71	3	27	8	51	96	**206**		84	0
Alisma plantago-aquatica	OBL	P	31	4	55	124	4	64	99	8	**118**	131

Table 10…

				Relative abundance of major taxa forming each HEPA class defined by CART groups								
Taxa	**Type**	**LH**	**Height (cm)**	**1**	**2**	**3**	**5**	**4**	**6**	**9**	**8**	**7**
				Wet meadow	Annual transition	Barren meadow	Open marsh	Scattered marsh	Mixed marsh	Closed marsh	Dense marsh	Submerged
Eleocharis acicularis	OBL	A	5	14	21		1		**60**	12	14	0
Nymphaea odorata	OBL	P	37		2		**455**		8		75	0
Nuphar variegata	OBL	P	47			1	**486**	21	1		**123**	2
Elodea spp	OBL	P	36			1	169	20	106	190	307	**942**
Myriophyllum spp	OBL	P	39			2	275	**485**	26	45	98	436
Potamogeton Richardsonii (bupleuroides, robinsii)	OBL	P	31			2	136	**323**	3		**410**	225
Heteranthera dubia	OBL	A	20			3	28	**243**	12		54	160
Vallisneria americana	OBL	P	16			25	**277**	48	2		67	171
Linear-leaved *Potamogeton (pectinatus, friesii, pusillus, zosteriformis)*	OBL	P	40				2				**27**	**73**
Chara spp	OBL	A	8			23	**168**	21			3	39
Filamentous algae	OBL	A	3	1	4	**39**	33	25	3		16	33

TABLE 11. Spearman correlation coefficients among hydrological variables (at Sorel) and wetlands characteristics derived from hydrological model of HEPA in Lake Saint-Pierre (1961-2002). Prob. < 0.01*, < 0.001**, < 0.0001***.

	Flood Date	Low Water Date	Flood Level	Low Water Level	High-Low Range	Mean Annual Level	Growth Season Level	Year	Total Area	1+2+3 Area	5+7 Area	4+6+8 +9 Area	Total Biomass	1+2+3 Biomass	5+7 Biomass	4+6+8 +9 Biomass
Low Water Date	0.40*															
Flood Level	0.21	0.21														
Low Water Level	0.35	0.28	0.66***													
High-Low Range	0.04	0.07	0.79***	0.12												
Mean Annual Level	0.23	0.22	0.76***	0.89***	0.32											
Growth Season Level	0.39	0.47*	0.79***	0.89***	0.36	0.91***										
Year	0.30	0.24	0.02	-0.03	0.08	-0.11	0.06									
Total Area	-0.32	-0.37	-0.61***	-0.92***	-0.11	-0.81***	-0.87***	-0.01								
1+2+3 Area	-0.26	-0.53**	-0.58***	-0.79***	-0.18	-0.74***	-0.85***	-0.13	0.91***							
5+7 Area	-0.31	-0.20	-0.69***	-0.48*	-0.49*	-0.61***	-0.68***	-0.08	0.49*	0.46*						
4+6+8+9 Area	0.35	0.28	0.37	0.14	0.30	0.32	0.38	0.15	-0.15	-0.26	-0.73***					
Total Biomass	0.04	-0.19	-0.13	-0.59***	0.20	-0.40*	-0.37	0.10	0.65***	0.57***	-0.27	0.54**				
1+2+3 Biomass	-0.28	-0.49*	-0.65***	-0.85***	-0.23	-0.76***	-0.87***	-0.10	0.93***	0.97***	0.46*	-0.21	0.58***			
5+7 Biomass	0.36	0.27	0.41*	0.16	0.33	0.35	0.41*	0.14	-0.17	-0.27	-0.75***	1.00***	0.53**	-0.23		
4+6+8+9 Biomass	-0.31	-0.20	-0.69***	-0.48*	-0.49*	-0.61***	-0.68***	-0.08	0.49*	0.46*	1.00***	-0.73***	-0.27	0.46*	-0.75***	
Shannon's Diversity	-0.13	-0.12	-0.55**	-0.48*	-0.36	-0.34	-0.41*	0.09	0.38	0.29	0.22	0.11	0.31	0.44*	0.08	0.22

TABLE 12. Linear regression equations between selected pairs of hydrological variables (at Sorel) and Lake Saint-Pierre wetland characteristics. All parameter estimates Prob. < 0.0001***.

Hydrological variable (m IGLD85)	Wetland characteristic	Intercept (± std err.)	Slope (± std err.)	r^2	N
Growing season level	Total Area	364.8 (27.3)	-58.8 (5.5)	0.743	42
Growing season level	1+ 2+ 3 Area	202.9 (16.5)	-37.3 (3.3)	0.761	42
Growing season level	1+ 2+ 3 Biomass	68364.2 (6021.2)	-12572.9 (1208.4)	0.730	42
Growing season level	4+ 6+ 8+ 9 Biomass	14652.9 (2341.5)	-2549.7 (469.9)	0.424	42
Spring flood level	4+ 6+ 8+ 9 Biomass	13325.3 (2207.7)	-1778.4 (345.0)	0.399	42
Spring flood level	Shannon Diversity	2.59 (0.35)	-0.24 (0.06)	0.316	42
Late summer-fall low-level	Total Area	397.9 (25.2)	-75.4 (5.8)	0.807	42
Late summer-fall low-level	1+ 2+ 3 Area	204.9 (20.3)	-43.4 (4.7)	0.681	42
Late summer-fall low-level	1+ 2+ 3 Biomass	68027.3 (8094.0)	-14419.7 (1871.2)	0.604	42