Models for submerged vegetation and related environmental changes induced by discharge (water level) variations in the St. Lawrence River (Québec, Canada)

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Abstract: The St. Lawrence River discharge has been regulated since the early 1960's using Plan 1958D (with deviations), which orders of approval for the downstream areas aim at protecting the interests of hydroelectric production, shipping traffic and riparian owners (Carpentier, 2003). In 2000, the Lake Ontario-St. Lawrence River (LO-SL) water level study was initiated to elaborate a new regulation plan ensuring long-term environmental health and sustainability (IJC, 1999). As a part of the LO-SL study, the Technical Working Group on the Environment (ETWG) identified the *Maintenance of habitat diversity* as one of the desired outcomes of an environmentally-sustainable water level regulation plan. The present study identifies, validates and tests several performance indicators (PI) linking hydrological variables to physical and biological components of wetland habitats. The performance indicators are the scientific basis to elaborate new regulation criteria for the environment and to test the environmental suitability of alternate regulation plans.

Eight sets of PI were elaborated between hydrological variables and water temperature, colour, turbidity, suspended solids concentration and light extinction coefficients; whenever feasible, separate relationships were identified for water originating from Lake Ontario and from the Ottawa River and other tributaries. Ten wetland habitat PI were then derived from various combinations of physical predictor variables such as level, discharge, water depth, transparency and exposure to wind. The maximum depth of macrophyte colonization, wetted surface area, percent cover of emergent plants and plant biomass were modelled for different water masses and sectors of the river. A particular emphasis was given to the Lake St. Pierre area, where the predictions derived from plant biomass models were generalised spatially using a GIS for 2000 and 2001. The feedback between submerged aquatic vegetation and physical environmental conditions was also documented by contrasting how plants affect light penetration and sediment characteristics in an exposed and a sheltered plant bed in Boucherville (1999-2001).

The predicted values of each PI were validated using field data acquired for the years 2000 and 2001. Inferred long-term (1960-2002) variations in physical and biological conditions in Lake St. Pierre show it alternated between a lake and a marsh over the past decades, making it highly sensitive to discharge regulation and to chronically low levels expected under climate change scenarios.

Résumé : Le débit du Saint-Laurent a été régularisé depuis les années ’60 suivant le plan 1958D (avec déviations), dont les ordonnances d’approbation pour la portion située en aval visent à sauvegarder les intérêts de la production hydroélectrique, du transport maritime et des riverains (Carpentier, 2003). En 2000, l’étude des niveaux du Lac Ontario-Saint-Laurent (LO-SL) a été amorcée pour élaborer un nouveau plan de régularisation assurant la santé et la pérennité de l’environnement (IJC, 1999). Le groupe de travail technique sur l’environnement (ETWG) de l’étude LO-SL a identifié le *Maintien de la diversité des habitats* comme l’un des objectifs à atteindre par le nouveau plan de régularisation pour assurer le maintien de l’environnement. La présente étude identifie, valide et teste plusieurs indicateurs de performance (PI) reliant les variables hydrologiques aux composantes physiques et biologiques de l’habitat des milieux humides. Les PI représentent la base scientifique permettant d’élaborer de nouveaux critères de régularisation pour l’environnement et de tester l’acceptabilité environnementale de plans de régularisation alternatifs.

Huit groupes de PI ont été élaborés entre les variables hydrologiques et la température, la couleur, la turbidité, la teneur en matières en suspension et le coefficient d’extinction lumineuse de l’eau ; lorsque c’était possible, des relations différentes ont été élaborées pour les eaux provenant du Lac Ontario et de la rivière des Outaouais et des autres tributaires. Dix groupes de PI ont ensuite été dérivés pour les milieux humides à partir de diverses combinaisons de variables physiques prédictives telles que le niveau d’eau, le débit, la profondeur, la transparence et l’exposition au vent. La profondeur maximale de la colonisation par les macrophytes, la superficie mouillée, le pourcentage de couverture des plantes émergentes et la biomasse des plantes ont été modélisées pour les différentes masses d’eau et les différents secteurs du fleuve. On a mis une emphase particulière au Lac Saint-Pierre, où la biomasse de plantes prédite en 2000 et 2001a été généralisée spatialement à l’aide d’un SIG. L’effet rétroactif des plantes submergées sur les conditions environnementales a aussi été documenté en comparant l’impact des plantes sur la pénétration lumineuse et les sédiments en milieux abrités et exposés (Boucherville, 1999-2001).

On a validé les valeurs prédites de chaque PI à l’aide de données de terrain acquises en 2000 et 2001. Les changements modélisés à long terme (1960-2002) des conditions physiques et biologiques au Lac Saint-Pierre indiquent que ce lac a alterné au cours des dernières décennies entre un milieu lacustre et un marais, ce qui le rend très sensible à la régularisation du débit ainsi qu’aux bas niveaux chroniques anticipés par les scénarios de changement climatique.

Errors using inadequate data are much less
than those using no data at all
Charles Babbage

INTRODUCTION

Submerged aquatic vegetation (SAV) represents an important, structurally-complex habitat for a wide range of aquatic fauna, supplying it with shelter from predators and providing a physical support to complex food webs (Tessier, 2002; Cyr and Downing, 1988; Weaver *et al*., 1997). SAV suitability as habitat for different faunal groups and their specific life history stage however depends upon a combination of plant species composition, vertical (canopy) structure and overall biomass (Lillie and Budd, 1992; Lalonde and Downing, 1992). Maintenance of wetlands and underwater habitat diversity therefore requires that a wide range of biomass and species richness be maintained across the system, from low-biomass, monospecific, single-layered SAV beds to high-biomass, plurispecific, multi-layered SAV beds.

The complex relationships between SAV and various environmental conditions are well documented (see review below). In temperate river systems, the seasonal variations of river discharge coincide with familiar changes in water quality: high discharge and associated water levels correspond to high suspended solids concentrations, high turbidity, high colour, low water transparency and high current speed, all of which are less favourable to SAV growth than conditions associated to low discharge regime (Figure 1).

In the St. Lawrence River, seasonal cycles, modulated by discharge regulation, are superimposed to long-term fluctuations (12-16-yr period) in mean annual discharge. Large-scale climatic conditions drive these trends, which correspond to dry and wet periods in the Great Lakes (Changnon, 1994). For example, over the 1912-1994 period, average yearly water level at Sorel varied between 0.5 (in 1964) and 1.84 (in 1973) metres above chart datum (DFO 2003), coinciding with periods of below- and above-average water supply to the Great Lakes. In turn, significant variations in the percent cover of emergent plants were observed downstream in Lake Saint-Pierre, changing one of its large bays from a large marsh (over 35% plant cover in 1965) to an open water area (less than 1% plant cover in 1976) (Hudon, 1997).

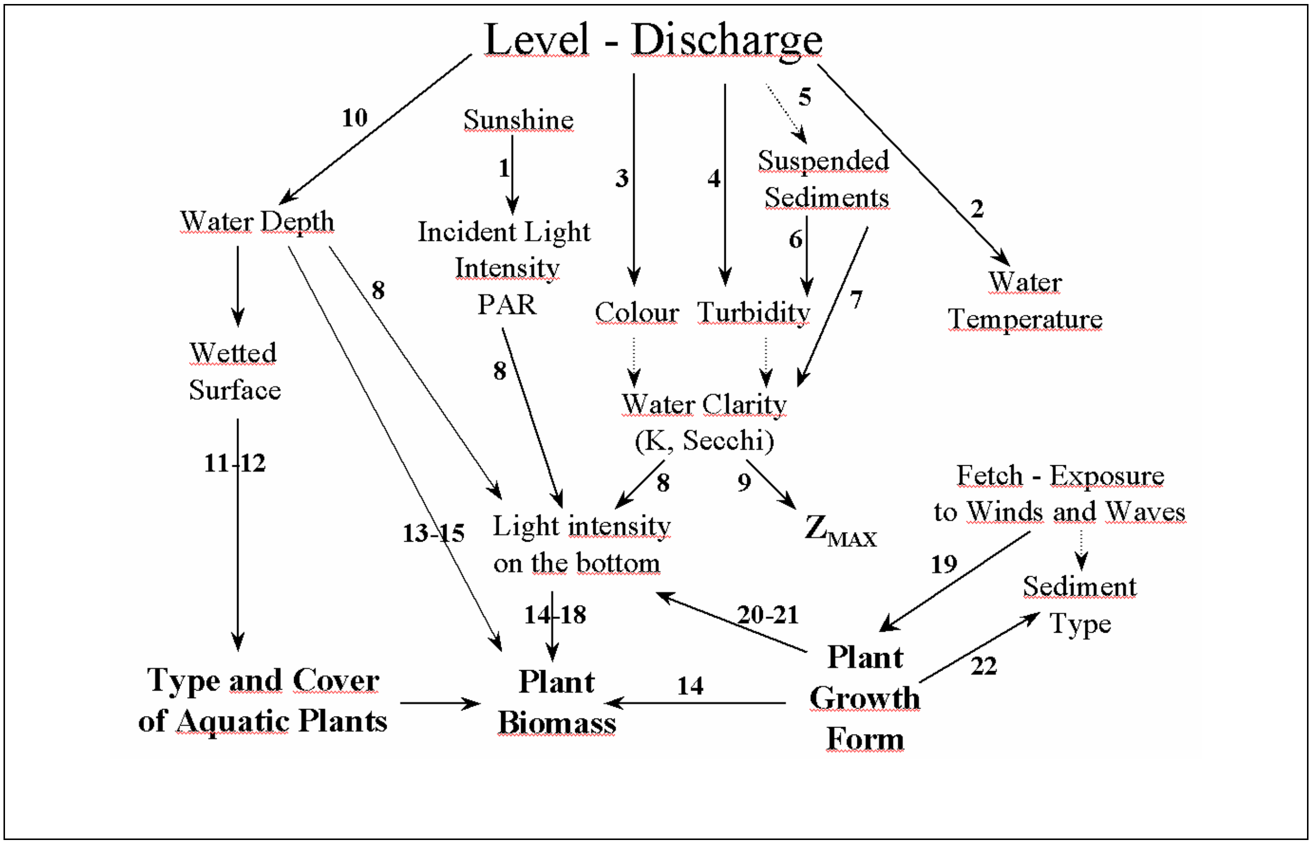

Figure 1 Relationships between physical environmental factors and SAV biomass and distribution. Numbers refer to equations presented in tables 6, 7 and 13

In the future, climatic influences on river hydrology are likely to become even more important owing to the acceleration of climate changes, further altering biological processes of aquatic fauna and of their habitats (Mortsch, 1998; Schindler, 2001). For the Great Lakes and St. Lawrence River basin, increased air temperature (by about 2°C) and duration of growth season are expected; in the Great Lakes, the resulting decline in ice cover duration and increased evaporation (12-17%) are expected to decrease lake levels by about 0.2 to 0.7 m (Lofgren *et al.*, 2002). Recurrent water deficit in the Great Lakes could in turn reduce Lake Ontario discharge to the St. Lawrence River by up to 40% of its long-term average with a concurrent 1.3 m decrease in water levels at Montreal (Mortsch and Quinn, 1996). The 1-m drop in mean annual levels experienced at Montreal harbour Jetty no. 1 in 1999 (5.93 m IGLD85) and 2001 (5.80 m IGLD85) (mean 1960-1998 levels = 6.79 m IGLD85), provided us with a unique opportunity to document their environmental consequences.

We hypothesize that discharge and level variations will affect SAV biomass and distribution, primarily through changes in water depth, transparency and current speed. In addition to the direct effects of environmental conditions on SAV, plants themselves affect their physical environment, especially when they reach high biomass. This feedback, when positive, could further amplify the effects of discharge regulation and of climate change on running water ecosystems by further altering aquatic habitats for fauna.

Effects of physical conditions on SAV

The physical factors influencing biomass and distribution of submerged aquatic vegetation (SAV) belong to three major categories: underwater light climate, water temperature and turbulent motion (Spence 1982). In temperate river systems, the variation of these physical factors is dominated by a seasonal cycle, to which SAV growth is also tightly coupled.

Underwater light intensity determines the depth of SAV colonization and maximum biomass; this response varies according to the combined effects of incident light intensity (PAR, photosynthetically active radiation), water depth and water clarity (K, light extinction coefficient) (Chambers and Kalff, 1985a, 1985b; Carter *et al*., 1994). From that standpoint, water levels represent a more meaningful hydrological variable than discharge, for many aquatic plants and faunal species. Water level and depth determine the light intensity available for plants, as well as access to the floodplain and availability of littoral areas for faunal species. In addition, historical variations in water levels include the cumulative effects of shoreline and river bed alterations, which are not accounted for by total discharge.

Water temperature influences primary (plant) productivity by controlling the rate at which photosynthesis and other chemical reactions take place, with peak production occurring within an optimal range of temperature for each species. In contrast with lakes, in which angiosperm colonisation is limited by thermocline depth (Chambers and Kalff, 1985a; Schwartz *et al*., 2000), water temperature does not change markedly with depth in large rivers

Current speed (Biggs, 1996; Chambers *et al*., 1991), exposure to winds and waves (fetch) (Duarte and Kalff, 1986) and river discharge (French and Chambers, 1997) alter the composition, biomass and vertical development (canopy formation) of SAV. Still-water sites sheltered from dominant winds exhibit high biomass of SAV in the shape of well developed canopies floating loosely under the surface, weakly attached to the bottom whereas sites exposed to swift currents or strong wind-wave effects support lower biomass of linear-leaved SAV species, which tend to be strongly anchored to the bottom (Haslam 1978). In the Nechako River, where both percent bottom cover and SAV biomass were negatively correlated to with mean summer current speed in the channel, modelled changes in SAV following flow reduction indicate that the biomass would increase more in slow reaches than in fast reaches (French and Chambers, 1997-see other refs in that paper).

In the natural environment, when nutrients are plentiful for plant growth, SAV species composition is most likely determined by the combination of light climate, thermal regime and current speed. Under laboratory conditions, two species of SAV of contrasting architectures were shown to have markedly different environmental efficiency with respect to optimum light intensity, temperature range and current (Table 1).

Table 1
Comparative environmental efficiency of *Vallisneria americana* and *Myriophyllum* spp. (modified from Titus and Adams, 1979)

Environmental attribute	***Vallisneria americana***	***Myriophyllum* spp.**
Architecture	Rosettes close to the bottom	Densely ramified stems forming an under surface canopy
Biomass distribution	Near the bottom	Near the surface
Leaves	Linear ribbon-like	Very finely dissected
Optimum light intensity	Low	High
Self-shading potential	Low	High
Response to changes in depth and turbidity	High	Low
Optimum temperature range	Narrow	Broad
Response to current	Good	Poor

Prairies of *Vallisneria americana* represent a typical example of monospecific, single layered, low-biomass SAV found in the St. Lawrence River. In contrast, dense assemblages of *Myriophyllum* spp., *Elodea canadensis* and *Potamogeton* spp. tend to form a thick canopy above the bottom, owing to their complex branching architecture, allowing them to reach very high biomass (see Figure 18). The sharp contrast in ecological range and preference of these architecturally different species led us to hypothesize that a change in environmental conditions in the river could lead to a shift in dominant species. Under high water level conditions, *Vallisneria americana* would tend to dominate the SAV assemblages, whereas *Myriophyllum* spp. and other canopy-forming species would become more important under extremely low-level conditions.

The combination of nested environmental factors, such as exposure to winds and waves, water depth and light intensity, explained 67% of the variance in SAV biomass in the St. Lawrence River (Hudon *et al*., 2000). We hypothesise that chronically low water levels and the associated changes in environmental conditions could generate an increase in total SAV biomass and a shift in its species composition towards canopy-forming species. The integrated response to low water levels should be fully expressed by late summer since SAV re-generate most of their aboveground biomass every year from the germination of belowground structures.

Feedback of SAV growth on environmental conditions

In addition to the complex responses of SAV to their environmental conditions, there is increasing evidence that, once they have colonized the bottom, SAV themselves alter their environment, thus exerting significant impacts on current speed, sediments, water clarity and light penetration through the water column (early literature is extensively reviewed by Sculthorpe, 1967). Dense SAV beds were shown to reduce current speed (Petticrew and Kalff, 1992; Leonard and Luther, 1995; Meeker, 1996), resulting in increases in sedimentation rate and water clarity within macrophyte beds (Vermaat *et al*., 2000). This sets in motion a cycle by which densely canopied SAV beds foster conditions favourable for their growth (Chamber and Kalff, 1985b) through internal, seasonal cycling of river nutrients (Clarke, 2002). Canopy-forming plants pile up under the surface and become extensively colonized by periphyton and filamentous algae (Hudon, unpubl. data), which further reduces water motion (Dodds and Biggs, 2002). The resulting assemblage efficiently obstructs light penetration (Westlake, 1964) and suppresses other SAV species (Madsen *et al*., 1991). Densely canopied SAV beds were also shown to increase spatial heterogeneity and induce daily cycles of water temperature, pH and oxygen concentration (Sand-Jensen *et al*., 1985; Frodge *et al*., 1990). Sharp gradients result from the isolation of dense SAV beds from the main water mass, creating an obstacle to water flow and thus inducing a steeper slope of water during the summer months (Sculthorpe, 1967; Morin and Bouchard, 2001). In summary, once densely canopied SAV beds are established, they induce additional changes in their physical environment and promote an overall shift in aquatic habitats, well beyond the simple, linear effects to be expected from the response to level/discharge variation.

Study Objectives

In this study we document the relationships between the St. Lawrence River water level/discharge and various environmental parameters that influence SAV growth (underwater light climate, water temperature, water movements). We then describe and assess the different models linking environmental parameters to various SAV characteristics (percent cover, maximum depth, biomass). Finally, we examine the feedback mechanisms between SAV and their physical environment. This is achieved by reviewing the literature, analysing multi-year monitoring data series and recently acquired original data taking advantage of the unusually low discharge pattern observed in 1999 and 2001. By integrating this information we will assess the response of SAV to St. Lawrence River discharge/level variations and provide insights on the possible effects of different regulation plans as well as chronic low water level conditions forecasted by climate change scenarios.

The specific objectives of this report are:

1) to quantify the relationships between physical environmental variables and St. Lawrence River water levels/discharge;
2) to model emergent and SAV response to physical environmental variables;
3) to describe the feedback mechanisms by which SAV alter their physical environment;
4) to document methods of data acquisition, model elaboration and validation;
5) to examine the range of physical and biological conditions stemming from previously experienced inter-annual variations of water discharge/level in the St. Lawrence River.

Study Area

The study area covers the St. Lawrence River, between Cornwall (outlet of Lake St. Lawrence), Carillon (outlet of Ottawa River) and Quebec city (Figure 2). Given the complexity of the St. Lawrence River system and the scope of this study, data originating from different segments of the study area were gathered to elaborate the various models.

Models were developed for different segments of the study area, depending on the specific questions asked and the available data, both of which conditioned the type of model selected and its level of precision. Specific information describing each site can be found in the previously published reports and articles or in the result section, for models developed in the present study.

1) The Cornwall-Trois-Rivières area (Hudon and Sylvestre, 1998; Hudon and Lalonde, 1998; Hudon *et al*., 2000; Hudon *et al*., 2003b);

2) Individual fluvial lakes: lakes St. Louis (Bibeault *et al*., 2004 – in prep) and St. Pierre (Hudon *et al*., 2003b; Vis *et al*., 2003; Tessier, 2002);

3) Sub-areas of Lake St. Pierre (Baie du Febvre: Hudon, 1997) and of the fluvial corridor near Montreal (Boucherville: Hudon, 2002, Gosselain *et al*., 2004; Repentigny-Varennes: Hudon and Sylvestre, 1998; Hudon, 2000).

The remainder of this section describes the location of data collection for each variable, the specific challenges they presented and the assumptions that had to be made in order to generalise the information.

1) Seasonal variations were accounted for by grouping data on a monthly or seasonal (3-month) bases, as winter (January-February-March), spring (April-May-June), summer (July-August-September) and fall (October-November-December). Interannual comparisons were made on the basis of plants' growth season, which was arbitrarily defined as the period extending between April 1 to September 30. This period roughly coincides with the period over which water temperature is $\geq 10^{o}C$ (Hudon *et al.*, 2003a).
2) Incident radiation (PAR) at the water surface was derived for the entire study area from daily measurements taken in the Montreal area (L'Assomption, Dorval and Saint-Hubert weather stations, DOE, 2003a). Since all models contrasted SAV distribution and biomass at the end

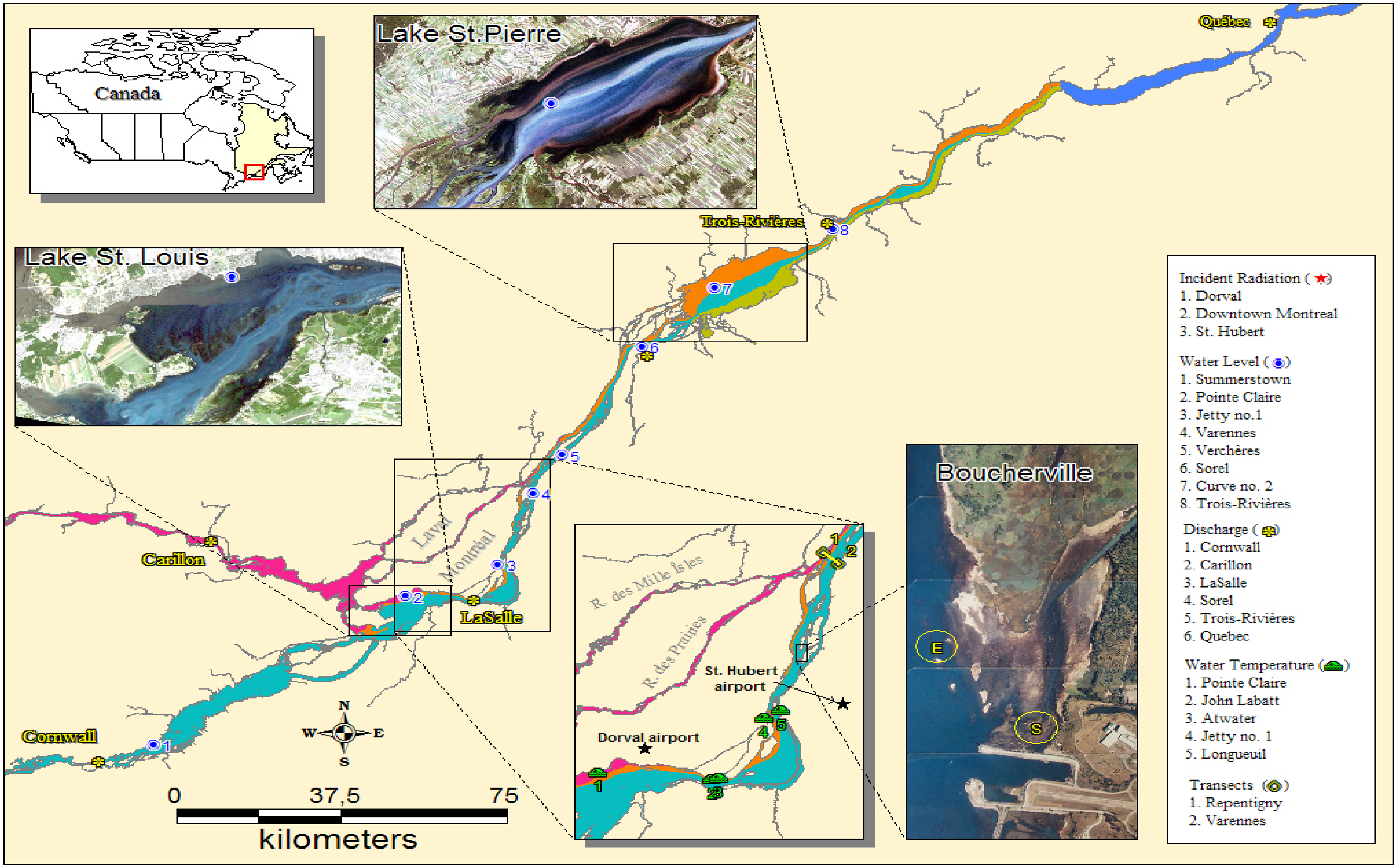

Figure 2 The Lower St. Lawrence River between Cornwall and Quebec City. Different water colours indicate the general distribution and mixing of waters originating from Lake Ontario, the Ottawa River (Carillon) and other tributaries (see text). Sites at which various physical data were acquired are indicated by different symbols for each variable. Photographic insets show the 3 major areas of SAV data acquisition: Lake St. Louis (LANDSAT Image, Aug. 2001), Lake St. Pierre (LANDSAT Image, Aug 1986), Boucherville islands (aerial photograph, Aug 1999).

of the growth season over different years, it was assumed that inter-annual variations of PAR were more important than local differences.

3) Water levels determine water depth at any given point and thus influence underwater light intensity. Daily water level values were obtained at seven locations (Pointe Claire, Montreal Harbour Jetty no. 1, Varennes, Verchères, Sorel, Lake St. Pierre and Trois-Rivières) (DFO, 2003); proximity to sampling sites determined the selection of the appropriate gauging station, which was used to transform measured sampling depth into elevation with respect to the appropriate datum (Chart Datum (CD), International Great Lakes Datum of 1985 (IGLD85), Mean Sea Level (MSL)).
4) Discharge is linked to water quality characteristics such as suspended sediment concentrations, colour and turbidity, all of which influence water transparency. Daily discharge values were obtained at several locations in the study area, either from hydroelectric production facilities (at Cornwall and Carillon dams), from calibrated level-discharge curves (LaSalle) or inferred from the sum of all upstream sources (Sorel, Trois-Rivières, Québec) (DOE, 2003b); proximity to sampling sites determined the selection of the appropriate station.
5) Underwater light climate is primarily controlled by the relative importance and mixing of waters originating from Lake Ontario, the Ottawa River and other tributaries, which differ from each other (and on a seasonal basis) in terms of their turbidity, suspended solids concentrations, colour and overall transparency. Local erosion injects fine clay particles into the water, which form distinct milky plumes perceptible for several km downstream of the erosion sites. The combination of these factors result in seasonally and spatially variable light quantity (and quality) on the bottom. Underwater light attenuation was measured directly in the field at each site at the time of sampling; analyses were made presuming that punctual measurements were representative of conditions prevailing during the plants' growth season.
6) Water currents differ among location according to fluvial morphology: narrow, fast-flowing fluvial corridors are subjected to variable current speed and direction; areas between islands and shallows are sheltered, whereas broad, shallow areas in slow-flowing fluvial lakes may be subjected to variable wind-waves actions depending on their orientation (fetch) with respect to dominant winds (NE-SW). Current speed was measured directly in the field at

each sampling site; fetch at each site was estimated by the distance to the nearest shore (or to a reference line perpendicular to the main river axis) along the direction of dominant winds.

7) Water temperature varies seasonally, among water masses, as a function of water depth and distance into the floodplain /shallow water areas. For the purposes of this study, we concentrated on water temperature variations in the main course of the river, which represent a large water volume(7000 to 12000 $m^3 s^{-1}$) which transits quickly (within a week) through the study area. Shallow littoral zones and the floodplain were excluded since they experience short term (diurnal) and small-scale (≤ km) temperature variations too fine for the scope of the present study. Daily/weekly water temperature measurements were obtained for six municipal (Pointe Claire, Atwater, Charles-J. Des Baillets, Longueuil, Sainte-Foy, Lévis) and one industrial (John Labatt Brewery) water intake sites Hourly temperature data was obtained for Canadian Coast Guard buoys S141 (near Sorel) and C65 (near Trois-Rivières) (Armellin *et al*., 2003; Hudon *et al.*, 2003a).. Since models contrasted SAV distribution and biomass at the end of the growth season over different years, it was assumed that inter-annual variations of water temperature were more important than local, short-term differences.
8) Nutrients were presumed to be in sufficient concentration for SAV growth, as supported by measurements of excess N and P concentrations in SAV tissues at all sites (Hudon *et al*., 2000; Hudon and Lalonde, 1998).
9) Substrate was presumed to be adequate for SAV growth over the entire study area, as supported by sediment sample analysis at several sites (Hudon *et al*., 2003b).

METHODS

Models presented in this study originate from three major sources (Table 2):

1) Previously published information;

2) Analysis of long-term monitoring data series obtained from various governmental and institutional sources;

3) Analysis of recent, unpublished field data re-analysed for the purpose of the present study.

Physical, climate and water quality data

Daily cumulative sunshine (h) was obtained from St. Hubert airport and was related to daily cumulative photosynthetically available radiation (PAR), which was measured during the summer of 1999 in Montreal (Hudon, unpubl. data). The relationships between water quantity (level, discharge) and physical water quality characteristics (temperature, turbidity, colour, light extinction coefficient) for the St. Lawrence River were determined from historical data (10-20 years) obtained for various locations in the St. Lawrence River (Table 2).

Daily water levels (7 gauging stations) were obtained from the Department of Fisheries and Oceans Marine Environment Data Service (DFO, 2003). Water level values were adjusted to navigation charts (hereafter referred to as chart datum reference level (CD), by subtracting station elevation from original data. Elevation of each SAV sample was measured at collection time using water depth and corrected according to daily water level at the nearest gauging station (without correction for the water slope), to estimate samples' elevation with respect to chart datum (CD). Daily discharge values (1960-2002) were obtained for Cornwall and Carillon hydroelectric dams and computed for LaSalle, Sorel, Trois-Rivières, Québec (DOE, 2003b).

An assessment of interannual and monthly variability of incident photosynthetically active radiation (PAR, Einstein m^{-2} d^{-1}) was required to assess the changes of underwater light intensity under different water level scenarios. Historical (1951-2002) hourly sunshine data was obtained for Saint-Hubert, l'Assomption and Dorval weather stations (DOE, 2003a) (Table 2). Incident radiation (I_0) was estimated from a linear regression predicting cumulative daily PAR from the average daily number of hours of sunshine (from April 1st to Sept. 30) in 1999. Cumulative daily photosynthetically active radiation (Li-Cor aerial probe LI-190SB and LI-1400 data logger) was measured in downtown Montreal in 1999 (April to October).

Table 2
Description of the sources of data used in this study

Variable (units)	Type of information	Location	Duration	Frequency	Source
Sunshine (h)	Field measurement	St. Hubert, Dorval , l'Assomption	1951-2002 (composite)	Cumulative daily	DOE, 2003a
Photosynthetically Active Radiation (PAR, Einstein m^{-2} d^{-1})	Field measurement	Montreal	1999	Hourly (integrated)	Hudon, unpubl. data
Discharge (Q, m^3 s^{-1})	Measurement Measurement Calculation Calculation Calculation Calculation	Carillon Cornwall LaSalle Sorel Trois-Rivières Québec	1960-2002	Daily	DOE, 2003b
Water level (m, IGLD85)	Field gauges	Pointe Claire Jetty no. 1 Verchères Varennes Sorel Curve no. 2 LSP Trois-Rivières	1912-2002 (year of beginning differs among gauging stations)	Daily	DFO, 2003
Water temperature (^{o}C)	Measurement at intake point Automated probe on buoy	Pointe Claire Atwater Charles-J. Des Baillets John Labatt Longueuil Sainte-Foy Lévis Sorel (Buoy S141) Trois-Rivières (Buoy C65)	1990-2001 1918-1998 1980-2001 1977-2001 1992-2002 1986-2001 1997-2001 1998-2002 1998-2002	Daily to Weekly (depending on period and station) Hourly	Armellin *et al*., 2003; Hudon *et al*., 2003a

Table 2

Variable (units)	Type of information	Location	Duration	Frequency	Source
True Colour (Pt-Co units)	Measurement at intake point	Charles-J. Des Baillets	1995-2001	Weekly	Armellin *et al*., 2003
Turbidity (NTU, Nephelometric turbidity units)	Measurement at intake point	Charles-J. Des Baillets	1981-2001	Daily	Armellin *et al*., 2003
Light extinction coefficient (K, m^{-1})	Field measurements	River	1993-2003	Concurrent with SAV sampling	Hudon and Sylvestre, 1998; Hudon, unpubl. data
Sediment characteristics (% composition)	Field collections and laboratory analyses	Lake St. Louis, Boucherville, Lake St. Pierre	2000-2001	Concurrent with SAV sampling	Hudon *et al*., 2003a; Hudon, unpubl. data
Digital elevation model (m above Mean Sea Level)	GIS map of surface elevation	Lake St. Pierre	2003	n.a.	DOE, 2003c
Cover of emergents (%)	Remote sensing and aerial photographs	Baie du Febvre	1965-1990	Annual	Lalonde and Létourneau, 1996
Limit of dense and of scattered emergents (X, Y coordinates)	Hydrofoil field survey with DGPS	Lake St. Pierre	2000-2003	Annual	Hudon, unpubl. data
Maximum SAV Biomass (g dry mass m^{-2})	Field collections and laboratory analyses	Various locations throughout the river	1993-2001	Annual (august-september)	Hudon and Lalonde, 1998; Hudon, 1997, Hudon and Amyot, unpubl. data

Light extinction coefficient (K, m^{-1}) in open water and within SAV monospecific canopies were derived from measurements of underwater light penetration (LI-COR aerial probe SA-LI188B and 4 π underwater probe SA-LI192SA) coupled to a data logger (Li-1000) and a pressure gauge (KPSI, Series 730) indicating water depth (within 1 cm). All probes were connected to the data logger for simultaneous recording. For measurements within SAV, the underwater light probe and depth gauge were mounted at the end of a 5-m-long retractable pole. The pole was entered diagonally through the plant bed, thus ensuring that the SAV canopy located directly above the measurement points, at increasing depth, remained undisturbed. These measurements were used to calculate the fraction (I_z/I_0) of surface light intensity (I_0) reaching each depth interval (I_z). Difference in the vertical distribution of SAV biomass resulting in changes in K with depth were detected by a shift in the slope of the relationship between depth (m) and ln I_z/I_0.

The characteristics of superficial sediments were determined by sampling the upper 10 cm of sediments at the time of SAV collections by divers in Lake St. Pierre (2000, N = 58; 2001, N= 60), Boucherville (2000, N = 7; 2001, N= 7), and Lake St. Louis (2001, N = 13). Percent composition in sand, silt and clay, particle size mean diameter (phi, µm), percent volatile solid (organic combustible; APHA 1995 method 2450 E) and nutrient (Kjeldahl organic nitrogen and total phosphorus) contents (APHA methods 4500 N_{org} B-C and 4500 P E.; respectively) and pH (APHA 1995, method 4500 H+B) were measured.

Biological data acquisition

Emergent plant cover at the end of the growth season (1965-1990) was assessed using standard aerial photography or numerical imagery acquired from an aircraft (MEIS) or a satellite (Landsat TM, IKONOS) (Lalonde and Létourneau, 1996; Jean *et al.,* 2002). Field assessment of emergent plant cover was also made using a hydrofoil at the end of the growth season (in August of 2000-2003), allowing to trace the limit of (with a DGPS) marshy areas in which emergent plants cover 50% or more of the available surface (which are clearly visible from remote sensing surveys) and the limit of emergent plants covering 1-50% of available surface area (which is not reliably detected from remote sensing surveys owing to the fact that plant patch sizes < pixel size). The reliability of field surveys is somewhat limited by the occurrence of adequate meteorological conditions (so that the smallest patches of emergent plants can be seen) and water levels. Late summer levels must be sufficiently high to allow passage in the shallowest, densely vegetated areas, yet sufficiently low to allow vegetation in deep-water to reach the surface. These weaknesses were compensated by the averaging out the results of multiple passages to survey more difficult areas over a given year.

Submerged vegetation was sampled at a number of sites in the St. Lawrence River between 1993 and 2002, to characterize the seasonal changes of species composition and biomass under a range of water levels. Submerged plant biomass (above and belowground structures) was collected in 25 x 25 cm quadrats harvested by SCUBA divers. Each site was sampled in clusters of 2-5 quadrats, depending on the level of heterogeneity at each site. Sites at which biomass was < 5 g dry mass m^{-2} of aboveground vegetation were defined as the maximum depth of macrophyte colonisation (Z_{MAX}).

All vegetation within the quadrat was collected by hand, occasionally using a knife to loosen the sediments and gently dislodge roots. Aboveground parts were identified and processed separately for each species, while underground biomass was pooled for each quadrat. Metaphyton (filamentous algae) was set aside as a separate category whenever found in sufficient abundance. Loose detritus, microscopic periphyton and sediment were carefully washed off plant matter, which was subsequently dried to a constant mass (at 80 ^{o}C) and weighed (0.001 g).

The effects of exposure to wind-waves and current on plant morphology and the feedback of SAV on physical environmental conditions (light extinction, sediment composition) were examined in more details at Boucherville (1999), by contrasting a sheltered (mostly colonized by *Myriophyllum* spp., *Elodea canadensis*) and an exposed (characterized by *Heteranthera dubia* and *Vallisneria americana*) site. Complete specimens were classified into stem types of homogeneous leaf density; for each specimen, the complete plant, bare stems, sparsely foliated stems, densely foliated stems and new leaves growing on bare stems (observed only after Sept. 29 1999) were measured, dried and weighted. These values allowed to reconstruct the seasonal changes in the proportion of total biomass and total plant length belonging to each plant segment category. The degree to which SAV were stretched underwater or piled up under the surface (stretching coefficient: SAV total length/water depth) was computed for specimen collected at exposed and sheltered sites at fortnightly intervals.

Statistical analyses

Quantitative relationships between physical, biological characteristics and water level/discharge at various locations of the St. Lawrence River were determined from linear and non-linear regressions available from standard statistical packages (SAS, Statgraphics, Excel, Jmp, SigmaPlot). Linear regressions between monthly level in Montreal Harbour and monthly water quality characteristics (temperature, colour and turbidity) were computed for the period of plant growth (April 1st-Sept. 30); separate regressions for each month were computed for water temperature to eliminate seasonal effects. Physical and biological conditions found at different sites subjected to contrasting environmental characteristics were assessed using comparisons of mean values among groups (ANOVAs) after transformation ($\log_{10}$ + minimum value/2) of variables whose variance differed among groups. Non parametric analyses such as Classification and Regression Tree (CART, Breiman *et al*., 1984) were used for binary, qualitative-categorical and semi-quantitative variables (see Hudon *et al*., 2000 for full description).

RESULTS

Relationships between water discharge, level and physical environmental characteristics

All equations described in this section are summarized in Table 6.

Sunshine and photosynthetically available radiation (PAR)

Equation 1 was computed to translate the number of daily hours of sunshine (*Sun*), into the amount of daily radiation available for plant photosynthesis (PAR, Einstein m^{-2} d^{-1}) (Table 6). This information is required to assess daily incident radiation at the surface of water (I_0), which allows to calculate the amount of radiation penetrating to the bottom (I_z), according to different combinations of water depth (Z) and transparency (K, m^{-1}) (equation 8, Table 6).

Equation 1

$$\boldsymbol{PAR = 9.68 + 3.17\,Sun} \qquad r^2 = 0.81,\ n = 165,\ p < 0.001$$

Water temperature

Water temperature is a parameter of great importance since it determines the rate of chemical reactions which control plant and animal metabolism, growth rate and the timing of their life history sequence. River discharge is the best hydrological variable to describe the relationship between the origin of water masses and water temperature, because it relates directly to volume and heat retention-transfer capacity. However, downstream of their confluence in the Montreal area, earlier studies have shown that the water masses originating from Lake Ontario and from the Ottawa River do not mix entirely but mostly retain their phycico-chemical and biological characteristics, within separate plumes (Hudon, 2000). Ottawa River waters tend to warm up earlier and to cool off earlier than waters originating from Lake Ontario (Hudon *et al*., 2003a).

Examination of daily water temperature data measured at different locations between Montreal (Pointe Claire), on buoys in the navigation channel (Sorel, Trois-Rivières) and near Quebec (Ste-Foy, Lévis) (Figure 3) shows the largely synchronous variations in temperature of the main river course as water travels downstream, suggesting that regional patterns of air temperature exert a major influence on river water temperature.

The mismatch in the seasonal temperature cycle of water masses originating from the Ottawa River and Lake Ontario was perceptible in the slightly warmer spring and colder fall water temperatures observed at Pointe Claire, which was influenced by a higher proportion of Ottawa River waters in periods of high discharge.

However, the high concordance of water temperature from all stations between April and September (within 1°C on average) prompted our use of long-term data series from filtration plants near Montreal to describe the relationships between level, discharge and water temperature for the St. Lawrence River. These relationships apply only to the main course of the river. Shallow littoral zones and the floodplain were excluded since they vary at temporal (daily) and spatial (km) scales which are too small for the scope of this study.

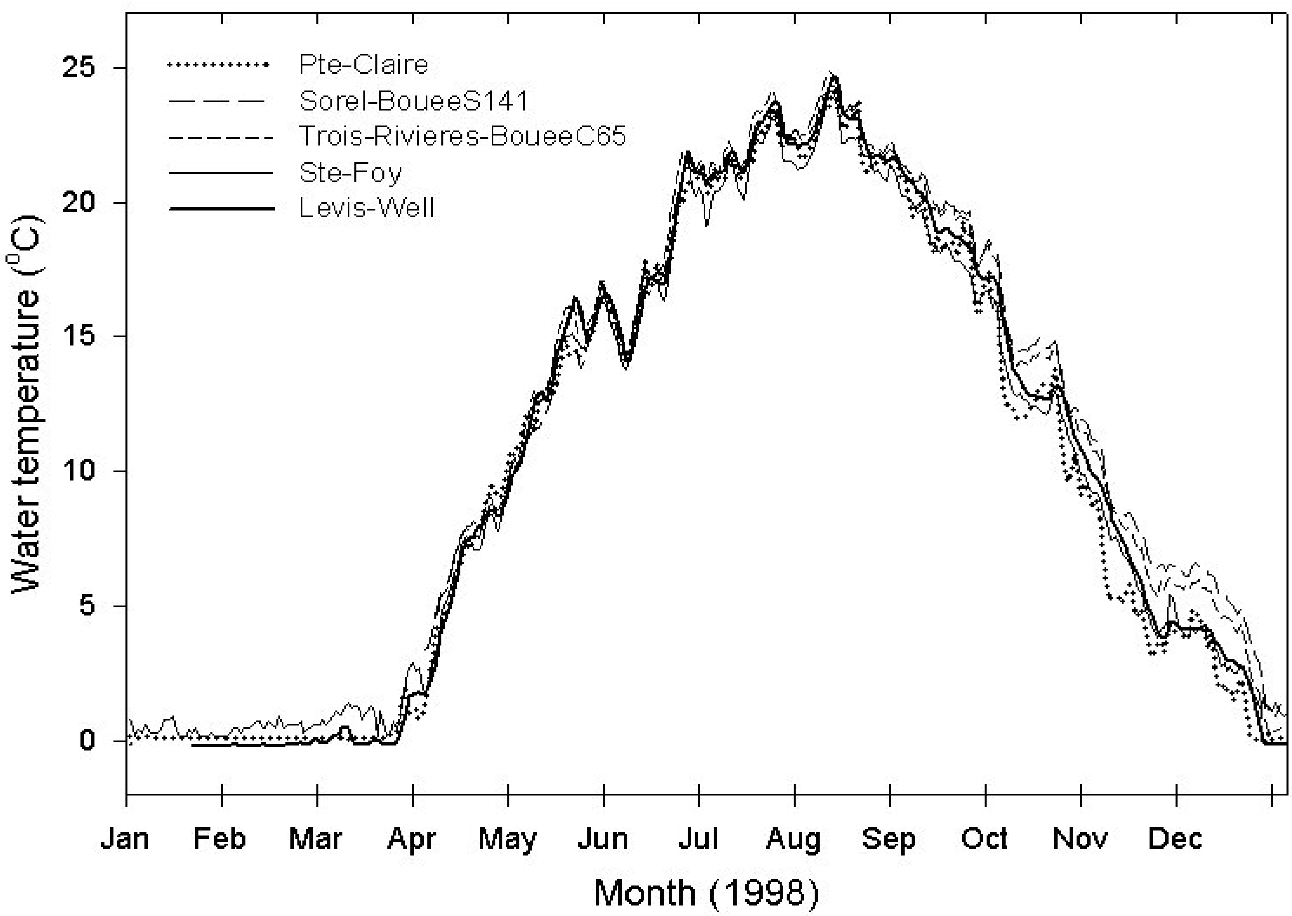

Figure 3 Water temperature variations recorded in 1998 in the main course of the St. Lawrence River between Montreal (Pointe Claire), Sorel, Trois-Rivières and the Quebec area (data from Armellin *et al.*, 2003)

The influence of the different water masses on daily water temperature was perceptible in the linear models developed for three of the water filtration plants in the Montreal area (Table 3, see also equations 2a in Table 6), all of which included significant terms for the Ottawa River discharge and the ratio of Ottawa to total river discharge, in addition to the common effects of daily air temperature and of a seasonal component (intercept).

Table 3
Linear models (equations 2a) predicting daily St. Lawrence River water temperature at three water filtration plants in the Montreal area. Multiple intercepts, common slopes regression coefficients (± standard error) are indicated: Average daily air temperature (Dorval airport), daily Ottawa River discharge at Carillon, daily ratio of Ottawa River to total river discharge (at Cornwall + Carillon)

Linear model parameters	Water filtration plants in the Montreal area Longueuil (1992-2002)	Charles-J. Des Baillets (1980-2001)	Atwater (1973-1998)
Intercept in Summer	16.1 ± 0.26	15.9 ± 0.26	15.5 ± 0.26
Intercept in Autumn	10.7 ± 0.26	10.6 ± 0.26	10.1 ± 0.26
Intercept in Winter	6.8 ± 0.26	6.7 ± 0.26	6.2 ± 0.26
Intercept in Spring	8.7 ± 0.26	8.6 ± 0.26	8.1 ± 0.26
Air temperature (^oC)	0.36 ± 0.006	0.36 ± 0.006	0.36 ± 0.006
Ottawa River Discharge ($m^3 s^{-1}$)	0.00048 ± 0.0001	0.00048 ± 0.0001	0.00048 ± 0.0001
Ratio of Ottawa River to total discharge	-20.55 ± 2.207	-20.55 ± 2.207	-20.55 ± 2.207

Note: For each water filtration plant, the time interval covered is specified. The proportion of the total explained variance, r^2= 89%. All terms are very highly significant (p < 0.001).

Examination of the relationship between monthly average water level and temperature for the Montreal area revealed significant, negative correlations for the months of May, June and September for the Charles-J. Des Baillets station (City of Montreal), which is primarily under the influence of water originating from Lake Ontario (Table 4, equation 2b).

Table 4
Linear regressions (equations 2b) between the mean monthly water level (L, m above chart datum) (Montreal Harbour Jetty no. 1) and the mean monthly water temperature (T, °C) at Montreal (Charles-J. Des Baillets water filtration plant), between 1981 and 2001 (from Hudon *et al.*, 2003a)

Month	Equation predicting mean monthly temperature	Mean 1981-2001 (s.d.)	*n*	r^2 (*p*)
April	$4.61 - 0.16\ L_{April}$	4.33 (1.26)	21	0.005 *n.s.*
May	$12.60 - 1.45\ L_{May}$	10.46 (2.29)	18	0.656***
June	$18.29 - 2.00\ L_{June}$	16.20 (1.52)	21	0.462***
July	$21.25 - 0.88\ L_{July}$	20.55 (1.37)	19	0.096 *n.s.*
August	$22.73 - 0.95\ L_{August}$	22.11 (1.10)	19	0.123 *n.s.*
September	$19.92 - 1.31\ L_{September}$	19.12 (1.13)	20	0.250*

Note: For each regression equation, the number of monthly mean values available for each regression (*n*), the fraction of the total variance explained (r^2) and the significance level of associated probability *(p)* are indicated: *($p < 0.05$); ***($p < 0.001$); *n.s.* (non significant).

Very similar, significant relationships were obtained for the months of May through September for the water intake of the John Labatt Brewery (Table 5, equation 2c),which is influenced by a mixture of Ottawa River and Lake Ontario waters. These results indicate that low discharge periods coincide with precocious warming in the spring and late cooling in the fall, which extent the growth season and elevate the cumulative number of degree-days.

In addition to relationships between monthly average values for a number of years, mean annual water temperature were examined in relation to mean annual water levels in the Montreal area, to ascertain whether the inverse relationships identified with discharge of the St. Lawrence and Ottawa rivers (equation 2d, Table 6) would remain perceptible once they were cumulated and translated into water level downstream of the confluence. As anticipated, a negative relationship ($p < 0.05$) was observed between average annual

Table 5
Linear regressions (equations 2c) between the average monthly water level (L, m above chart datum) (Montreal Harbour Jetty no. 1) and the average monthly water temperature (T, ^{o}C) at Montreal (John Labatt Brewery water filtration plant), between 1977 and 2001 (from Hudon *et al*., 2003a)

Month	Equation predicting mean monthly temperature	Mean 1977-2001 (s.d.)	*n*	r^2 (*p*)
April	$5.80–0.40\ L_{April}$	5.07 (1.52)	24	0.02 *n.s.*
May	$14.57–1.45\ L_{May}$	12.34 (1.28)	25	0.504***
June	$19.33–1.74\ L_{June}$	17.51 (1.81)	25	0.221*
July	$22.70–0.85\ L_{July}$	21.99 (0.92)	25	0.176*
August	$23.29–0.92\ L_{August}$	22.61 (0.97)	25	0.160*
September	$19.69–1.21\ L_{September}$	18.87 (0.89)	25	0.325**

Note: For each regression equation, the number of monthly mean values available for each regression (*n*), the fraction of the total variance explained (r^2) and the significance level of associated probability (*p*) are indicated: * ($p < 0$ .05); **($p < 0.01$); ***($p < 0.001$); *n.s.* (non-significant).

water temperature (T_{Year}, ºC) at the two City of Montreal water filtration plants (Atwater 1919-1998 and Charles-J. DesBaillets 1998-2001) and mean annual level (L_{Year}, m above CD) at Montreal Harbour (Jetty no. 1), described by the equation 2d :

Equation 2d

$$\boldsymbol{T_{Year} = 10.36 - 0.53\ L_{Year}} \qquad r^2 = 0.16,\quad n = 63,\quad p < 0.01,\ (1919\text{-}2001)$$

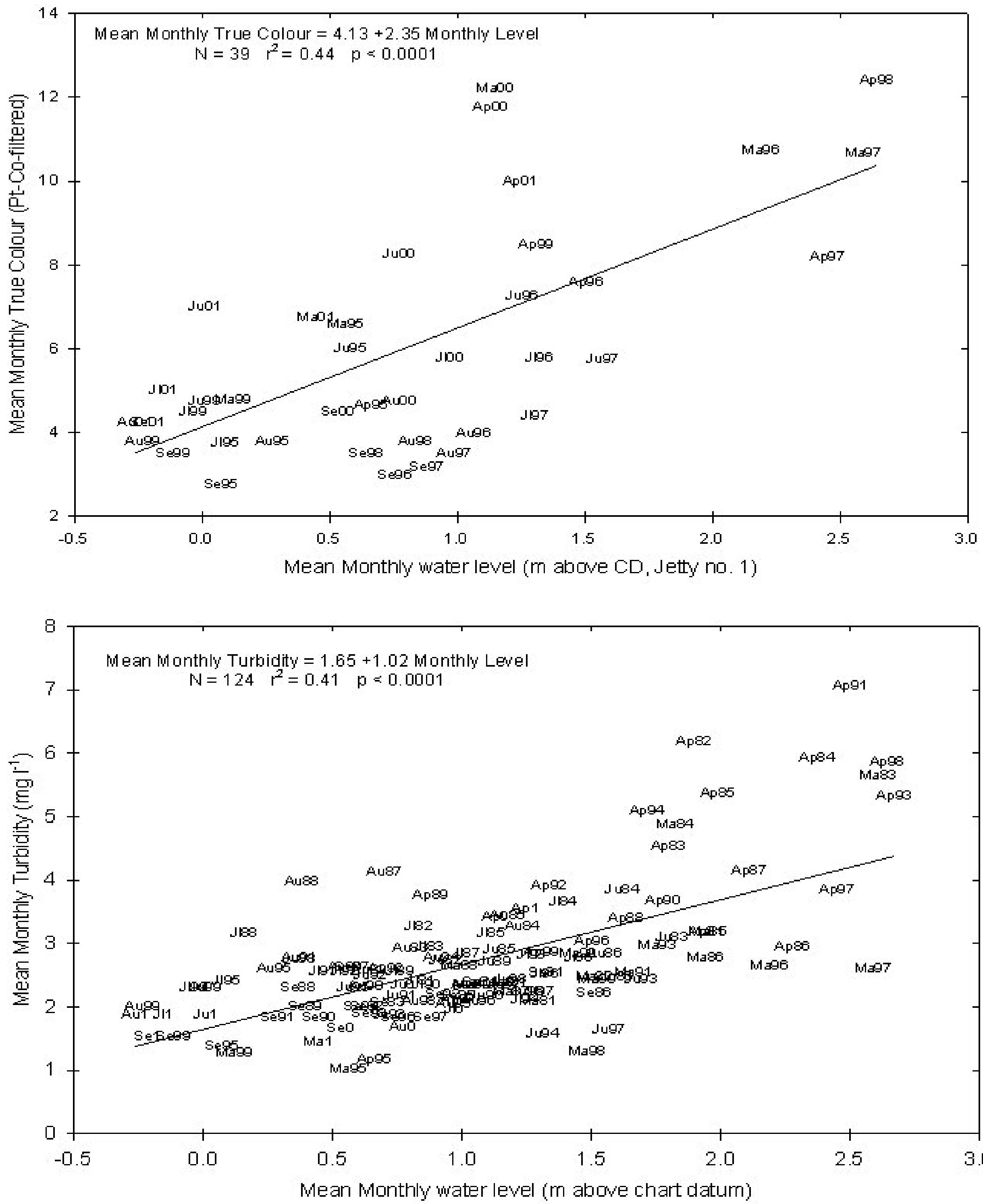

Figure 4 Quantitative relationships between monthly average water level (Montreal Harbour Jetty no. 1) and water colour (upper panel, equation 3) and turbidity (lower panel, equation 4) at the Charles-J. Des Baillets water filtration plant near Montreal.

Water colour and turbidity

The penetration of light through water was also influenced by water levels, both in terms of water colour (dissolved substances, Pt-Co units, 1997-2001) as well as turbidity (suspended solids, NTU, nephelometric turbidity units, 1982-2001)(Figure 4, top and bottom panels). Significant positive relationships were found between the monthly average water level at Montreal Harbour Jetty no. 1 and monthly (April-Sept.) average true colour and turbidity values measured at the intake of the City of Montreal (Charles-J. Des Baillets) water filtration plant. Spring months (April-May) correspond to highest levels of colour and turbidity whereas lowest values are observed over the summer months (July-August-September). The relationship was estimated for the months of April to September only, which coincide with the SAV growing period in the St. Lawrence River. Increased colour and turbidity in the spring likely results from an increase in the proportion of water that affects the City of Montreal (Charles-J. Des Baillets) water filtration plant originating from the Ottawa River (equations 3 and 4, Table 6).

Suspended solids concentration

The low transparency of river waters resulting from increased concentrations of dissolved and particulate materials carried during periods of high discharge/water levels is a well-documented phenomenon. Various equations linking discharge to turbidity, turbidity to suspended solids (Rondeau et al., 2000) and suspended solids to light extinction coefficient (Hudon and Sylvestre, 1998) are available for the St. Lawrence River waters at different locations along its course (equations 5a, 5b, 5c, 5d and 6, Table 6). At Cornwall, turbidity and suspended solids of St. Lawrence River waters were not related to discharge, because of the decanting effect of Lake Ontario, letting out only a constant suspended solids concentration of 1 mg SS l^{-1}. By the time river water reached Repentigny-Varennes (downstream of the Montreal archipelago), median annual suspended solids concentration in waters flowing in the navigation channel rose to 4.4 mg l^{-1} (mean = 6 mg l^{-1}), but was still not correlated to discharge at Beauharnois (Hudon and Sylvestre, 1998). This confirmed the steady level of erosion occurring in the river between Cornwall and the Beauharnois area (mainly in the Beauharnois channel and off de la Paix archipelago) and the dominance of more variable sources of erosion between

Beauharnois and Repentigny (some of which are visible on the Landsat TM image of Lake St. Louis, see Figure 2). The sum of erosion sources is important enough to quadruple the suspended solid concentrations even under summer discharge conditions. In contrast, strong, positive relationships were observed between discharge and suspended solids concentration for the Ottawa River and other tributaries draining in the St. Lawrence (equations 5c and 5d, Table 6); a complete list of equations for individual tributaries is available in Rondeau *et al.* (2000). At Lévis (across from Quebec city), automatic monitoring of water turbidity is a valuable tool to assess short-term variations of suspended solids loads flowing out of the river to the estuary (equation 6, Table 6).

Transparency and light extinction coefficient

The transparency of water varies according to the combination of its colour and the amount of suspended particles it contains. The simplest and oldest measurement of water transparency is the depth at which a white disk disappears from sight (Secchi depth). Waters originating from Lake Ontario, which flow in the navigation channel, are clearer (low colour, low turbidity, low suspended sediments) than those originating from the Ottawa River and other tributaries, which flow along the north shore of the river. At the river cross section between Varennes and Repentigny, waters in the navigation channel (Varennes) were more transparent (median Secchi depth of 2.5 m) than those found across the river (Repentigny) along the north shore (median Secchi depth of 1 m) (Hudon and Sylvestre, 1998).

Water transparency is inversely related to light extinction coefficient; the higher the clarity, the lower the light extinction coefficient (K). Separate equations linking the suspended solids concentrations to K were developed for waters originating from Lake Ontario (in the navigation channel) and for waters originating from the Ottawa River and other tributaries (along the north shore), allow allowing to identify the contribution of colour and of particulate matter in light extinction (Figure 5, equations 7a, 7b, 7c).

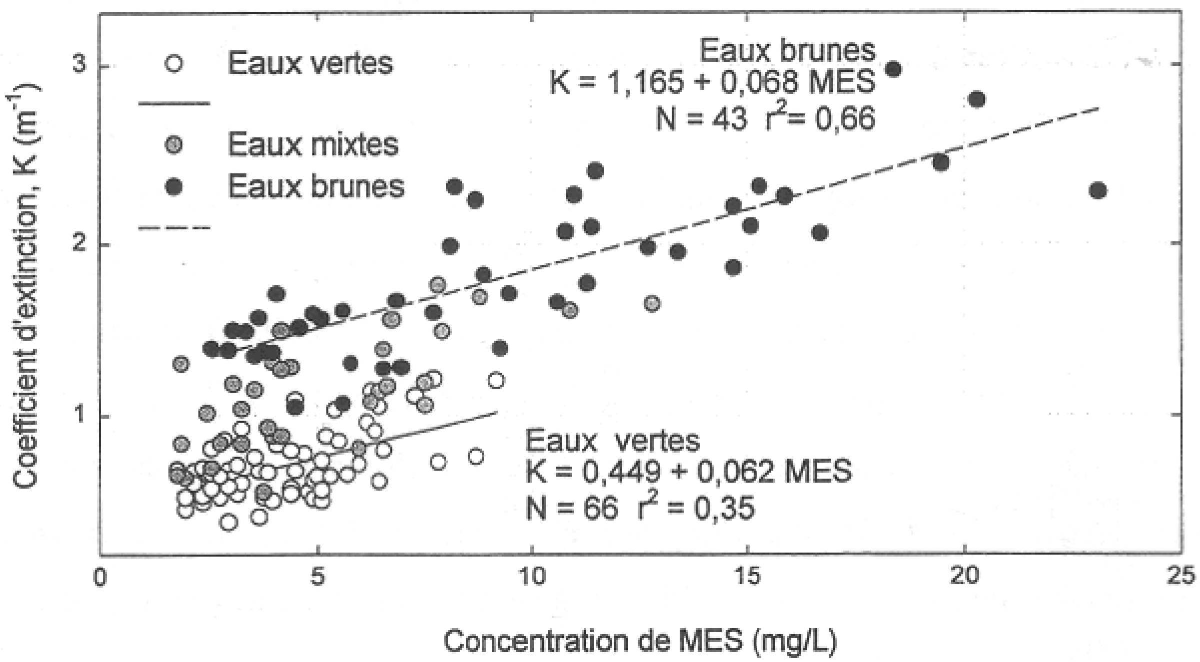

Figure 5 Quantitative relationships (equations 7a and 7c) between suspended solids concentrations and light extinction coefficient (*K*) in waters originating from Upper St. Lawrence River (open circles) and waters originating from the Ottawa River (full circles). The relationship for mixed waters (grey circles, equation 7b) is not indicated.

The linearity of these relationships shows that Beer's law is respected at the observed concentration levels whereas the parallelism of the curves indicates that particles from both water masses have similar optical properties. The main difference shown by these relationships is in the light absorption of colloids and dissolved materials between waters from the two main sources of the St. Lawrence. These equations show that, for a suspended solids concentration of 5 mg l^{-1}, *K* would equal 0.76 in the navigation channel (at Varennes) and 1.51 in waters originating from the Ottawa River across the river (at Repentigny), revealing that light is absorbed twice as fast in the milky tea brown waters of the north shore tributaries (Ottawa, des Mille-Iles, des Prairies and L'Assomption rivers). The equation for mixed waters, which lies between the two equations describing the two original water masses, may vary according to the proportion of mixing of each water mass.

The fraction (Iz/I0) of surface light intensity

The fraction (Iz/I0) of surface light intensity reaching a given depth is determined by the combination of water depth (Z, m) and light extinction coefficient (K, m^{-1}) through Lambert's law of absorption. When K is constant, such as in well mixed river waters, the equation 8 relating these quantities is:

Equation 8

$$I_Z / I_0 = e^{-KZ}$$

In which ***e*** is the natural base of logarithms. This equation is commonly used in limnology to calculate the depth at which 1% of the incident light intensity persists, which is the threshold above which primary production by micro-algae and SAV can take place.

The equations linking water levels to physical environmental conditions in the St. Lawrence River (summarised in Table 6) allow to determine the extent and direction of the changes in SAV growth conditions resulting from a wide range of water level conditions. For example, under chronically low water level conditions, water depth would decrease whereas water clarity would increase (less suspended solids and less colour), thus increasing the light intensity reaching the bottom. In addition, the coincidence of low level conditions with warmer water temperatures would stimulate biological productivity and favour certain SAV species better adapted to warm waters. These compounded effects could thus result in a biomass increase and a shift in species composition, abundance and distribution, setting in a chain of events by which profound changes to the aquatic ecosystem could occur. The following sections assess some of these hypotheses and examine the feedback effects of SAV on their physical environment.

Table 6

Quantitative relationships between environmental factors in the St. Lawrence River as schematised in Figure 1. Relationships differing among waters originating from St. Lawrence River (SLR), for waters originating from the Ottawa River (Ottawa) or mixed waters (mixed) are identified, unless inappropriate (*n.a.*)

Equation (Fig. 1)	Water mass	Dependent Variable at specified location	Equation at specified location	r^2	*p*	*n*	Reference Data source
1	*n.a.*	PAR at Montreal	9.68 + 3.17 Sun at Saint-Hubert	0.81	<0.001	165	This study
2a	SLR and mixed	T_{Day} at Montreal	a_{season} + 0.36 T_{Air} + 0.00048 $Q_{Carillon}$ -20.55 ($Q_{Carillon}$ / ($Q_{Carillon}$ + $Q_{Cornwall}$))	0.89	< 0.001	> 3500	Hudon *et al.*, 2003a Table 3
2b	SLR	T_{Month} at Charles-J. DesBaillets	a_{Month} – b L_{Month} at Montreal	0.005 to 0.66	*n.s.* to < 0.001	18 to 21	Hudon *et al.*, 2003a Table 4
2c	Mixed	T_{Month} at John Labatt	a_{Month} – b L_{Month} at Montreal	0.02 to 0.50	*n.s.* to < 0.001	24 to 25	Hudon *et al.*, 2003a Table 5
2d	SLR	T_{Year} at Atwater- Charles-J. DesBaillets	10.36 – 0.53 L_{Year} at Montreal	0.16	< 0.01	63	This study (correction to Hudon *et al.*, 2003a)
3	SLR	Co at Montreal	4.13 + 2.35 L_{Month} at Montreal	0.45	< 0.001	39	This study
4	SLR	Tu at Montreal	1.65 + 1.02 L_{Month} at Montreal	0.41	< 0.001	124	This study – eq. 3
5a	SLR	SS at Cornwall mean = 1 mg l^{-1}	$Q_{Cornwall}$	n.a.	n.s.	39	Rondeau *et al.*, 2000
5b	SLR	$\log_{10}$ SS at Varennes mean = 6 mg l^{-1}	$Q_{Cornwall}$ and $Q_{Beauharnois}$	n.a.	n.s.	57	Hudon and Sylvestre, 1998

Table 6

Equation (Fig. 1)	**Water mass**	**Dependent Variable at specified location**	**Equation at specified location**	r^2	p	n	**Reference Data source**
5c	Ottawa	SS at Carillon	$0.002Q_{Carillon}^{1.07}$	0.44	< 0.001	39	Rondeau *et al*., 2000
5d	Ottawa	log $_{10}$ SS at Repentigny	-2.2996 + 1.0341 $\log_{10} Q_{Carillon}$	0.27	< 0.001	56	Hudon and Sylvestre, 1998
6	Mixed	SS at Lévis	0.748 $Tu^{1.158}$ at Lévis	0.79	< 0.001	230	Rondeau *et al*., 2000
7a	SLR	K	0.449 + 0.062 SS at Varennes	0.35	< 0.001	66	Hudon and Sylvestre, 1998
7b	Mixed	K	0.720 + 0.084 SS at Repentigny-Varennes	0.45	< 0.001	35	Hudon and Sylvestre, 1998
7c	Ottawa	K	1.165 + 0.068 SS at Repentigny	0.66	< 0.001	43	Hudon and Sylvestre, 1998
8	SLR, mixed and Ottawa	I_z / I_0	e^{-KZ}	n.a.			

See notes on the following page.

Variables and measurement units for Table 6 are defined as follows, for specified locations:
a_{Season} : Intercept for each seasonal, 3-months periods,
a_{Month} : Intercept for each month,
b: slope of the relationship,
Co: daily colour at Montreal (Pt-Co units),
I_z/I_0 : fraction of daily surface light intensity (I_0) reaching the bottom or a specified depth (I_z),
L_{Month} : mean monthly water level at Montreal Harbour Jetty no. 1 (m above chart datum),
PAR : cumulative daily photosynthetically active radiation at Montreal (Einstein m^{-2} d^{-1}),
$Q_{Carillon}$: daily discharge at Carillon (and other specified locations) (m^3 s^{-1}),
SS: daily suspended sediment concentration at specified location (mg l^{-1}),
S : cumulative daily hours of sunshine at Saint-Hubert (h),
T_{Day}: mean daily water temperature at Montreal (water filtration plants Longueuil, Charles-J. Des Baillets, Atwater) (^oC),
T_{Month}: mean monthly water temperature at Montreal (water filtration plants Charles-J. Des Baillets, John Labatt) (^oC),
T_{Year}: mean annual water temperature at Montreal (water filtration plant Atwater) (^oC),
T_{Air} : mean daily air temperature at Dorval airport (^oC),
Tu : daily turbidity at specified location (nephelometric turbidity units),
Z: water depth (m)

Modelling SAV distribution and biomass from physical variables

Presence-absence of SAV – Maximum depth of colonisation.

In the St. Lawrence, the depth limit of SAV colonisation is primarily controlled by water clarity, expressed either as a function of Secchi depth (m) or as light extinction coefficient (*K*, m^1) (Figure 6, equations 9a and 9b). shore) axes.

These equations set the lower bound at which SAV biomass models were applicable, which varied with location in the St. Lawrence River, on the longitudinal (upstream-downstream) as well as the transversal (across the river, from shore to shore). For example, within the water mass originating from Lake Ontario, the maximum depth at which SAV were found (Z_{max}) was 6-10 m in Lake St. François, 5-7 m in Lake St. Louis and 4-5 m from Montreal to Verchères. Such progressive decrease in the depth range of SAV resulted from the progressive increase in suspended sediment concentration in the waters of the navigation channel as they flow downstream. Across Lake St. Louis, Z_{max} shifted from 5-7 m in the clear Lake Ontario waters flowing in the southern sector, to 3.5 m in the northern sector under the influence of brown, turbid Ottawa River waters.

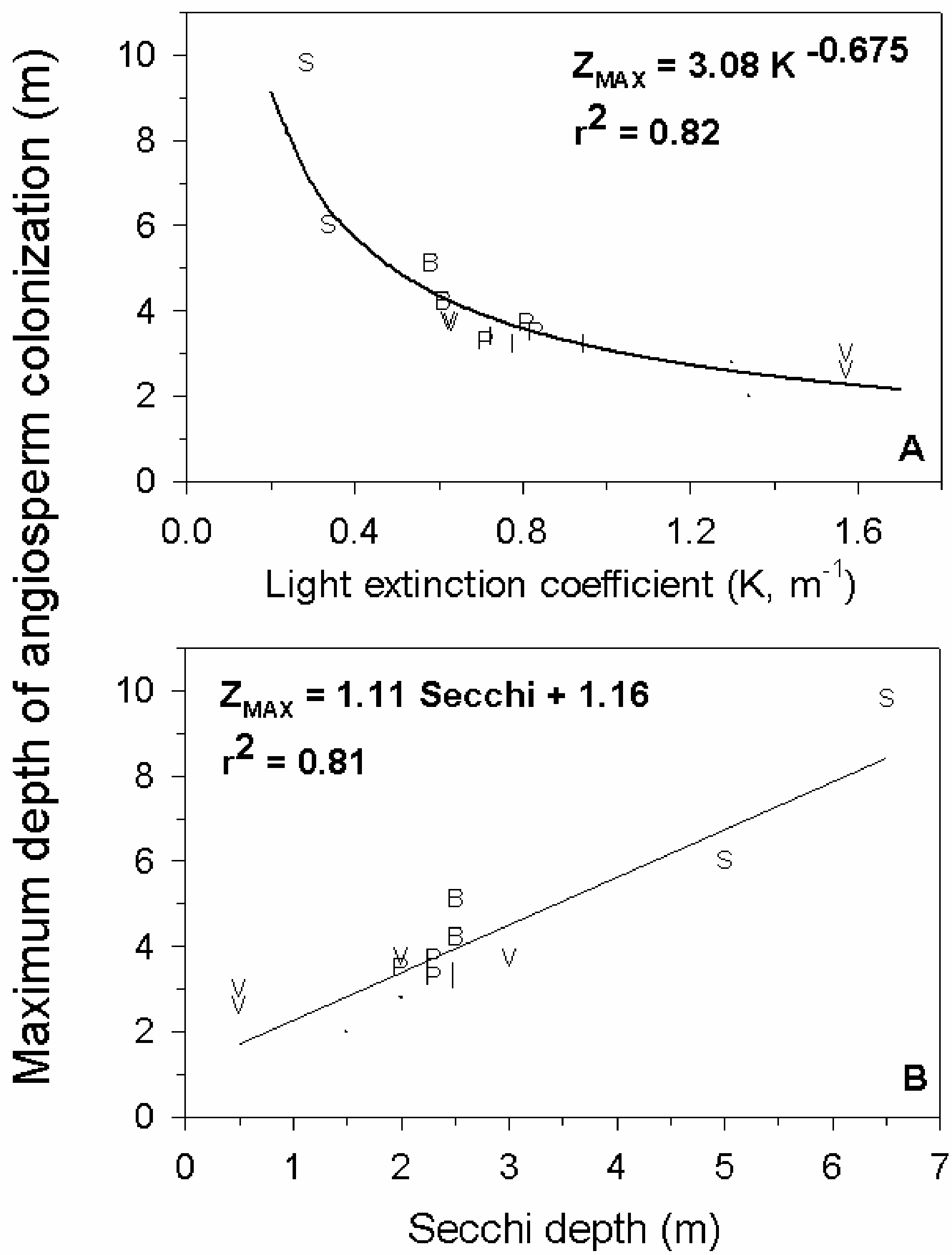

Figure 6 Relationships (equations 9a and 9b) between the maximum depth of angiosperm colonization and (A) the light extinction coefficient and (B) Secchi depth. Letters identify sites: S, Lake St. Francis; D, Lake des Deux-Montagnes; B, Boucherville; P, Pointe-aux-Trembles; I, Île aux Cerfeuils; V, Verchères (from Hudon *et al.*, 2000)

The effective maximum depth of macrophyte colonisation, Z_{max}, was usually measured at the end of the growth season (August-September), when plants reached their maximum development; as such, Z_{max} integrated the sum of all day-to-day lighting conditions, which varied on seasonal as well as short-term (< daily) bases.

Wetted surface area and total cover of emergent wetlands

Water levels obviously influence the surface area that can be colonized by SAV and emergent wetland vegetation through the simple relationship between levels and wetted surface area, which is a direct function of the slope of the river bed and shoreline. The gentler the slope, the larger the increment of wetted surface per unit of level-discharge rise. The wetted surface area of Lake St. Pierre and archipelago under increasingly high water levels and discharge at Sorel was assessed in two independent ways: first, empirically, by calculating the total surface area of the lake from the numerical elevation model (DOE, 2003c) for 10-cm increments of water level and second, by simulating wetted surface area from the hydrodynamic model (DOE, 2003d), for five summer and eight spring water discharge scenarios (Morin and Bouchard, 2001).

Empirical assessment. Historical thresholds of emergent and submerged plant vertical distribution were identified on the elevation profile of Lake St. Pierre (Figure 7). For the sake of simplicity and uniformity across this large water body, all elevations were expressed relatively to Average Sea Level (ASL). In Lake St. Pierre, areas that were too deep and thus too dark on the bottom to support SAV ranged from 18 below to 1.67 m above ASL and covered a total surface area of about 100 km^2.

The elevations over which plants were found in Lake St. Pierre (from 1.67 to 8.13 m above ASL) defined the lower (Z_{max}) and upper (floodplain limit) bounds of the 700 km^2 of lake surface area over which wetlands could develop. Across this range of elevation, wetted surface area increased linearly with water levels at 83.15 km^2 m^{-1}. SAV colonised the river bed from a depth of 5 m (1.67 m below ASL) to 2.94 ASL, followed by a belt (2.94 to 4.4 m ASL) in which SAV coexisted with emergent vegetation. For the purposes of this study, the floodplain was defined by the area extending from the shoreline (2-yr flood recurrence) to a height of about 8.13 m ASL, which was the highest flood level reached at Sorel in the 1960-1997 period.

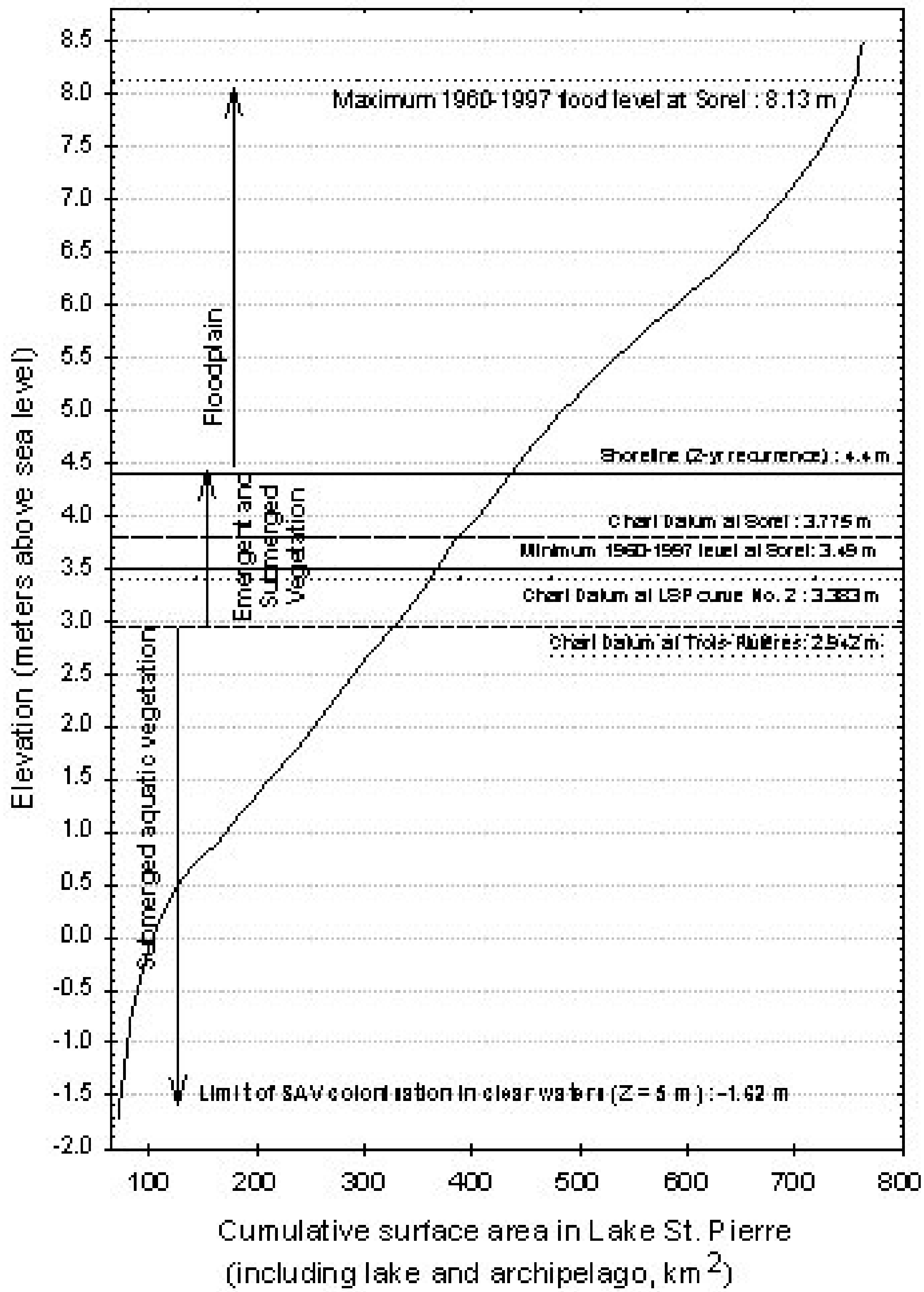

Figure 7 Wetted surface area of Lake St. Pierre (km^2) with increasing water level above sea level (ASL). Historical elevation thresholds defining the areas colonized by submerged aquatic vegetation (-1.67 to 2.94 m ASL), the belt of emergent and submerged vegetation (2.94 to 4.4 m ASL) and the floodplain (4.4 to 8.13 m ASL) are indicated.

Wetted surface area (S_{water}, km^2) increased linearly with water level at Sorel (L_{Sorel}, m ASL) following the empirical relationship (equation 10a) :

Equation 10 a

$$S_{water} = 85.47 + 83.15\, L_{Sorel} \qquad r^2 = 0.99,\ n = 98,\ p = 0.001$$

which described the portion of figure 7 between –1.7 and 8.5 m ASL.

Simulations. Simulated water level scenarios also showed a strong, nearly linear relationship between wetted surface area of Lake St. Pierre (km^2) and St. Lawrence River discharge at Sorel (m^3 s^{-1}), for the eight spring scenarios (without the influence of SAV) as well as for the five summer scenarios (accounting for the effect of SAV) (Morin and Bouchard, 2001)(Figure 8). Over the course of the growth season, water flow was progressively obstructed by increasing SAV biomass, accentuating the water surface slope between the inlet and outlet of Lake St. Pierre in late summer in comparison with spring (no SAV). Results from the simulations showed that, for a given discharge, summer scenarios resulted in a slightly smaller (by an average of 9 km^2, about 2%) wetted surface area than for corresponding spring scenarios. Such lack of difference between seasons likely resulted from the fact that gains and losses of wetted areas balanced each other out with seasonal changes in water slope: the presence of plants caused upstream wetlands to be more flooded in summer whereas downstream wetlands experienced slightly lower inundation than for a comparable level in the spring.

Implications for Lake St. Pierre water level management. Examination of the average monthly difference between pre-project levels and regulation plan 1958D with deviations (1900-2001 simulations, DOE 2003e) revealed a strong seasonal pattern. Discharge regulation at Cornwall induced a reduction in water levels at Sorel in January, April, May, June and July and induced an increase in level at Sorel in February-March, August-November. This pattern is coherent with spring flood reduction to protect shoreline properties and with level increase in late summer and fall to maintain commercial navigation. These practices reduce the total vertical range of seasonal variations in water levels, which systematically reduce the wetted surface area of Lake St. Pierre and thus affect wetland surface area.

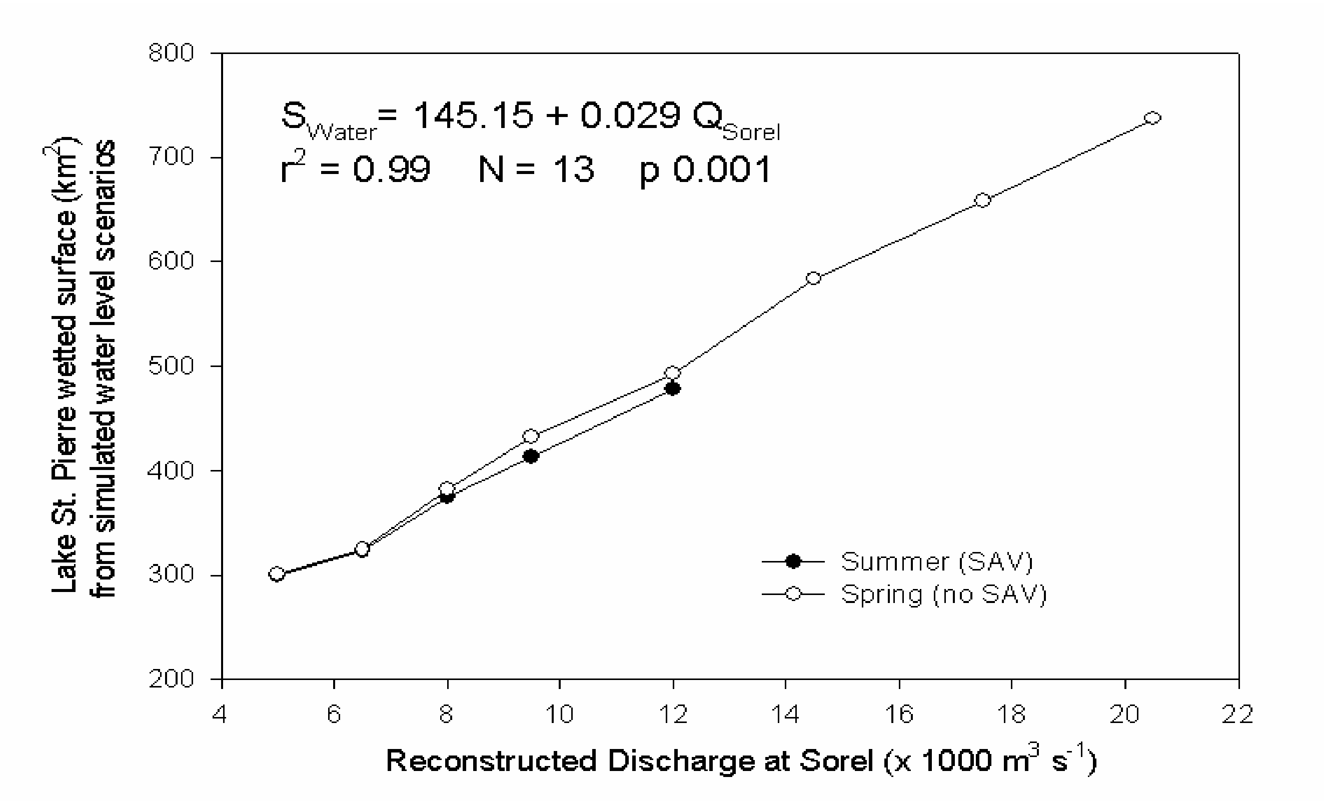

Figure 8 Relationship (equation 10b) between discharge at Sorel (Q_{Sorel}, m^3 s^{-1}) and wetted surface area (S_{water}, km^2) of Lake St. Pierre from simulations for eight spring (no SAV) and five summer (with SAV) discharge regimes. A single linear relationship was fitted between S_{water} and Q_{Sorel}

The monthly pattern of differences is nearly a mirror-image to that of the proportion of Cornwall discharge to total discharge at Sorel. On average, discharge at Cornwall represented 73% of the long-term (1965-1997) river discharge at Sorel. In April and May, discharge at Cornwall represented only 60 and 65 % (respectively) of discharge at Sorel, owing to the high discharge of the Ottawa River and tributaries. Conversely, from August through November, discharge at Cornwall represented the highest fraction (74-82%) of discharge at Sorel.

It should be stressed however, that these monthly proportions are most likely to change in the future, owing to the combined effects of changing water demands (hydroelectric production, commercial and recreational navigation, drinking water supply) and alteration of water budget stemming from climate change (lower water supply to Lake Ontario, occurrence of winter thawing events, change in tributary discharge patterns).

The relationship between water level and discharge at Sorel involves three different regimes. First, ice conditions in winter greatly interfere with water flow between December 20 and March 31st, a complex hydrological period which will not concern us further. During the rest of the year, the factor that mostly affects water flow patterns is SAV, mainly present in the months of July to October and absent during the rest of the year. Once the period of ice-cover was excluded, separate regression equations linking level to discharge at Sorel (1965-1997) were derived for conditions without (April, May, June, November, December) and with (July-October) vegetation (equations 10c and 10d):

Equations 10c and 10d

10c	$Level = 2.10 + 0.243Q + 0.00267Q^2$	no vegetation	April, May, June, Nov., Dec.
10d	$Level = 2.24 + 0.222Q + 0.00267Q^2$	with vegetation	July, Aug., Sept., Oct.

r^2=0.92, $p<0.0001$

As shown on Figure 7 and equation 10a, lake level is linearly related to wetted area. Also, the water flow entering the fluvial system at Cornwall was considered to reach Lake St. Pierre (at Sorel) without loss (after a certain time delay), where it constituted 73% of the flow, on average. These considerations, along with equations 10c and 10d, allowed the derivation of a simple flood control model describing the effects of outflow management (km^2 per 1000 m^3 s^{-1} unit) in terms of change in Lake St. Pierre flooded surface, without (Equation 10e) and with (Equation 10f) vegetation (Figure 9, smooth bold lines):

Equations 10e and 10f

10e	$\partial Level / \partial Q = 8.6\sqrt{Level + 3.42}$	no vegetation	April, May, June, Nov., Dec.
10f	$\partial Level / \partial Q = 8.6\sqrt{Level + 2.38}$	with vegetation	July, Aug, Sept, Oct.

These two equations reveal how the increment in wetted surface becomes more important as the baseline lake level increases. For example, a 1000 m^3 s^{-1} increase in discharge at Cornwall would increase Lake St. Pierre wetted area by about 22 km^2 if lake level equalled 4 m ASL, whereas a 27 km^2 gain would be generated when lake level equalled 7 m ASL. For a given lake level, gains would always be slightly higher (by about 2 km^2) during the spring and late autumn months (without plants).The previous estimates rely on the assumption of a linear relationship between wetted surface area and lake level (Figure 7). The same flow control effect, when estimated from detailed lake topography (i.e. the data in Figure 7, instead of the trend) reveals the sensitivity of control diagrams to minor shifts from overall trends (Figure 9, fine, broken line plots). It proves so far difficult to translate the uncertainty in topography measurements into an assessment of the optimal level of smoothing required to properly describe lake level control.

The wetted surface area of Lake St. Pierre ultimately determines the fraction of its surface which can be colonized by emergent marsh vegetation, an important component of faunal habitats. Emergent macrophyte wetland vegetation represents the sum of meadow marsh, robust emergents, thin-leaved emergents and transition marsh habitat types, which cover the lower fringe of emergent plants, from water-logged soils down to the submersion depth limit (about 1 m in late summer). Aerial photographs and remote sensing imagery are most conducive to large-scale, global assessment of total surface area covered by emergent vegetation, although such techniques cannot reliably quantify the coverage of plants at lower densities. Depending on the quality of aerial imagery (spatial resolution, spectral separation and coverage) various emergent plant assemblages can be distinguished, allowing further refinement to wetland monitoring once the images have been validated with field surveys. This technique is not applicable however to submerged vegetation in the St. Lawrence River, owing to variable water transparency and colour.

A combination of aerial photographs and remote sensing imagery were used to identify a significant, negative relationship between the proportion of emergent plant cover at Baie du Febvre and water levels at Sorel during the growth season (April 1-September 30) (Hudon,1997) (Figure 10, equation 11, Table 7). Between 1965 and 1990, average April-September water levels ranged between 0.36 and 2.26 m above chart datum whereas emergent plants occupied 1-38% of the surface area. As with Z_{max}, interpretation of this relationship relies on the assumption that the distribution of emergent plants by the end of their growth season reflects the sum of the seasonal effects induced by short-term (daily) water level variations. Baie du Febvre is a 62 km^2 area located in south-eastern Lake St. Pierre, (Figure 11). The speed at which emergent plant assemblages responded to shifts in water levels was previously estimated at 2-5 years (Hudon, 1997); recent field observations made over consecutive years (2000, 2002, 2003) using a hydrofoil (Figure 11) indicate that changes in emergent plant cover can be detected over a period of 2-3 years. In the St. Lawrence River, aquatic plants were shown to be established over a broad range of water depth and can thus adapt rapidly to changing water levels (Hudon, 1997).

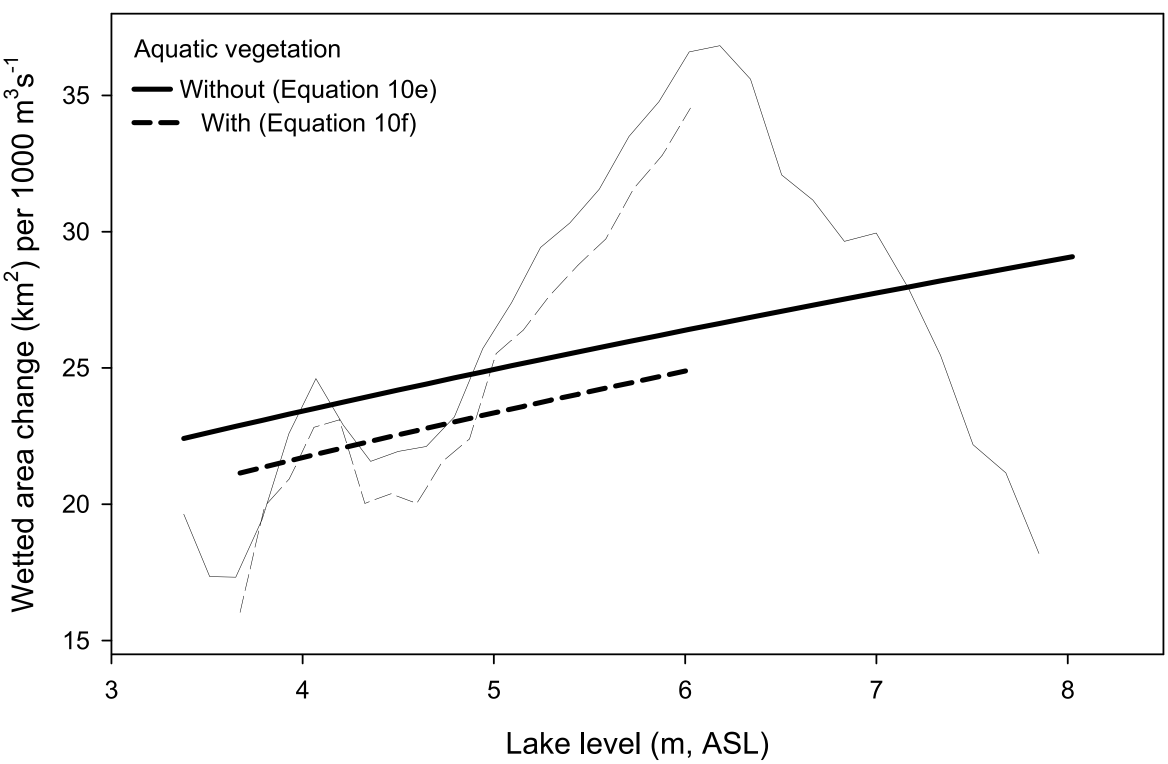

Figure 9 Flooding control model for Lake St. Pierre relating the effect of changing the inflow at Cornwall by 1000 m^3s^{-1} on the lake wetted surface area (change in km^2) as a function of the Sorel water level (m ASL), with (dashed lines) and without plants (full lines). Smooth relationships (bold lines) are based on average lake slope (equations 10e and 10f); broken line plots (finer lines) are based on detailed topography (Figure 7).

The equation linking percent plant cover to water levels will be improved using recent data for Lake St. Pierre, acquired by remote-sensing (2000, 2002), field surveys (1999, 2000, 2002, 2003) and modelling (Hudon *et al.*, 2003b, Hudon *et al.*, in prep). This future segment of the study will allow to predict the surface area covered by each major emergent wetland plant communities, corresponding to the habitat sub-types occupying the lower fringe of wetlands: Low water level allow sparse emergent vegetation to become denser, whereas high levels thin out the dense emergent cover, meadow marsh, robust emergents, thin-leaved emergents, transition marsh, barren grounds, floating leaves and shallow submerged aquatic vegetation. The occurrence of plant communities was found to be related to four hydrological variables through

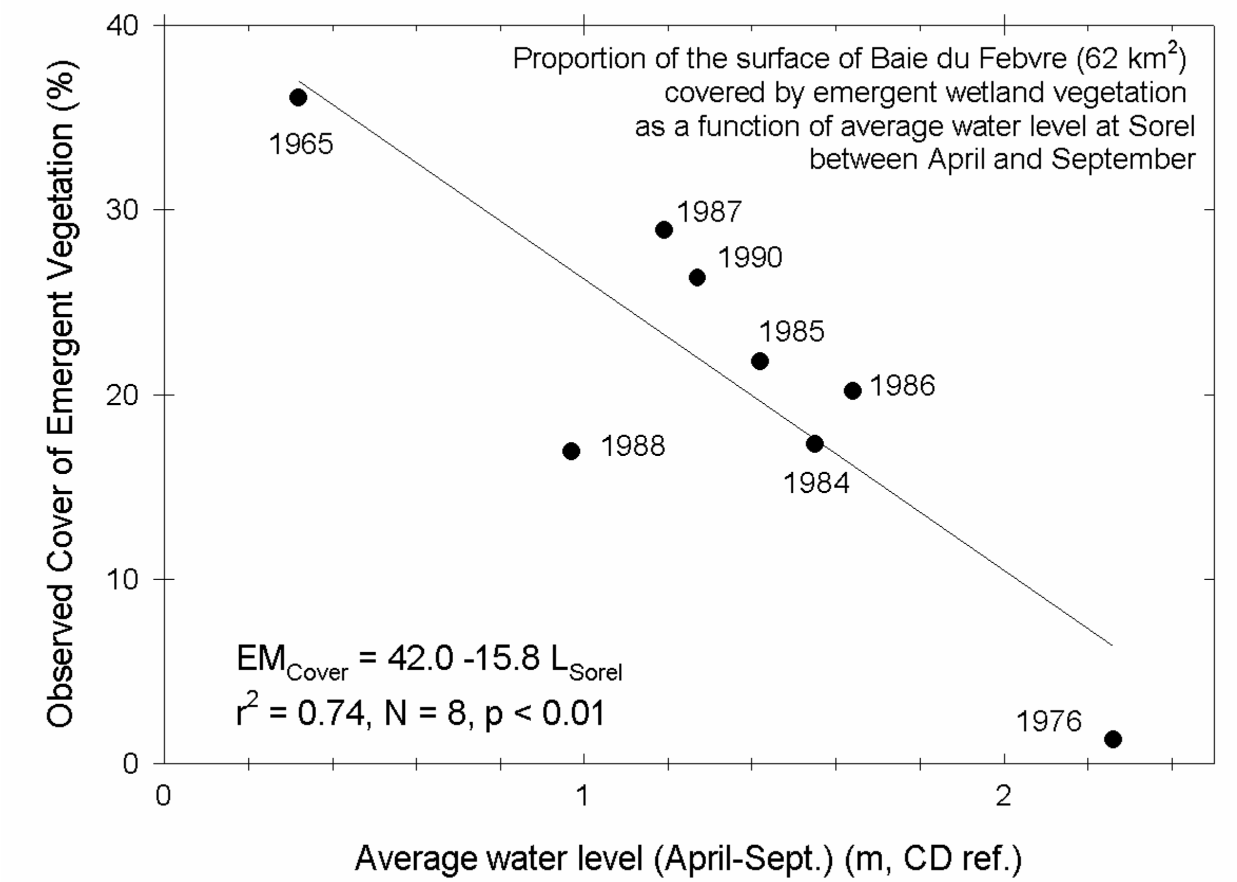

Figure 10 Relationship (equation 11) between the proportion of total surface area covered by emergent marshes at Baie du Febvre (south-eastern Lake St. Pierre) and average water level during the macrophyte growth period (April 1-September 30) at Sorel for eight summers between 1965 and 1990 (from Lalonde and Létourneau, 1996; Hudon, 1997).

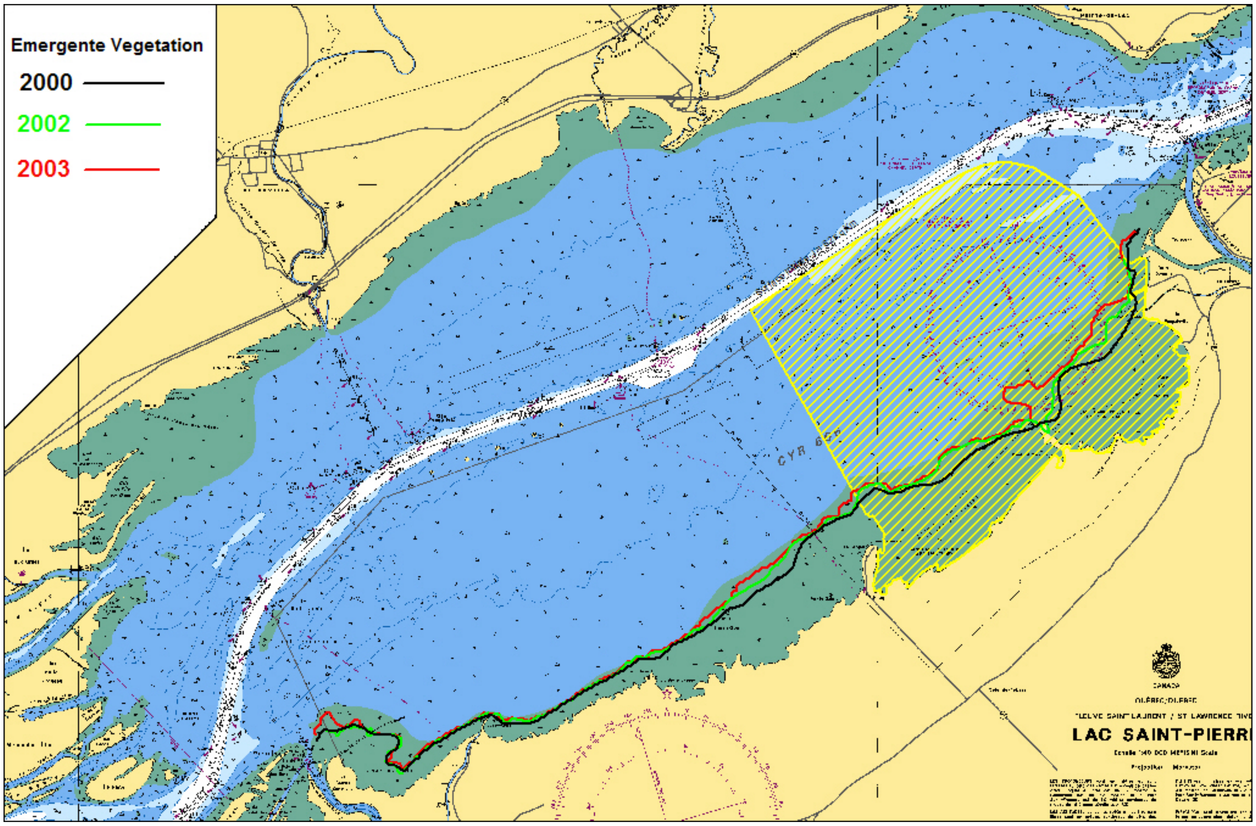

Figure 11 Inter-annual variations (2000, 2002, 2003) of the offshore edge of high (> 50%) cover of emergent vegetation in southern Lake St. Pierre, as surveyed by hydrofoil at the end of the growth season. Survey could not be completed in 2001 owing to exceedingly low water levels. Shaded enclosure indicates the Baie du Febvre 62 km^2 area used to develop equation 11 from Figure 10.

a hierarchical model (Classification and Regression Trees, CART, Breiman *et al*., 1984). The best predictors were combinations of elevation of a point above or below the average water line in July, average water depth over the previous growth season, number of days under water over the previous growth season, standard deviation of water depth, for which critical thresholds determine to which group a given area will be allocated (Hudon *et al*., 2003b, equation 12, Figure 12).

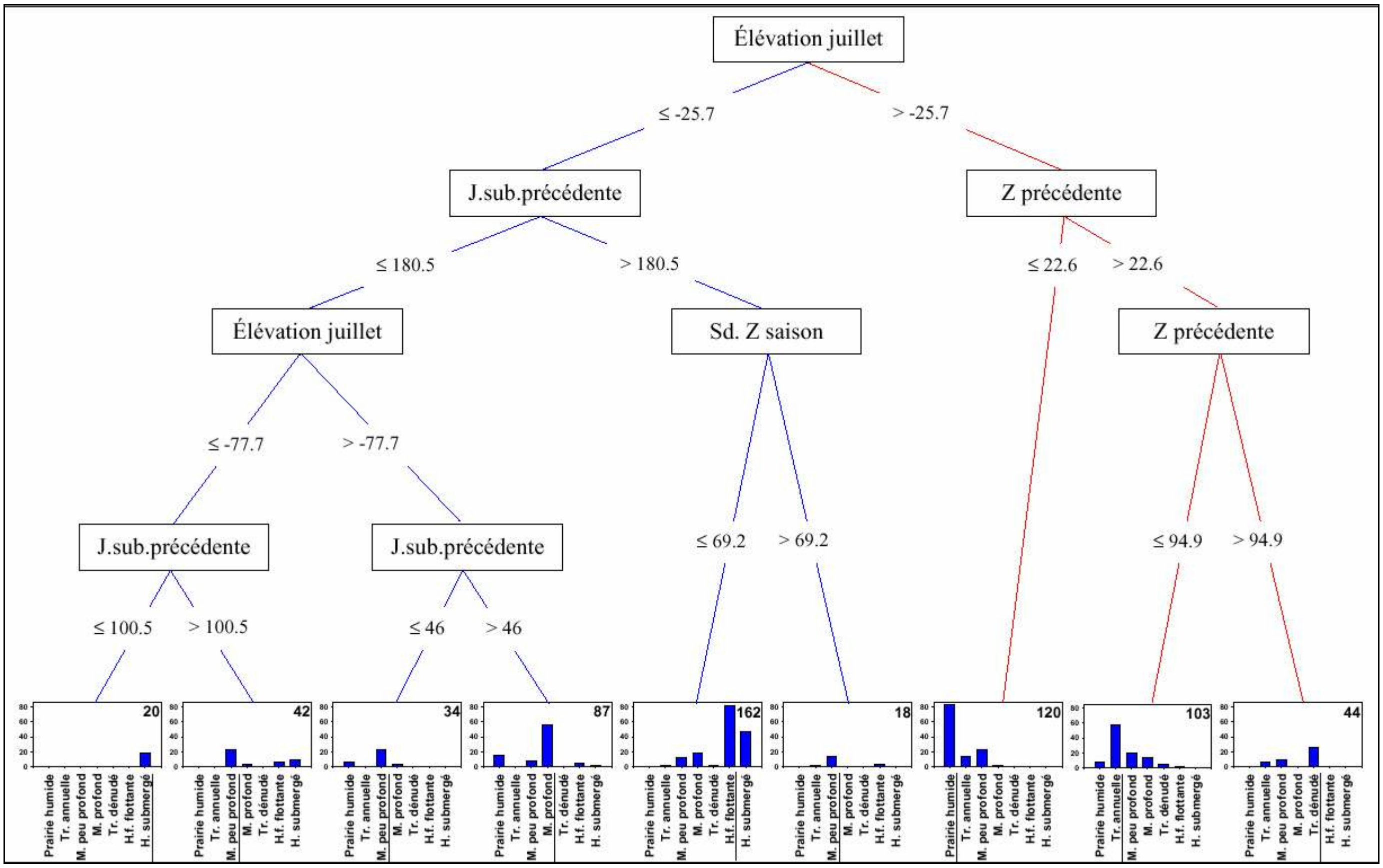

Figure 12 Binary CART model (equation 12) allowing to predict wetland vegetation type from a combination of hydrological variables (from Hudon et al. 2003b).

General estimates of SAV biomass for the St. Lawrence River

General relationships (equation 13) describing the changes of aboveground biomass of emergent and submerged vegetation across a broad depth range (*Z*, 0 to 5 m below average level in September) in the St. Lawrence River were first developed (Hudon, 1997).

Equation 13

$$Log_{10} B = -0.65 - 0.75 \log_{10}Z - 0.23 (\log_{10}Z)^2 \qquad r^2 = 0.31, \ n = 252, \ p < 0.001$$

Although this equation provided a rough approximation of plant biomass across all river sites, its low r^2 (proportion of the variance explained) likely resulted from the use of a single variable, without consideration for the other environmental variables (exposure and current conditions, water mass, water clarity) which likely influence aquatic plant biomass.

Subsequent models (Hudon *et al*., 2000; Figure 13, equation 14) including the effects of exposure, plant canopy formation and water transparency, in addition to water depth, were successful in explaining twice as much variance in biomass ($r^2 = 0.67$) over the same depth range. This model represented an improvement over the initial multiple regression model using depth alone (Equation 13), however, the classification and regression tree predicted discontinuous values of aquatic plant biomass for 10 groups of biomass categories. Each category represented a distinct combination of environmental variables, for which binary thresholds were identified. Such discontinuous predictions (average biomass ± standard deviation) were quite remote from natural situations in which plant assemblages grade progressively into each other rather than being delimited by sharp boundaries. In addition, application of the CART model to predict aquatic plant biomass under a new set of environmental conditions (either at a different site or for earlier periods) presented the problem of assessing plant canopy formation, which necessarily required field observations, echo-sounding surveys or remote sensing data. These shortcomings emphasized the need for more area-specific, practically applicable predictive models. Such area-specific models were especially needed for fluvial lakes, which were likely to be the areas most strongly affected by changing water levels. Fluvial lakes encompass the wetland areas most intensively used by humans (Lake St. Louis) and are of utmost importance as faunal habitats (Lake St. Pierre).

Lake-specific models of SAV biomass

<u>Lake St. Louis</u>. With the exception of a few wetland areas located on islands (particularly de la Paix, Saint-Bernard and Dowker islands), most of the emergent vegetation of Lake St. Louis has been destroyed by shoreline urbanisation. The modelling effort thus focussed on submerged aquatic vegetation which covers large expanses of the bottom of Lake St. Louis. Lake St. Louis is characterised by a wide range of water depth (max depth 25 m). The deep, central navigation channel separates two shallow basins partly isolated from the main channel by the Iles de la Paix archipelago (to the south) and by Perrot Island as well as shallow banks of dredge spoil deposits

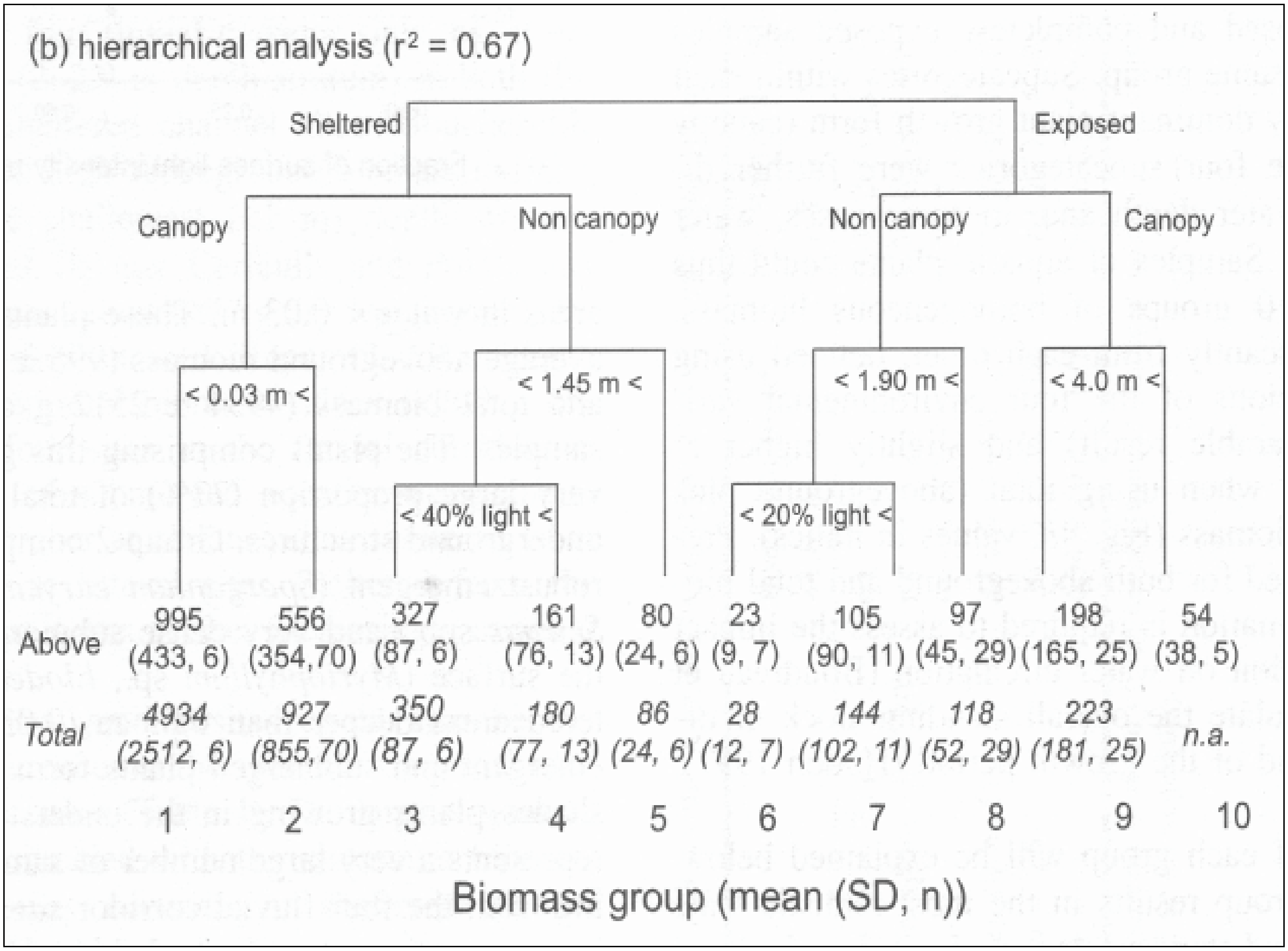

Figure 13 Characterization of average aboveground macrophyte biomass obtained from the binary, hierarchical classification of exposure conditions, plant canopy formation, water depth and transparency. Average (s.d.) of non transformed biomass values are presented to facilitate comparison; the model was derived from $\log_{10}$ transformed values (from Hudon *et al*., 2000; equation 14)

(to the north). A large fraction of the lake is thus sheltered from strong currents and wind action. In addition, the inflow of Ottawa River waters along the north shore of Lake St. Louis generates two readily identifiable water masses which contrast sharply against each other (see Landsat TM image on Figure 2).

Two linear regression models (equations 15 a and 15b, Table 7) linking water depth (Z, m) to aboveground biomass of SAV (B, $\log_{10}$ g dry mass m^{-2}) for waters originating from Lake Ontario

(K = 1.61 m^{-1}) and from the Ottawa River (K = 0.40 - 0.65 m^{-1}) were developed for Lake St. Louis (35 samples from 14 sites in the northern basin, August 2001) (Figure 14). Inclusion of other physical variables measured at the time of sampling (current speed, sediment composition, grain size, N, P and organic content,) did not yield significant improvements in the relationships.

These two simple equations provide an estimation of the maximum SAV biomass reached by the end of the growth season and are valid within a depth range between 1 m and corresponding Z_{max} values for each water mass. The regression models predict that at a depth of 1 m, SAV can reach 760 and 150 g dry mass m^{-2} in Lake Ontario and Ottawa River waters, respectively. Predictions will be most accurate on a broad spatial scale however, owing to the notoriously high variability of SAV biomass in the field, as evidenced by the broad scatter of observations (across almost one order of magnitude) around the regression lines (Figure 14).

<u>Lake St. Pierre</u>. The main water body of Lake St. Pierre is considerably shallower and less dissected than Lake St. Louis: the central navigation channel (>11.3 m deep) bisects two shallow (< 4 m deep) lateral basins. In contrast with Lake St. Louis, the shallow sloping shores and the rural setting of Lake St. Pierre favour the development of large expanses of emergent and submerged aquatic vegetation, which cover most of the lake's surface.

In Lake St. Pierre, part of the complexity of modelling SAV is due to the presence of distinct water masses originating from various tributaries flowing into the St. Lawrence River. Turbid, brown waters from the Ottawa River and other tributaries draining the Precambrian Shield flow along the north shore and partially mix with waters originating from Lake Ontario. The clearer waters of the main stem of the St. Lawrence River flow in the central (navigation) channel and partly spill over the adjacent shallow southern areas. Along the south shore of Lake St. Pierre, tributaries draining farmlands (Richelieu, Yamaska, Saint-François rivers) bring turbid, brown and nutrient-rich waters to the shallow areas of its southern basin. Landsat imagery (Figure 15) further demonstrates the complexity of the water masses that occur in Lake St. Pierre, which likely shift laterally on a seasonal basis, with the relative importance of the discharge of its tributary components.

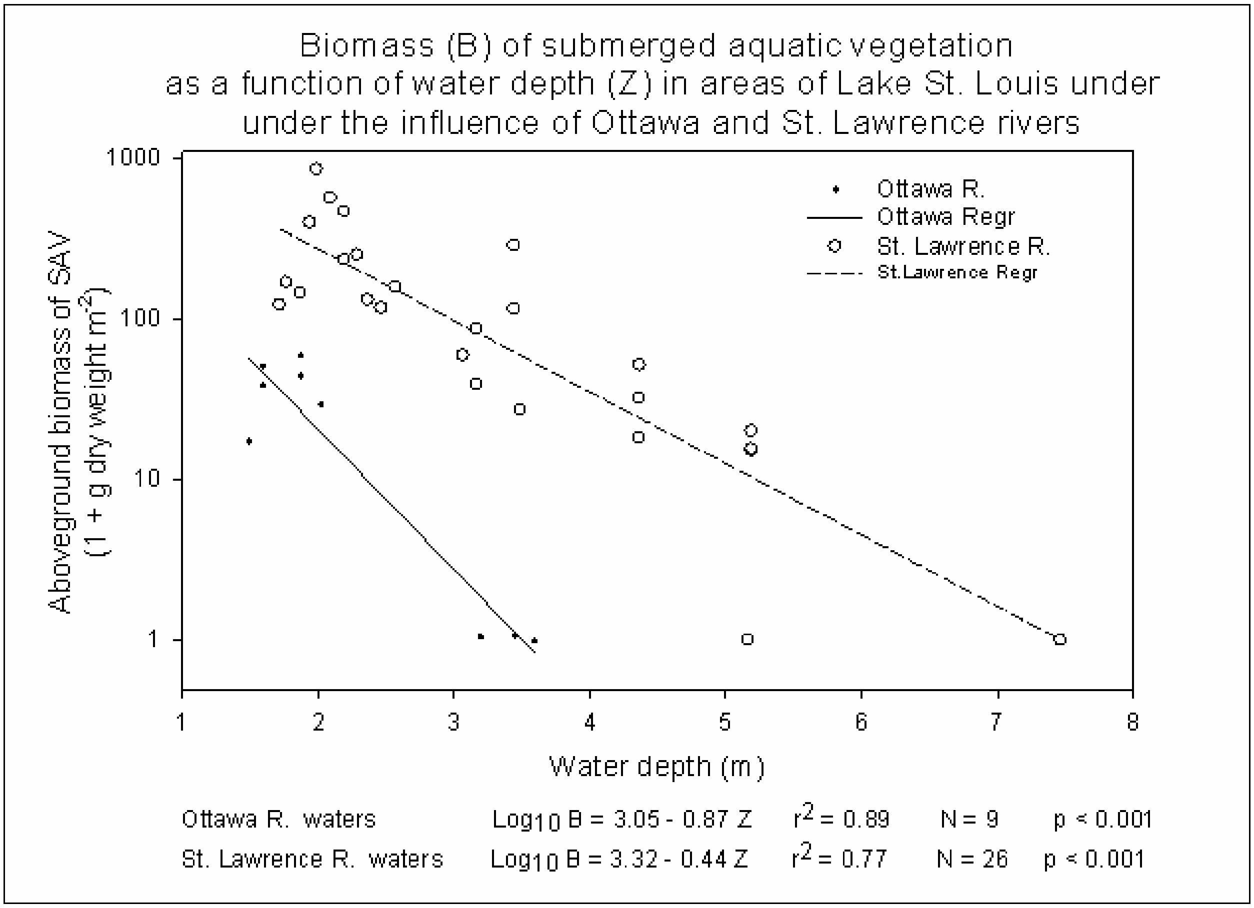

Figure 14 Linear relationships (equations 15 a and 15b) between water depth (*Z*) and biomass of SAV (*B*) in sectors of Lake St. Louis under the influence of waters originating from the Ottawa River (full circles) and from Lake Ontario (open circles) (2001)

Although most of the river water flows through the central channel, echo-sounding surveys (Fortin *et al*., 1993) identified SAV free side-channels maintained clear by the passage of water; these channels were not defined by bathymetry but corresponded to faster measured currents and lower SAV biomass than in adjacent areas. The exact mechanism responsible for the maintenance of these side channels (ice, current) is not clear at this stage.

Downstream of the Berthier-Sorel archipelago, the smooth shoreline morphology and shallow depth of Lake St. Pierre make it vulnerable to the effects of dominant wind and waves directed roughly along the lake main axis (SW direction). This large fluvial lake therefore presents a diverse combination of physical characteristics (water mass, current, wind and waves) which are expected to influence the distribution and biomass of SAV over large spatial scales.

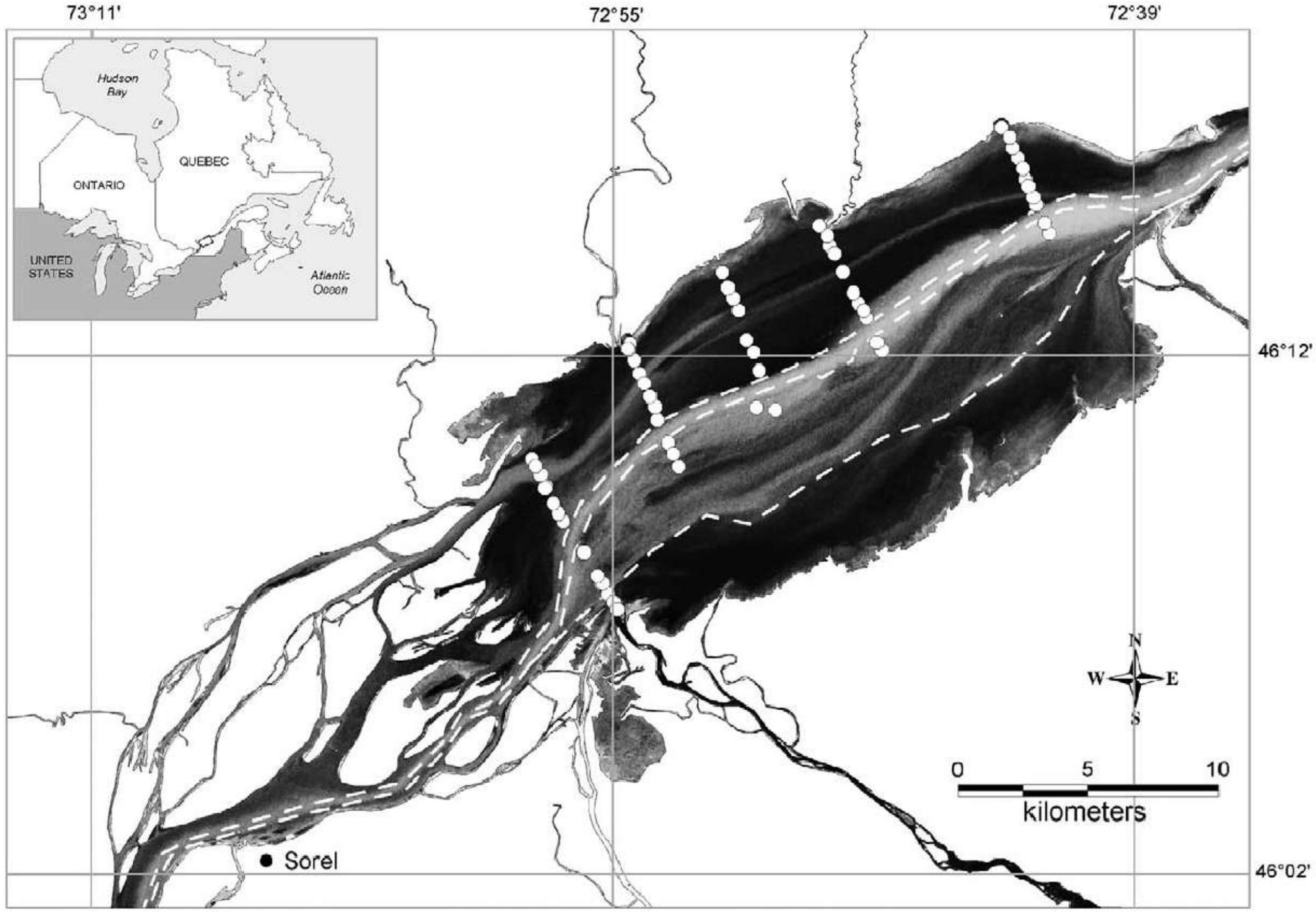

Figure 15 Landsat TM image of Lake St. Pierre's (September 1988) illustrating its tributaries and the distribution of water masses. The location of field survey sites (circles) and the boundaries of each water mass (hatched white lines) are indicated. The water masses are, from north to south: the north shore, the navigation channel, the central area and the south shore (from Vis *et al*., 2003).

SAV biomass and associated physical environmental characteristics (water depth, *K*, current speed, surface sediments) were sampled in 2000 and 2001 in Lake St. Pierre. Divers collected samples along 5 transects in 2000 (*n*= 62 sites, 154 samples) and 2001 (*n* = 58 sites, 140 samples), 39 of which were visited both in 2000 and 2001. Four of the five transects extended only across the northern half-width of the lake because access to the southern part of the lake is prohibited by the Dept. of National Defence of Canada. Two-way scatter diagrams (not shown) did not show strong bivariate relationship between physical variables (light intensity, sediment characteristics, current speed) and SAV biomass, suggesting the effect of multiple-variable interactions and the compounding effect of wind (fetch).

The effect of current was accounted for by identifying and excluding from the regression models the sites located in side channels identified on echo-sounding maps (Fortin *et al*., 1993), where low SAV biomass coincided with high current speed. The effect of wind and fetch was accounted for by introducing a proxy variable for fetch, corresponding to the distance (in metres) of each site from a line running perpendicular across the lake at the eastern (downstream) edge of the Berthier-Sorel archipelago. This coincided with the long axis of the lake and the south-westerly wind direction which predominates in the St. Lawrence River valley. Since the effect of wind on the bottom is inversely proportional to water depth, separate models were fitted for shallow and deep waters; the depth threshold was determined by optimizing r^2.

Two regression models were thus identified to predict SAV biomass in Lake St. Pierre corresponding with shallow (1-1.7 m, equation 16) and deep (> 1.7 m, equation 17) waters. In the shallow-water model, fetch was the only variable linked (negatively) to SAV biomass, indicating that long fetch and corresponding wind driven turbulent motion was associated with low SAV biomass. This model's explanation of SAV biomass, albeit significant ($p = 0.02$), explained only 23% of SAV (adjusted) variance, owing to the combined effects of large spatial variability and small sample size. Fetch may have played an overly strong role in the shallow-water model since most samples were collected from the north shore, which is comparatively more exposed to wind than the south shore of Lake St. Pierre.

In the deep-water regression model (< 1.7 m, equation 17), fetch was also negatively related to SAV biomass, in addition to water depth (Z) and light extinction coefficient (K), which explained together 57% of total (adjusted) variance in SAV biomass (Table 7, $p < 0.001$). As previously seen in Lake St. Louis, this model revealed that Lake St. Pierre sites subjected to strong wind, deep or turbid waters tended to have low SAV biomass. Repeated measurements in Lake St. Pierre however showed K to be temporally variable with tributary discharge, especially during heavy rain episodes

In order to capture the integrated effect of the differences in water quality (transparency, nutrients, dissolved substances, pH) on SAV across lake St. Pierre, the deep-water model was reformulated using dummy variables defining four distinct water masses. The north, mixed, central, and south water masses were delineated from the examination of 2 Landsat MSS and TM satellite images obtained for different dates (1973-1990) during the growing season (Vis *et al*., 2003). The resulting multiple regression model was also highly significant, but explained a lower (44%) proportion of the total (adjusted) SAV variance (equations 18 a, 18b, 18c, 18d, Table 7). Although less efficient in explaining total variance than the model using K, the model using water mass is more realistic from an ecological standpoint as well as more convenient for modelling the variations of SAV distribution and biomass submitted to different water level conditions.

Global estimation of SAV biomass in Lake St. Pierre (2000-2001) using GIS

Models predicting of SAV biomass must be generalised spatially to obtain an overall estimation of the changes induced by environmental conditions over the Lake St. Pierre area, using a geographic information system (GIS). For this, water levels were simulated over the entire Lake St. Pierre surface, for the conditions prevailing in 2000 and 2001 and the surface area of the lake was divided among different depth strata, for which plant biomass was assessed using the appropriate model (Figure 16). The external limit of emergent plant assemblages in 2000 and 2001 were determined on the basis of the hydrofoil surveys – in the future, the limits of the different types of emergent plant assemblages will be modelled (Equation 12) – and an average biomass value was attributed to each of the depth strata (Table 8), to a depth of 1m.

Figure 16 outlines the sequence of decisions leading to the allocation the surface of Lake St. Pierre to the different vegetation models. For the emergent vegetation (0-1 m depth zone), work is currently under way to use model output (Hudon *et al*., 2003b) rather than hydrofoil field surveys to determine the distribution and types of emergent plant assemblages (Hudon *et al*., in preparation).

For the purpose of the present report, the limits of emergent vegetation cover were defined from hydrofoil field surveys, which distinguished between shallow (> 50% continuous emergent plant cover, Z = 0- 0.5 m) and deep marsh (< 50% continuous emergent plant cover, Z = 0.5- 1 m). Under the low-level conditions experienced in 2001, dried up areas of shallow marsh and of river bed shifted to transition annual vegetation and barren zones, respectively (Hudon *et al*., 2002).

Table 7
Quantitative relationships between environmental factors and SAV characteristics in the St. Lawrence River. For each relationship, the sector of the St. Lawrence River to which it applies is given

Equation	Area (water mass)	Dependent variable	Equation	Elevation range (m CD)	r^2	$p <$	*n*	Reference Data source
9a	River	Z_{max}	$3.08\ K^{-0.675}$	*n.a.*	0.82	0.001	16	Hudon *et al.*, 2000 Fig. 6a
9b	River	Z_{max}	1.11 Secchi + 1.16	*n.a.*	0.81	0.001	16	Hudon *et al.*, 2000 Fig. 6b
10a	LSP	S_{Water}	$85.47 + 83.15\ L_{Sorel}$ Empirical model	+ 8.5 m to - 1.7 m	0.99	0.001	98	This study- Fig. 7
10b	LSP	S_{Water}	$145.15 + 0.029\ Q_{Sorel}$ Simulated Scenarios	*n.a.*	0.99	0.001	13	This study- Fig. 8
10c	LSP	L_{Sorel} No SAV	$2.10 + 0.243\ Q_{Sorel} + 0.00267\ Q_{Sorel}^2$	*n.a.*	0.92	0.0001		This study – See text
10d	LSP	L_{Sorel} With SAV	$2.24 + 0.222\ Q_{Sorel} + 0.00267\ Q_{Sorel}^2$	*n.a.*	0.92	0.0001		This study – See text
10 e	LSP	$\Delta\ S_{Water}$ No SAV	$8.6\ (L_{Sorel} + 3.42)^{0.5}$	3.5 to 8 m ASL	*n.a.*	*n.a.*		This study – Fig. 9
10 f	LSP	$\Delta\ S_{Water}$ With SAV	$8.6\ (L_{Sorel} + 2.38)^{0.5}$	3.5 to 8 m ASL	*n.a.*	*n.a.*		This study – Fig. 9
11	Baie du Febvre	EM_{Cover}	$42.0 - 15.8\ L_{Sorel}$ Mean 1April- 30 September	+ 2 m to 0 m	0.74	0.01	8	Hudon, 1997 Fig. 10
12	LSP	EM_{Type}	Binary CART model : E, Z	+1 to -1m	*n.a.*	*n.a.*	630	Hudon *et al.*, 2003b Fig. 11
13	River	$Log_{10}\ B$	$-0.65 - 0.75\ \log_{10}Z - 0.23\ (\log_{10}Z)^2$	+1 m to Z_{max}	0.31	0.001	252	Hudon, 1997 Fig. 12
14	River	B	Binary CART model : F_{Class}, C, Z, I_z/I_0	+1 m to Z_{max}	0.67	0.001	178	Hudon *et al.*, 2000 Fig. 13
15a	LSL-Ottawa R.	$Log_{10}B$	3.05 - 0.87 Z	-0.5 m to Z_{max}	0.89	0.001	9	This study- Fig. 14
15b	LSL-SLR	$Log_{10}B$	3.32 - 0.44 Z	-0.5 m to Z_{max}	0.77	0.001	26	This study- Fig. 14

Table 7								
Equation	**Area (water mass)**	**Dependent variable**	**Equation**	**Elevation range (m CD)**	**r^2**	***p* <**	***n***	**Reference Data source**
16	LSP	B	$120.31 - 0.0025\ F_{Distance}$	-1 to -1.7 m	0.28	0.02	18	This study – see text
17	LSP	B	$374.44 - 0.003\ F_{Distance} - 35.91\ Z - 101.27\ K$	-1.7 m to Z_{max}	0.57	0.0001	51	This study- see text
18a	LSP- North	B	$221.05 - 0.0022\ F_{Distance} – 49.67\ Z$	-1.7 m to Z_{max}	0.49	0.0001	51	This study- See text –Fig. 15
18b	LSP- Mixed	B	$273.75 - 0.0022\ F_{Distance} – 49.67\ Z$	-1.7 m to Z_{max}	0.49	0.0001	51	This study- See text–Fig. 15
18c	LSP- Central	B	$254.57 - 0.0022\ F_{Distance} – 49.67\ Z$	-1.7 m to Z_{max}	0.49	0.0001	51	This study- See text –Fig. 15
18d	LSP- South	B	$124.51 - 0.0022\ F_{Distance} – 49.67\ Z$	-1.7 m to Z_{max}	0.49	0.0001	51	This study- See text –Fig. 15

See notes on the following page.

Variables and measurement units of Table 7 are defined as follows :

B : total aboveground biomass (all SAV species, g dry mass m^{-2}),
B(V) : total aboveground biomass per unit of water volume (all SAV species, g dry mass m^{-3}),
B_{Myr} : aboveground biomass of *Myriophyllum* spp. (g dry mass m^{-2}).
C: canopy (presence or absence),
E : elevation (m) of a point above or below the average water line in July,
EM_{Cover} : total cover of all types of emergent macrophyte wetlands (% of total surface area),
EM_{Type} : surface area (km^2) of each type of emergent macrophyte wetlands: meadow marsh, robust emergents, thin-leaved emergents and transition marsh,
F_{Class}: classes of fetch from the SW wind direction (225°) : fetch < 3000 m = sheltered site; fetch > 3000 m = exposed site,
$F_{Distance}$: continuous distance (m) values of fetch along the longest axis of Lake St. Pierre (245°), downstream from the cross-section of the archipelago at Sorel,
I_z/I_0 : fraction of incident light intensity reaching the bottom,
K : light extinction coefficient in open water (m^{-1}),
L : river water level (m above chart datum) at specified location and time interval,
Q : river discharge ($m^3 s^{-1}$) at specified location and time interval,
Secchi: depth at which a standard 20 cm diameter Secchi disk is visible in the shade (m),
S_{Water} : Cumulative surface area underwater (wetted surface)
Z_{max} : maximum depth of SAV colonization in the St. Lawrence River (m),
Z: water depth (m),
n.a. not appropriate.

As specified earlier (see previous section), the areas corresponding to channels in which water circulated within each of the shallower basins located on each side of the central navigation channel were excluded from the modelling exercise and were attributed a biomass of 0 (Table 8).

Areas of Lake St. Pierre submerged by > 1 m of water during the summer were allocated to the SAV models (outlined in the previous section). The shallow -water SAV model (Equation 16) was applied to the 1 - 1.7 m depth stratum and the deep-water SAV models (Equation 18a, 18b, 18c and 18d) were applied to the waters deeper than 1.7 m, within the limits defined for each of the four water mass in Lake St. Pierre.

The exercise generated estimations of the total surface area on which different emergent and submerged plant assemblages were found (Figure 17), leading to the calculation of the biomass for each assemblage (Table 9). In 2000, the emergent plant assemblages were dominated by

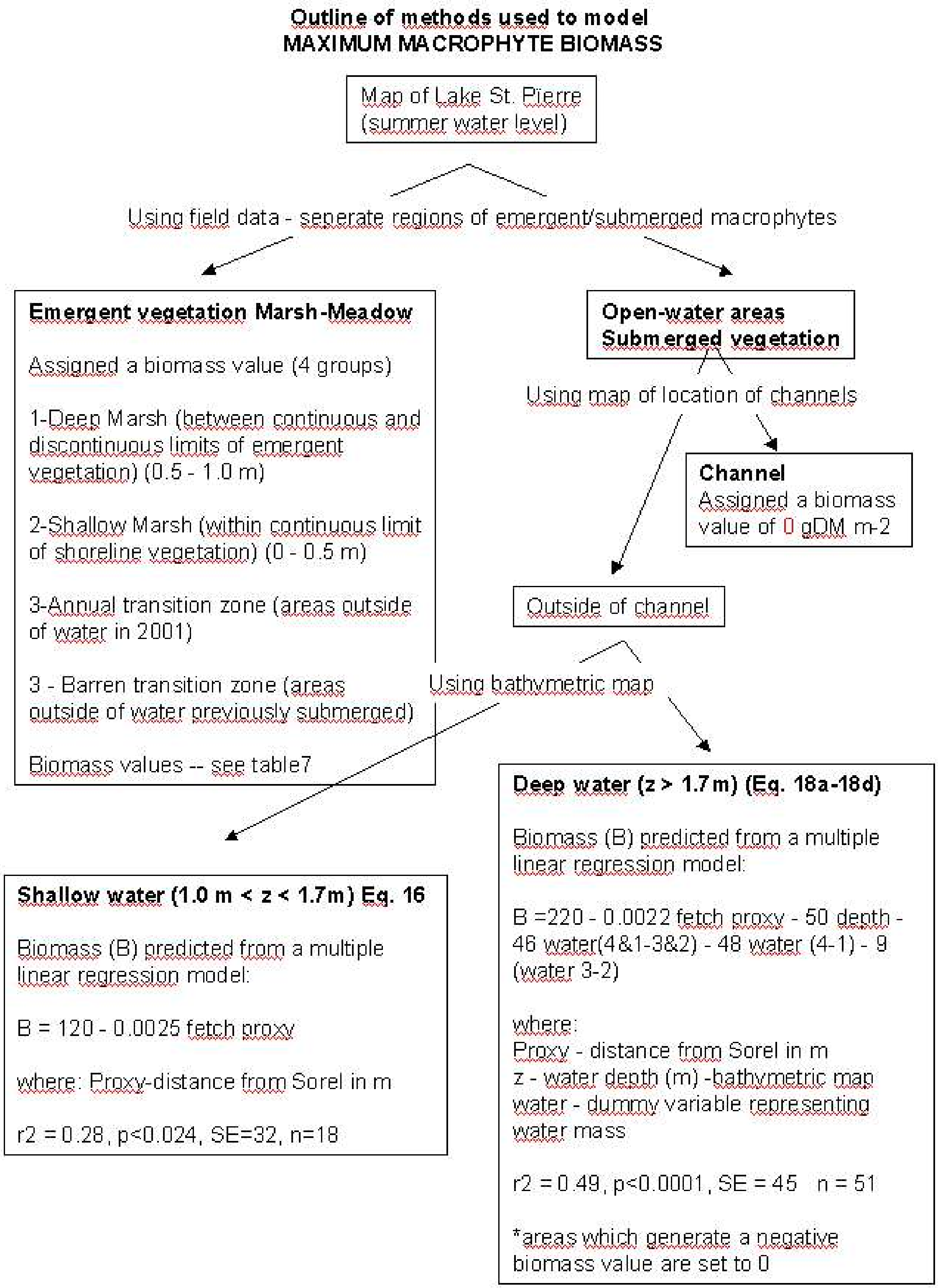

Figure 16 Decision process leading to the modelling of maximum biomass of submerged and emergent aquatic vegetation in Lake St. Pierre (from Vis, in prep.)

Table 8
Biomass values allocated to emergent vegetation assemblages for the calculation of Lake St. Pierre production in 2000 and 2001 (from Vis, in prep.)

Emergent plant assemblage	Depth Interval (m)	Mean Depth (s.d., n)	Average biomass (g dry mass m^{-2}) (s.e.) Emergent	Sub-merged	Filamen-tous algae	Litter
Annual transition (Dried marsh)	0	0 (0, 74)	750 (80)	0	1 (1)	480 (50)
Shallow Marsh (Thin-leaved emergents, small rush)	0 - 0.5	0.24 (0.14, 74)	410 (60)	90 (20)	20 (6)	280 (54)
Deep Marsh (Robust emergents, tall rush)	0.5 - 1	0.69 (0.14, 56)	220 (40)	230 (40)	8 (3)	110 (40)
Barren zone	0	0 (0, 28)	20 (10)	10 (6)	30 (8)	30 (9)

thin-leaved and robust emergents, which occupied together a surface of 86 km^2 and represented a biomass of 40710 tons. The 0.5 m drop in average water level in 2001 led to the drying out of 23.4 km^2 of lake bottom, most of which (22.4 km^2) became overgrown by a transitional marsh assemblage characterized by a higher average biomass (Table 9) and a small surface (1 km^2) of barren ground consisting of dried out submerged vegetation (Figure 17). In conjunction with the remaining surface of thin-leaved and robust marsh vegetation, these four emergent plant assemblages covered in 2001 a surface of 110 km^2 (30% increase from 2000) over the entire lake area, representing a total biomass of 57160 tons (40% increase).

For the submerged aquatic vegetation, the surface area decreased from 157.4 km^2 in 2000 to 132.7 km^2 in 2001, with a concurrent decrease of biomass from 6570 tons to 6350 tons ; these inter-annual differences translate into an overall rise of average SAV biomass from 41.7 to 47.8 g dry mass m^{-2}, which is entirely coherent with our field measurements.

Table 9
Comparison of mean depth (m), surface area (km^2) and total biomass (tons) of emergent and submerged vegetation in Lake St. Pierre in 2000 and 2001 (from Vis, in prep.)

Plant assemblage	Depth Interval (m)	Mean Depth (s.d)	Surface area (km^2)	Total Biomass (tons)	Mean Depth (s.d.)	Surface area (km^2)	Total Biomass (tons)
			2000			2001	
Annual transition (Dried marsh)	0	*n.a.*			0.22 (0.15) above water	22.4	16760
Shallow Marsh (Thin-leaved emergents, small rush)	0 - 0.5	0.51 (0.25)	39.6	19820	0.18 (0.13)	20.0	10010
Deep Marsh (Robust emergents, tall rush)	0.5 - 1	1.10 (0.38)	46.4	20890	0.88 (0.54)	67.5	30360
Barren zone	0	*n.a.*			0.08 (0.45) above water	1.0	30
Shallow SAV	1 - 1.7	1.30 (0.36)	15.7	730	1.25 (0.39)	21.6	1090
Deep SAV	> 1.7	3.04 (0.79)	141.7	5840	2.78 (0.66)	111.1	5260
Channels		6.5 (3.7)	56.5		6.0 (3.7)	56.5	
TOTAL			299.9	47280		299.8	63510

Feedback of SAV on their physical environment

The Boucherville wetland is located across the river from Montreal harbour, under the influence of the waters originating from Lake Ontario. Between Lake St. Louis and Boucherville, water clarity declines by more than half and light extinction coefficient drops from 1.6 to 0.72 m-1 (seasonal range of K = 0.39 - 1.29) owing to the increase of fine suspended clay eroded from upstream areas. This sector was significantly altered by major construction projects in the

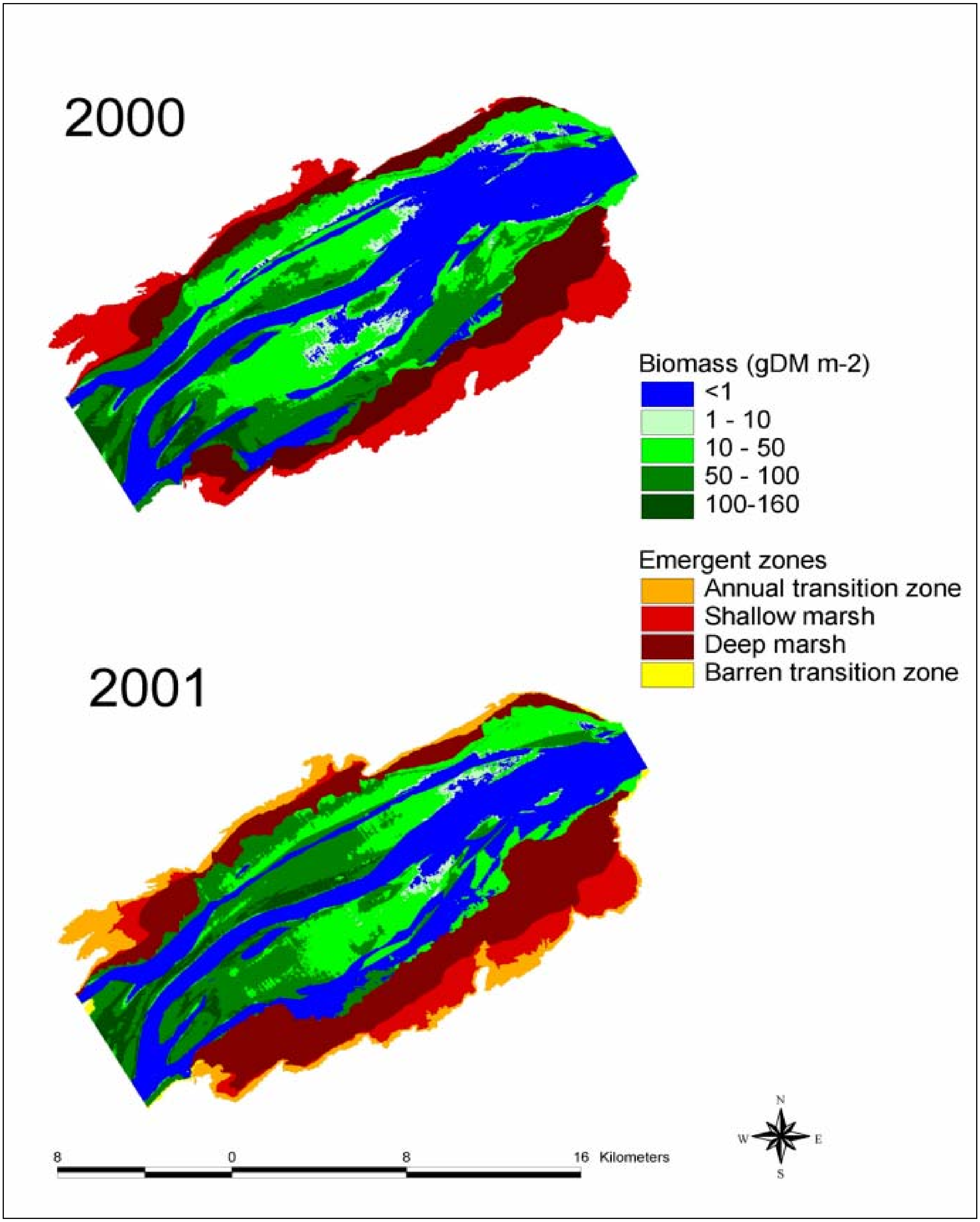

Figure 17 Spatial distribution of the different emergent and submerged plant assemblages in 2000 and 2001, modelled in Lake St. Pierre using GIS (from Vis, in prep.)

1960's including the excavation of the Montreal Harbour, the St. Lawrence Seaway and the Louis-Hippolyte Lafontaine tunnel. Dredge spoil was used to shield the nearby shoreline, build up jetties and islands, fill in wetlands and develop highways and urban areas along the Longueuil-Boucherville shoreline. Such alteration in the bathymetry and shoreline profile most likely diverted water towards the harbour area, with a concomitant reduction in flow through the Boucherville islands.

The resulting river configuration conveniently defined two adjacent, exposed and sheltered sampling sites, to test the effects of current and fetch (winds and waves) on SAV biomass and canopy formation (Table 10). Detailed observations on SAV architecture, seasonal sequence of development and the associated physical environmental conditions were made at both sites in 1999 (June to November), 2000 and 2001 (August). Such sharply contrasting SAV plant assemblages growing within the same water mass were selected to highlight the complex interactions and feedback of SAV with local underwater light climate, current and sediment composition.

Table 10
Comparison of physical characteristics (mean (s.d.) (min-max)) for the exposed and sheltered sites of the Boucherville wetland in 1999-2001

	Sheltered site	**Exposed site**
Mean Elevation CD (mean) (s.d.) (min-max)	-2.07 (0.31) (-1.33 to -3.29)	-2.05 (0.22) (-1.23 to -2.72)
Current speed (m s^{-1}) (min-max)	0 - 0.43	0.1 - 1
Fetch from the SW direction (km)	< 0.1	5 - 8
Light extinction coefficient (open water, K, m^{-1})	0.72 (0.39 - 1.29)	0.72 (0.39 - 1.29)
Sediment type	Soft mud (40-50 cm deep)	Sand and gravel on compacted clay
Dominant taxa	*Myriophyllum* spp. and *Elodea canadensis*	*Vallisneria americana* and *Heteranthera dubia*
Spatial arrangement	Dense mosaic of macrophytes patches, forming a thick canopy under the surface	Open mosaic of patches of different taxa forming a loose, shifting vertical cover

Plant architecture, morphology and canopy formation

Submerged plant composition and biomass differed markedly between sites. The sheltered macrophyte bed was dominated (0.4-1.2 kg DM m^{-2}) by canopy forming species such as *Myriophyllum* spp. *Elodea canadensis*, *Ceratophyllum demersum*, *Potamogeton* spp., whereas a lower biomass (0.2-0.5 kg DM m^{-2}) of *Vallisneria americana* and *Heteranthera dubia* occupied the exposed site. These species differed markedly in morphology and in the vertical distribution of their biomass (Figure 18).

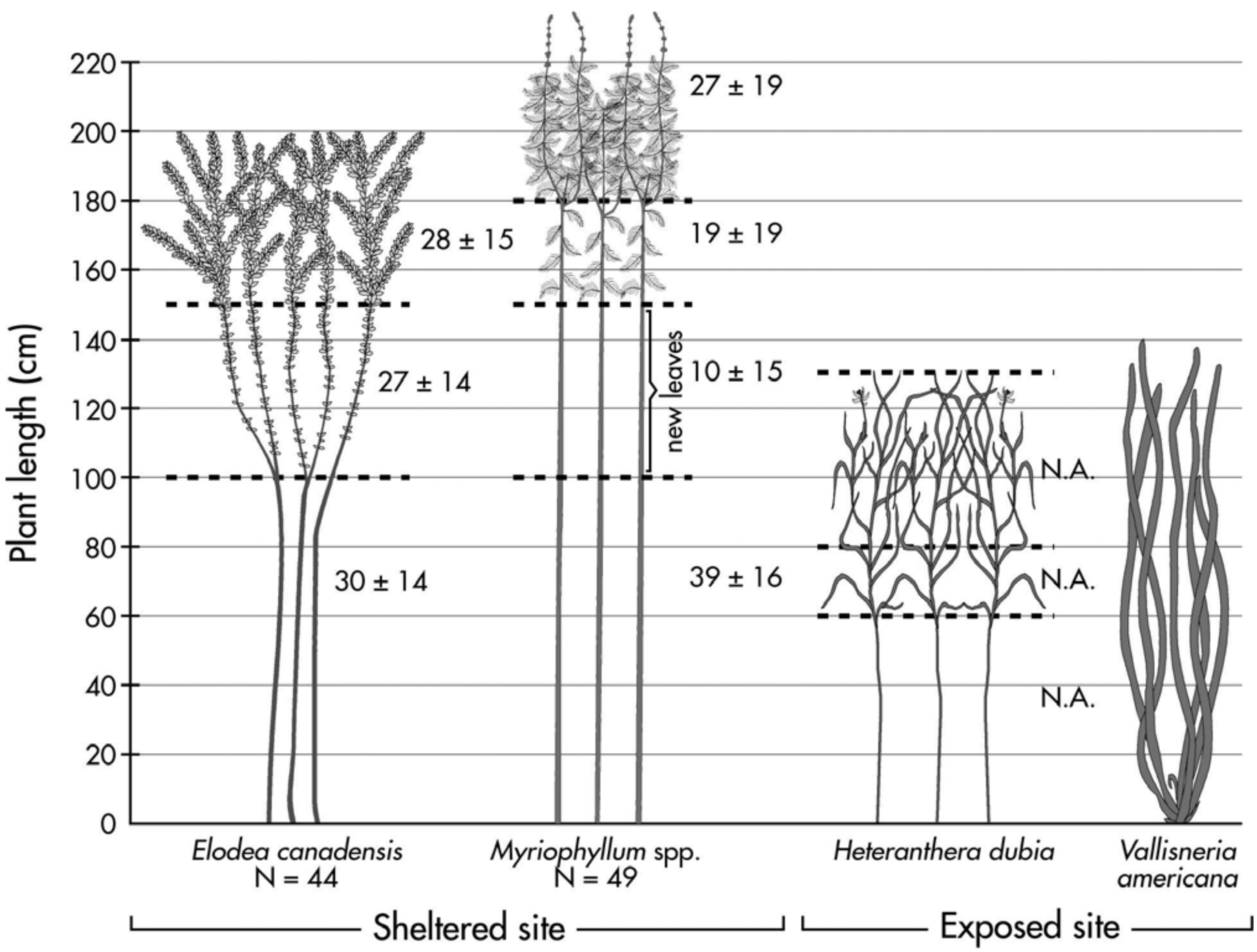

Figure 18 Comparison of plant architecture, height and vertical distribution of biomass (mean % of total biomass ± s.d.) of plant species dominant at the sheltered and exposed sites in Boucherville. N.A = measurements not available.

Plant morphology and vertical distribution of biomass differed markedly among species dominatingat sheltered and exposed sites. Both *Myriophyllum* spp. and *Elodea canadensis* reached total height > 180 cm and supported different stem types at increasing depth below the surface. Dense leaves and multiple ramifications were found in the upper 40 cm (28% of total biomass), leaves became less dense in the following 30-50 cm (19-27%) and stems devoid of leaves (30-39%) occupied the last meter to the bottom (Figure 18).

This distribution did not change through the season except for the germination of new leaves on the upper part of bare stems of *Myriophyllum* spp. in October, after the near- surface canopy became scattered by plant decay. Similar, although less pronounced vertical zonation was observed for *Heteranthera dubia* at the exposed site; this species and *Vallisneria americana* reached 120 cm of total height (Figure 18).

The sheltered site supported nearly three times the total and aboveground biomass found at the exposed site (Table 11). This difference was mostly due to the abundance of most canopy forming species under sheltered conditions. All canopy-forming species (except for *Potamogeton* spp.) exhibited significantly higher biomass at the sheltered than at the exposed site. *Vallisneria americana, Potamogeton* spp. and *Heteranthera dubia* dominated at the exposed site whereas *Myriophyllum* spp. and *Elodea canadensis* were consistently more abundant at the sheltered site. Total belowground (root) biomass was significantly higher under exposed conditions, revealing the need for strong anchoring of plants against current, in spite of their smaller aboveground biomass. A 3-fold difference was found in the proportion of belowground to total biomass between the sheltered (5.95 ± 2.1%) and the exposed (19.5 ± 2.2%) sites.when levels went down. This phenomenon was most important for pronounced for *Vallisneria americana* at the exposed site. Water level variations observed during the summer of 1999 exerted a compaction effect on SAV stems located closest to the surface (Figure 19) ; densely leafed canopy near the surface went up and down with rise and fall of water levels, making stems pile up together in a dense mat when levels went down.

Such compaction effect increased SAV biomass density under the surface and contributed to the shading effect induced by high biomass of SAV, especially important in sheltered areas in

Table 11

Comparison of maximum biomass (g DM m^{-2}) in early August for different species and groups of SAV (1999-2000-2001) sampled at an exposed and a sheltered site in the Boucherville wetland. Differences between sites were tested using one-way ANOVAs with a correction for multiple tests. Significance of the probability (p) associated to the F value : $p > 0.05$ not significant, *n.s.* ; $0.01 < p < 0.05$, * ; $0.001 < p < 0.01$, **, $p < 0.001$, ***

	Sheltered Site Mean biomass (s.d.) *n* = 29	**Exposed site Mean biomass (s.d.) *n* = 29**	**Effect of Exposure F value (*p*)**
Filamentous algae	0.06 (0.25)	0.01 (0.03)	0.81
Chara spp.	0 (0)	1.44 (5.62)	14.74***
Butomus umbellatus[1] var. *vallisneriifolius*	0.29 (1.10)	14.14 (54.12)	0.44
Ceratophyllum demersum	10.66 (16.91)	0.39 (1.35)	16.16***
Elodea canadensis	963.62 (1082.10)	50.11 (134.04)	36.68***
Heteranthera dubia	0.77 (2.67)	33.89 (89.45)	0.35
Myriophyllum spp.	274.5 (333.77)	5.32 (23.01)	32.34***
Potamogeton spp.	2.57 (5.17)	66.54 (172.23)	11.11**
Vallisneria americana	0.86 (2.20)	180.21 (143.95)	78.37***
Canopy-forming taxa[2]	1252.18 (971.53)	15.26 (225.40, 29)	20.38***
Non Canopy-forming taxa[3]	1.22 (3.03)	195.79 (147.16, 29)	79.73***
Total Aboveground biomass	1253.40 (972.21)	352.05 (213.38)	11.52**
Total Belowground biomass	29.34 (17.41)	75.05 (64.58)	15.98***
Litter	3.35 (8.14)	4.40 (8.42)	0.24
Total Biomass	1286.09 (980.07)	431.50 (216.69)	7.15**

(1) Two samples of 162 and 248 g DM m^{-2} in August 2000

(2) Sum of *Myriophyllum* spp., *Elodea canadensis, Ceratophyllum demersum, Potamogeton* spp., *Heteranthera dubia*

(3) Sum of *Vallisneria americana*, filamentous algae*, Characea, Butomus umbellatus* var. *vallisneriifolius*

Effects of SAV biomass/canopy on underwater light climate

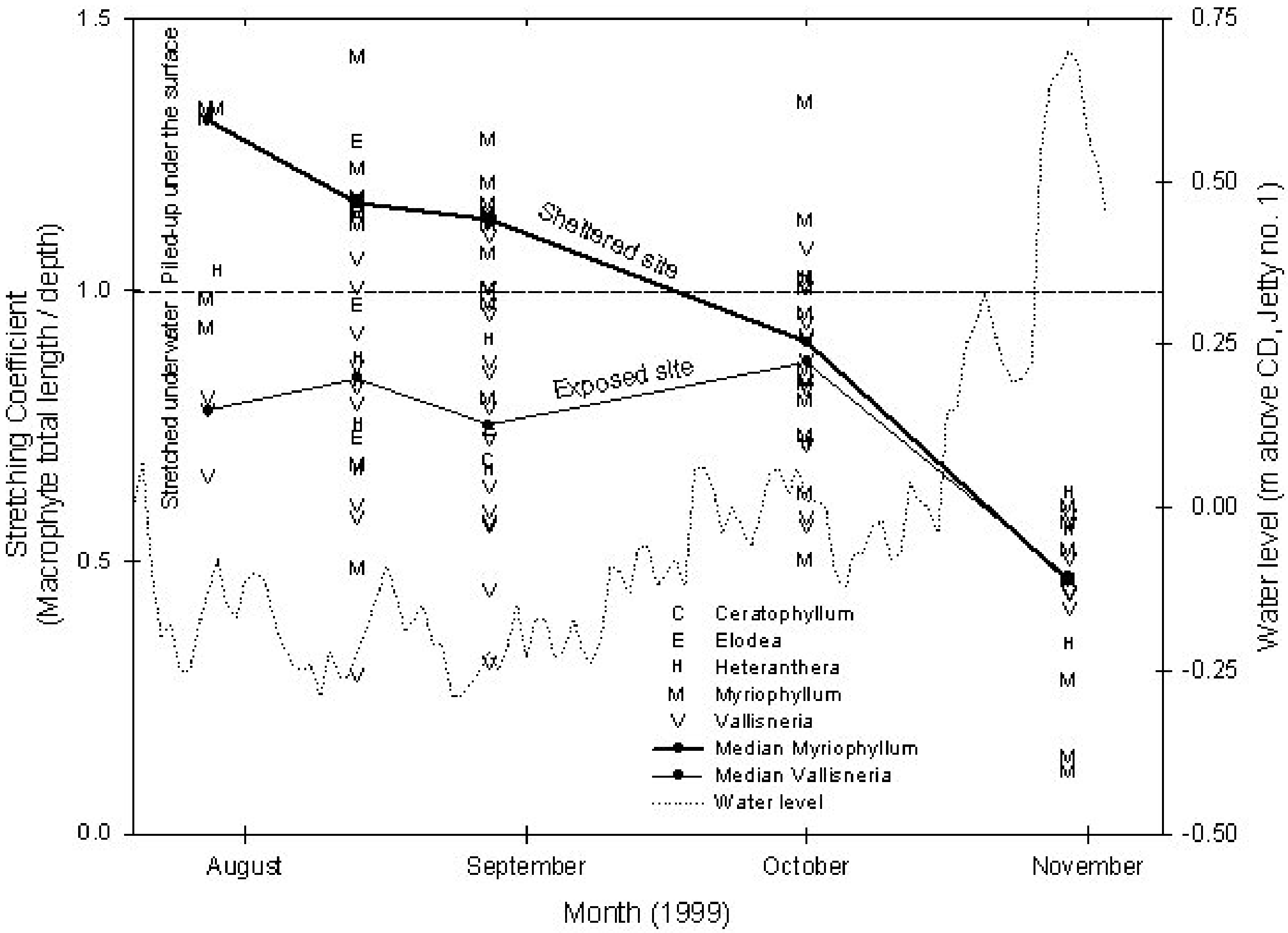

Figure 19 Seasonal variations in the vertical distribution and stretching coefficient (vertical compaction) of stems of the dominant SAV species found in exposed and sheltered sites in Boucherville (1999) as a function of daily water level variations at Montreal

which canopy-forming taxa were predominant (Figure 19). Canopy-forming species dominant at the sheltered site tended to form thick subsurface canopies which monopolized incident light and generated a sharp decrease in light intensity with depth; a strong relationship was observed between the biomass of *Myriophyllum* spp. and light extinction coefficient through the canopy (Figure. 20). Maximum mid-summer (July 28-Aug. 24) biomass of *Myriophyllum* spp. (300-400 g dry mass m^{-2}) coincided with light extinction coefficients > 15 in the upper 30 cm of the water column, thus allowing less than 1% of the incident light to penetrate underneath. Decreasing biomass (100-200 g dry mass m^{-2}) and rising water levels in October resulted in a more open canopy and lower light extinction coefficients (< 10 m^{-1}) due to plants, which allowed 8-85% of incident light below the canopy (Figure. 20). At the exposed site, maximum biomass of *Vallisneria americana* (220 g dry mass m^{-2}) coincided with a *K* value of 2.5, confirming the comparatively tenuous light obstruction produced by its linear leaves floating at the surface.

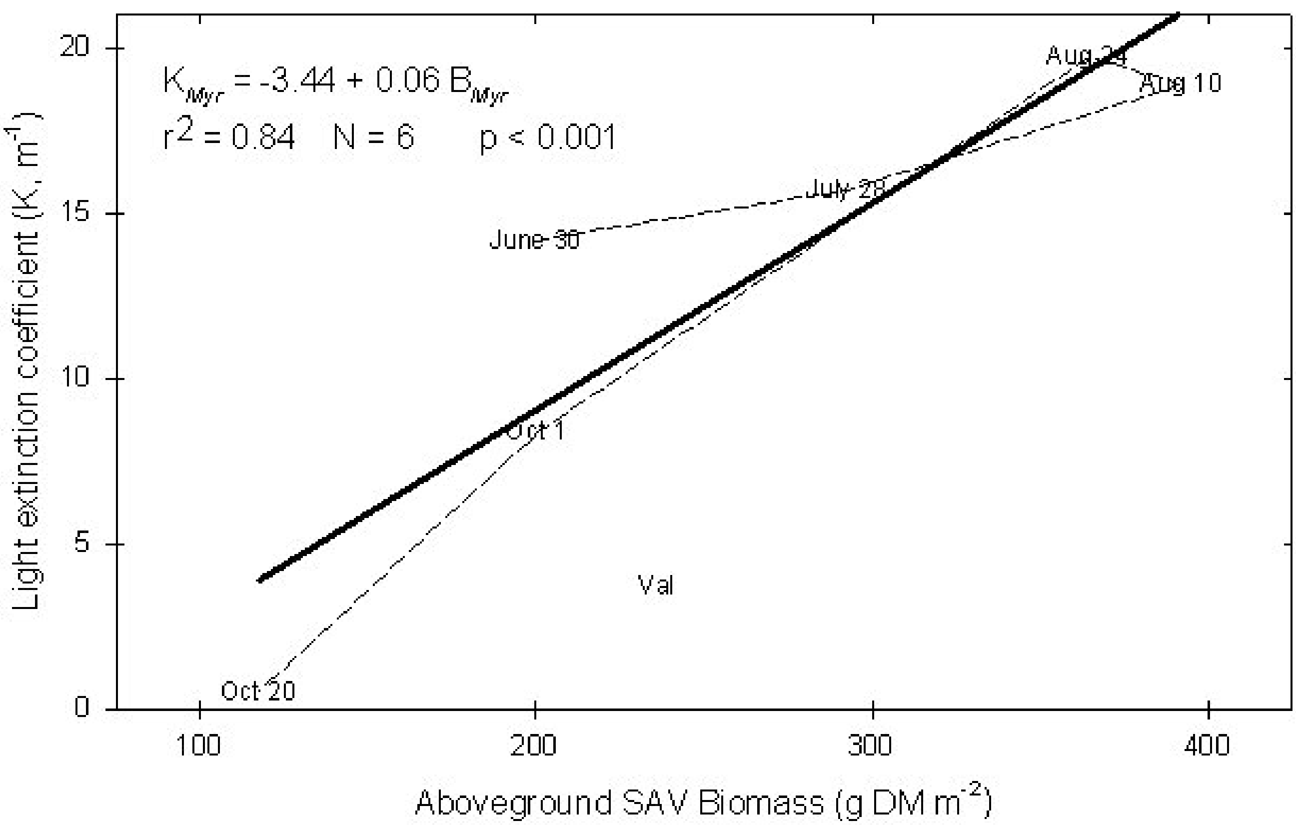

Figure 20 Seasonal variations (equation 20) in aboveground biomass of *Myriophyllum* spp. in Boucherville (1999) and the concurrent changes in light penetration through the SAV bed at the same dates. A value for *Vallisneria americana* (Val) is shown for comparison

The same pattern was observed when a broader range of SAV biomass values, representing multi-specific plant assemblages from various locations (Lake St. Louis, Lake St. Pierre and Boucherville) were examined (Figure 21). Distinct quantitative relationships between aboveground SAV biomass and light extinction coefficient were identified for canopy-forming and non-canopy forming assemblages; relationships were significant whether SAV biomass was expressed per unit of surface area (top diagram) or per volumetric units (bottom diagram). These relationships demonstrate the efficiency of different SAV assemblages in monopolizing light, regardless of species composition. Furthermore, these relationships could be useful in obtaining a rough assessment of SAV biomass from relatively simple K_{SAV} measurements in the field.

Effects of exposure and SAV biomass/canopy on sediment properties

Dense canopy also appear to be extremely efficient at intercepting particulate material from the water ; after its passage through the dense canopy of SAV at Boucherville water transparency increased and K decreased from 0.7 (upstream of the SAV bed) to 0.6 m^{-1} (downstream of the SAV bed). Differences in SAV biomass and species composition between the exposed and sheltered sites also coincided with significant differences in sediment texture, composition and nutrient contents. At the sheltered site, sediment comprised 33% less silt, 3 times more volatile organic matter and 3 times more nitrogen than at the exposed site, for both 2000 and 2001 (Table 12). Retention by canopy of imported suspended matter and of locally-produced dead plant matter thus improved plant growing conditions, through the accumulation of thick, silty, nitrogen-rich, organic sediment (Table 12, Clarke, 2002). Conversely, the exposed site had higher sediment compaction and mineral contents, which coincided with a 4-fold increase in the fraction of total biomass devoted to anchoring belowground structures (Table 11).

Cumulative effects of water levels on the physical environment of aquatic plants

Validation of models using 2000-2001 field data

Equations described in the previous sections were combined to illustrate the cumulative effects of water levels on long-term (1960-2003) variations of physical and biological characteristics in Lake St. Pierre. This required the application of information on the equations and predictor variables (table 14), to a hypothetical point located at an elevation of 2 m below chart datum, mid-way downstream of the lake, exposed to a fetch of 26 km from Sorel. These specific thresholds were selected because they corresponded to the overall average elevation and fetch of the stations sampled in Lake St. Pierre in 2000 and 2001(previous section). All calculations were made for the period of the growth season (April 1 to Sept. 30). Whenever possible, contrasting values for each variable expected for St. Lawrence River and Ottawa River

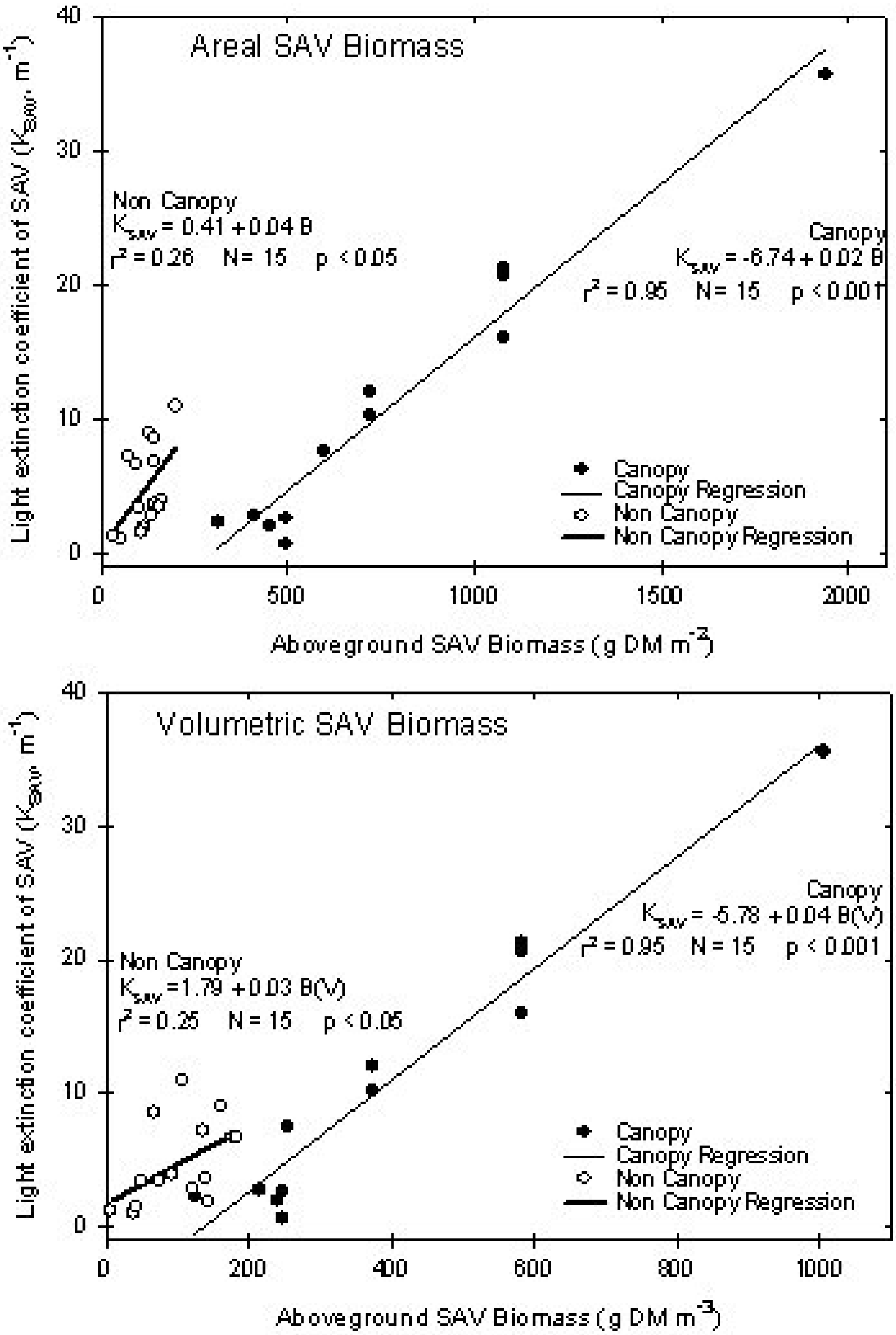

Figure 21 Quantitative relationships (equations 21 a, 21b, 21c, 21d, Table 13) linking areal and volumetric biomass of SAV of canopy and non-canopy species to light extinction coefficients resulting from the obstruction of light by plant material in the water column – *K* values for open water were subtracted from the calculation. Measurements originate from Lake St. Louis, Lake St. Pierre and Boucherville in 2001

Table 12
Comparison of physical variables and sediment (2000-2001) characteristics at an exposed and a sheltered site in the Boucherville archipelago. Differences between years and sites were tested using one-way ANOVA with a correction for multiple tests. ANOVA was not performed on current speed and fetch values (*n.a.*)

	Exposed Site mean (s.d.,) *n* = 7	**Sheltered site mean (s.d.) *n* = 7**	**Effect of Exposure**
Depth (cm)	-200.8 (20.5)	-188.6 (20.5)	*n.s.*
Elevation (cm below CD)	-204.4 (20.5)	-192.1 (20.5)	*n.s.*
Current speed (m s^{-1})(min-max)	0.1 - 1	0 - 0.4	*n.a.*
SW Fetch (km)	5 - 8	< 0.1	*n.a.*
% Sand	7.2 (8.4)	31.0 (9.1)	*n.s.*
% Silt	69.0 (6.9)	45.8 (7.5)	0.05*
% Clay	23.9 (4.2)	23.3 (4.6)	*n.s.*
Phi (particle diameter, μm)	22.2 (78.9)	189.8 (85.3)	*n.s.*
% Volatile Solids	7.4 (0.6)	2.6 (0.6)	0.00002***
Organic Nitrogen (μg N g^{-1} dry sediment)	3028.6 (301.3)	1057.1 (301.3)	0.007**
Total Phosphorus (μg P g^{-1} dry sediment)	861.4 (92.5)	764.3 (92.5)	*n.s.*
pH	7.4 (0.06)	7.6 (0.06)	0.05*

Table 13
Quantitative relationships describing the feedback of SAV on physical environmental conditions in the St. Lawrence River. For each relationship, the sector of the St. Lawrence River to which it applies is given

Equation	Area	Dependent Variable	Equation	Biomass range (g dry mass m^{-2})	r^2	*p* <	*n*	Reference Data source
19	Boucherville	$B_{Species}$	Significant difference between exposed and sheltered sites	0 - 1500	*n.a.*	0.001	29	This study-Table 11
20	River	K_{Myr}	$-3.44 + 0.06\ B_{Myr}$	125-400	0.84	0.001	6	This study- Fig. 20
21a	River	Canopy K_{SAV}	$-6.74 + 0.02\ B$	300-1800	0.95	0.001	15	This study- Fig. 21
21b	River	Non Canopy K_{SAV}	$0.41 + 0.04\ B$	20-250	0.26	0.05	15	This study- Fig. 21
21c	River	Canopy K_{SAV}	$-5.78 + 0.04\ B(V)$	100-1000 g dry mass m^{-3}	0.95	0.001	15	This study- Fig. 21
21d	River	Non Canopy K_{SAV}	$1.79 + 0.03\ B(V)$	10 - 200 g dry mass m^{-3}	0.25	0.05	15	This study- Fig. 21
22	Boucherville	Sediment	Significant difference between exposed and sheltered sites	*n.a.*	*n.a.*	0.05 to 0.00001	7	This study-Table 12

See notes on the following page.

Variables and measurement units of Table 13 are defined as follows :
B : total aboveground biomass (all SAV species, g dry mass m^{-2}),
B(V) : total aboveground biomass per unit of water volume (all SAV species, g dry mass m^{-3}),
B_{Myr} : aboveground biomass of *Myriophyllum* spp. (g dry mass m^{-2}).
$B_{Species}$: aboveground biomass of individual SAV species (g dry mass m^{-2}),
K: light extinction coefficient (K) of open water (m^{-1}),
K_{Myr} : light extinction coefficient (K) due to the presence of *Myriophyllum* spp. in the water column (m^{-1}),
K_{SAV} : light extinction coefficient (K) due to the presence of dense SAV in the water column (m^{-1}),
L_{Sorel}, : mean river water level at Sorel (m above chart datum),
Sediment = Sediment characteristics (% silt, % organic contents, Organic N, pH)

waters were calculated, so as to obtain an image of the widest range of conditions that could be experienced under the influence of different water masses, all other factors remaining equal.

The number of hours of sunshine was used to derive PAR values (I_0, Equation 1, Table 6), defining the average incident photosynthetically active radiation at the surface of the water during the growth season. Water temperature was determined from water levels at Montreal Harbour Jetty no. 1, using the monthly equations derived for waters originating from Lake Ontario (Equation 2b) and for waters mixed with Ottawa River (Equation 2c). Water clarity was also calculated separately for the two major water masses found in the river. For waters under the influence of Lake Ontario waters, an average suspended solids concentration of 6 mg l^{-1} (Equation. 5b) served as the basis for calculation of *K* (Equation 7a). For water under the influence of the Ottawa River, daily discharge at Carillon was used to predict suspended solids concentration (Equation 5c), which served as input to predict light extinction coefficient *K* (Equation 7c).

In combination with *Z* and the PAR value (I_0), the estimates of *K* for each water mass lead to the calculation, using Equation 8, of the fraction of incident light (I_Z / I_0) and of the irradiance (I_Z) at an elevation of 2 m below CD. These variables constituted the physical variables from which emergent and submerged aquatic vegetation were predicted and validated against observations (Table 15). The maximum depth of submerged macrophyte (SAV) colonization (Z_{MAX}) was predicted from the *K* value derived for each water mass using Equation 9a. The

Table 14
Predictor variables used in the equations used to model temporal changes of physical and biological characteristics in Lake St. Pierre (1960-2003). For each variable, a mean value for the growing season (1 April to 30 September) was derived from daily values averaged monthly. Mean values measured in 2000 and 2001 are indicated for comparison

Equation	Predictor variable (units)	Location (Interval)	Mean min- max	2000	2001
10a, 11	Water level (m above CD)	Sorel (1960-2003)	1.19 (0.28 - 2.05)	1.06	0.52
n.a.	Depth of a point located at an elevation of - 2m CD	Sorel (1960-2003)	3.19 (2.28 - 4.05)	3.06	2.52
1	Sunshine (h)	Montreal area (1960-2003)	7.2 (6.4 - 8.2)	6.7	8.2
2b, 2c	Daily water level (m above CD)	Montreal Harbour (1960-2002)	1.12 (-0.03 - 2.18)	0.89	0.18
5b	Suspended Solids (mg l^{-1})	Varennes (1994-1996)	6.0 (median 4.4) (1.0 - 61.7)	6.0	6.0
5c	Daily Discharge (m^3 s^{-1})	Carillon (1963-2002)	2041 (1341 - 3218)	1922	1429
10b	Daily Discharge (m^3 s^{-1})	Sorel (1960-2002)	10590 (7532 - 13450)	10159	8470
18a, 18b, 18c, 18d	Fetch (m)	Sorel (*n.a.*)	26188 (17291-395270	26000	26000

wetted surface of Lake St. Pierre for the growth period was determined using both the equations obtainedempirically from level at Sorel (Equation 10a) and from simulations using discharge at Sorel (Equation 10b). Level at Sorel was also used to predict the percent cover of emergent vegetation at Baie du Febvre (Equation 11). Finally, the biomass of SAV at an elevation of -2 m CD and exposed to a mid-lake fetch (26000 m from Sorel) was predicted for each of the four water masses of Lake St. Pierre using Equation 18a – 18d.

The values predicted for the years 2000 and 2001 were compared to measurements, to ascertain that predictions fell within the proper range and whether or not the forecasted differences between years were in the proper direction. This was done using the results of field

Table 15
Comparison of physical and biological characteristics measured at 39 stations in Lake St. Pierre sampled in August 2000 and 2001. Significance of the probability (unilateral test) (*p*) associated to the F value : $p > 0.05$ not significant, *n.s.* ; $0.01 < p < 0.05$, * ; $0.001 < p < 0.01$, **, $p < 0.001$, *. Test cannot be performed, not appropriate or not available (*n.a.*)**

	Measurements mean (s.d.) min-max		Paired t-test	Equations	Predictions	
	2000	2001	t		2000	2001
Sample depth (m)	2.61 (0.82) 0.86 -3.90	1.80 (0.70) 0.50 -3.40	-8.95 ***	*n.a.*	3.06	2.52
Sample elevation with respect to CD (m)	-1.96 (0.80) -3.16 to -0.05	-1.84 (0.70) -3.40 to -0.51	-1.46 n.s.	*n.a.*	-2.00	-2.00
Water temperature (°C)[1]	17.48 (4.73)	18.98 (4.67)	-14.08 ***	2b – 2c	15.6-16.6	16.5-17.5
Current speed ($m\ s^{-1}$)	0.22 (0.14) 0.0 - 0.6	0.11 (0.08) 0.0 - 0.4	4.80 ***	*n.a.*	*n.a.*	*n.a.*
Light extinction coefficient (K, m^{-1})	1.67 (0.29) 0.9 - 3.5	1.34 (0.29) 0.8 - 3.1	-3.38 ***	5b – 5d 7a – 7c	0.8 - 2.6	0.8 - 2.2
Fraction of incident light reaching the bottom (I_Z / I_0, %)	4.06 (6.18) 0.0 - 28.8	13.36 (7.28) 0.9 - 31.5	-7.41 ***	8	< 1 -8.1	< 1 -12.7
Light intensity reaching the bottom (I_Z, Einstein $m^{-2}\ d^{-1}$)	1.25 (1.90) 0 - 8.9	4.76 (2.79) 0.3 - 11.2	-8.14 ***	8	0.01 - 2.5	0.14 - 4.5
Z_{max} (m)[2]	2.23 (0.88) 0.50 - 3.50	1.89 (0.70) 0.73 - 3.40	1.41 *n.s.*	9a	1.6 - 3.5	1.8 - 3.5
Cover of emergent plants (%)	25.4	2002 : 28.3 2003 : 30.8	*n.a.*	11	25.2 (2-yr mean = 29.3)	33.9 (2-yr mean = 29.5)
SAV biomass (g dry mass m^{-2})	33.1 (35.6) 0 - 108.2	45.3 (53.6) 0 - 201.3	-1.64 *	18a, 18b. 18c, 18d	0 - 64	0 - 92

[1] Daily mean comparison computed from hourly temperature data recorded at Canadian Coast Guard Buoy C-65, located in the navigation channel near Trois-Rivières, between April 20 and September 30.
[2] T-Test (non-paired) made on all Lake St. Pierre stations at which total sampled SAV biomass > 0 g dry mass m^{-2} < 5 in 2000 and 2001.

measurements made at 39 stations in Lake St. Pierre distributed among 5 transects perpendicular to the shoreline (see methods). Although the predictions were made for individual water masses, validation was carried out for all samples together, since dividing the samples among water masses would have greatly reduced the sample size. Physical measurements (water depth, water temperature, *K*, I_Z/I_0, I_Z) were entirely independent from our model development data sets.

Biological measurements were independent in some cases (Z_{max}, cover of emergent plants) but not in others (total SAV biomass); in the latter case, the samples used to test the predictions represented a subset of samples used to derive the equations predicting total aboveground biomass. However, additional between-year comparisons were made to contrast the biomass of individual species' and of structural groups (canopy vs non canopy forming), thus representing independent subsets.

The samples used to validate the predictions of the different models were taken at the same locations over the months of August 2000 and 2001 (Table 15); the 54 cm lower level observed in 2001 resulted in significantly lower average sample depth although the elevation measurements of the samples did not differ significantly among years. This ensured that the comparison of the samples represented contrasting water level conditions.

Overall, the absolute values, direction and relative magnitude of the changes predicted in 2000 and 2001 coincided well with observed changes (Table 15). As predicted by the temperature model, water temperature in 2001 was significantly warmer than in 2000; the higher than expected difference in temperature (1.5^{o}C observed instead of the expected 1^{o}C) in part results from the lack of the first three weeks of April in the measured temperature series. Reduced discharge and level in 2001 also halved current speed in 2001. Our measurements also showed Lake St. Pierre's water to be significantly more transparent in 2001 than in 2000, allowing three times the amount of light to reach the bottom under low level conditions. Predictions were in the proper direction although somewhat conservative in absolute terms for the three variables describing underwater light conditions.

No significant change was recorded in the maximum depth of SAV colonization; although a marginal increase (by 0.2 m) was anticipated for stations subjected to Ottawa River waters, no change were forecasted for stations influenced by St. Lawrence River waters, which coincided with observations (3.5 m). Percent cover of emergent vegetation was very close to expectations and showed a significant increase (by 50%) as a response to low levels. The anticipated 2001 increase of SAV total biomass was indeed observed, showing a stronger measured response than anticipated.

Closer comparison between sub-components of SAV samples (Table 16) revealed that the 50% increase in biomass was due to a significant increase in the biomass of *Vallisneria americana,* *Heteranthera dubia* and of filamentous algae. This coincided with a significant increase in non canopy-forming species.

Table 16
Comparison of SAV biomass (mean g DM m^{-2}, s.d.) recorded at 39 stations in Lake St. Pierre sampled in August 2000 and 2001 (value for each station is the mean of 1-5 samples). Significance of the probability (*p*) associated to the F value : *p*> 0.05 not significant, *n.s.* ; 0.01 < *p*< 0.05, * ; 0.001 < *p* < 0.01, **, *p*< 0.001, ***

	Effect of year/level		Paired t-test	*p*
	2000	2001	Year	
Potamogeton spp.	4.81 (11.34)	3.21 (11.87)	0.78	0.22 *n.s.*
Elodea canadensis	0.0008 (0.004)	0.002 (0.09)	-1.35	0.09 *n.s.*
Heteranthera dubia	0.24 (1.35)	5.54 (18.96)	-1.74	0.05*
Myriophyllum spp.	0.001 (0.009)	0.008 (0.03)	-1.06	0.15 *n.s.*
Ceratophyllum demersum	0	0.0007 (0.004)	-1	1.69 *n.s.*
Vallisneria americana	23.25 (32.39)	57.23 (50.36)	-4.35	0.00005***
Butomus umbellatus var. *vallisneriifolius*	0.07 (0.46)	0.14 (0.87)	-0.41	0.34 *n.s.*
Nitella spp.	3.66 (16.98)	4.21 (9.59)	-0.14	0.45 *n.s.*
Chara spp.	0.003 (0.01)	0.09 (0.55)	-0.96	0.17 *n.s.*
Filamentous algae	0.03 (0.14)	2.50 (6.34)	-2.40	0.009**
Canopy-forming taxa[1]	5.05 (11.38)	8.79 (21.53)	-0.99	0.16 *n.s.*
Non-canopy forming taxa[2]	27.01 (34.25)	64.18 (57.51)	-4.38	0.00005***
Total Aboveground	33.14 (35.57)	45.31 (53.61)	-1.64	0.05*

(1) Sum of *Myriophyllum* spp., *Elodea canadensis*, *Ceratophyllum demersum*, *Potamogeton* spp., *Heteranthera dubia*
(2) Sum of *Vallisneria americana*, filamentous algae, *Chara*, *Nitella*, *Butomus umbellatus* var. *vallisneriifolius*

Propagation of physical effects

In the 1960-2003 interval, water level at Sorel during the growth period followed a broad range of variations (Figure 22), with a minimum of 0.28 m (in 1965) and maximum values of 2.05 (in 1974) above CD, translating in a depth range of 2.28 to 4.05 m for a point located 2 m below chart datum over the same period. The average number of hours of sunshine ranged from 6.4 to 8.2 hours daily (Table 17), exhibiting a year-to-year variation as a mirror image to that of water levels. Water temperature followed a similar pattern, suggesting that years of low level coincide with generally sunny, dry and warm weather. Waters originating from Lake Ontario followed inter-annual variations (spanning 2.5 ^{o}C) parallel to those originating from the Ottawa River, the latter being warmer by about 1^{o}C. Following Ottawa River discharge and suspended solids concentrations, the light extinction coefficient of Ottawa River waters ranged between 2.1 and 3.7, whereas that of St. Lawrence River waters were constant at 0.8 m^{-1}, owing to the lack of correlation between Cornwall-Beauharnois discharge and suspended solids concentrations.

The fraction of surface light intensity (I_Z / I_0) as well as the absolute amount of light (I_Z) reaching a point located at an elevation of -2 m (CD) was influenced by depth variations (Z) only in St. Lawrence River waters (K being constant) whereas both Z and K varied in Ottawa River waters. The point located at -2 m CD was exposed to considerably more light passing through St. Lawrence River waters (3.6 – 15 % of surface irradiance) received consistently higher illumination than through Ottawa River waters (< 1%) (Table 17).

The quantitative relationships among environmental factors, between physical factors and SAV and the retroactive action of SAV on the environment identified for the St. Lawrence River in the present report (Tables 6, 7, 13) allow to parameterise the magnitude of the anticipated effects of different water level and climate (sunshine) scenarios on SAV biomass.

In comparison with the 1960-2003 mean, the values observed and predicted (table 15 and Figure 22) for most variables over the years 2000 and 2001 coincide with ± 1 standard deviation on either side of the 43-yr mean. In addition, the warm, sunny, low water level conditions observed in 2001 coincide both in direction and relative magnitude with the changes forecasted by the CGCM 2 x CO_2 climate change scenario for the Great Lakes - St. Lawrence Basin

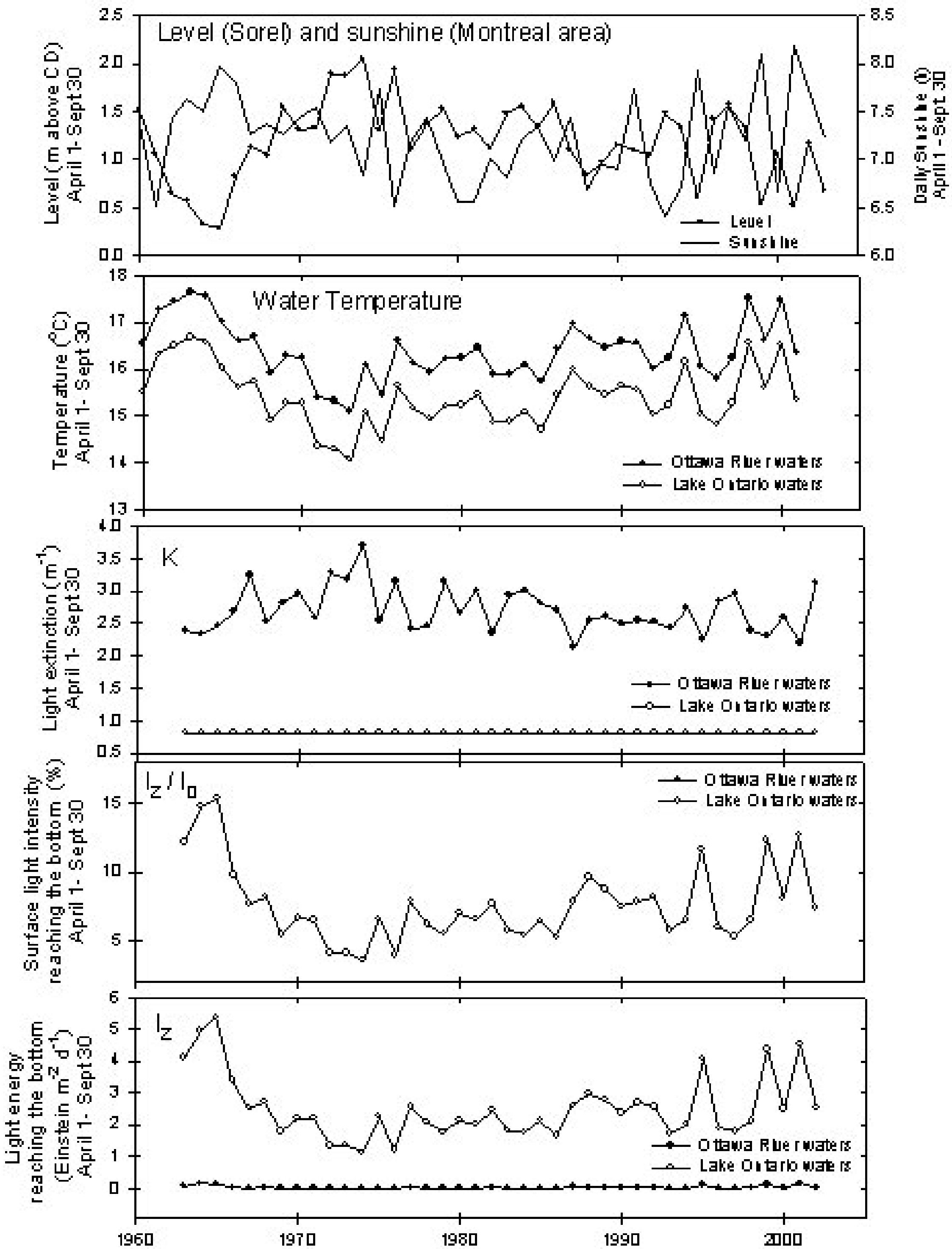

Figure 22 Temporal variations (1960-2003) of physical characteristics influencing SAV distribution and biomass during the growth season (1 April to 30 September) in Lake St. Pierre, predicted from the equations presented in Table 6 and predictor variables (Table 14). When applicable, values were computed separately for different water masses

Table 17
Predicted values of the physical characteristics in Lake St. Pierre (1960-2003), for the growing season (1 April to 30 September). Mean values predicted for 2000 and 2001 are indicated for comparison with measured values (Table 15)

Predicted variable (units)	Water mass originating from	1960-2003 mean min-max	2000 Predicted	2001 Predicted
Incident PAR (I_0, Einstein m^{-2} d^{-1})	*n.a.*	32.6 (30.0 - 35.6)	30.8	35.6
Water temperature (^oC)	Ottawa River	16.4 (15.1 -17.6)	16.6	17.5
	St. Lawrence River	15.4 (14.1 - 16. 7)	15.6	16.5
Suspended Solids concentration (mg l^{-1})	Ottawa River	22.6 (14.2 - 37.2)	21.1	15.2
	St. Lawrence River	6.0	6.0	6.0
Light extinction coefficient (K, m^{-1})	Ottawa River	2.7 (2.1 - 3.7)	2.6	2.2
	St. Lawrence River	0.8	0.8	0.8
Fraction of incident light reaching an elevation of -2 m CD (I_Z / I_0, %)	Ottawa River	< 1 (0 - 0.4)	< 1	< 1
	St. Lawrence River	7.6 (3.6 - 15.0)	8.1	12.7
Light intensity reaching an elevation of -2 m CD (I_Z, Einstein m^{-2} d^{-1})	Ottawa River	0.02 (0 - 0.15)	0.01	0.14
	St. Lawrence River	2.5 (1.1 - 5.4)	2.5	4.5

(Mortsch, 1998). Also consistent with this scenario was the decline in water levels and rise in water temperature during the 2001 growth season, as a consequence of reduced precipitations and increased evaporation in the upper part of the watershed. The combination of low discharge and high sunshine result in lower water depth and higher incident radiation; low precipitation also reduce the amounts of dissolved and particulate matter carried into the river and thus increase water clarity.

Predicted biological variables responded accordingly to physical environmental changes (Figure 23, Table 18). The maximum depth of SAV colonisation (Z_{max}) was stable (3.5 m) in St. Lawrence River waters as a function of constant *K* values, whereas it varied from 1.3 to 1.9 m in areas under the influence of Ottawa River waters. The wetted surface of Lake St. Pierre was forecasted to increase by 30% between years of high and low levels; the small but consistent (10%) difference in total area recorded between empirical and simulation methods likely resulted from the consideration of the slope of waters over the length of the lake, which is not considered in the former method. Accordingly, emergent plants were expected to cover 10 to 38% of the surface of Baie du Febvre. Models of biomass of submerged aquatic vegetation in each of four water masses of Lake St. Pierre indicated higher biomass in the mixed and central areas of the lake than along the more turbid north (influenced by the Ottawa River) and south (influenced by south shore tributaries) shores.

As with the physical variables, differences in biological characteristics anticipated between 2000 and 2001 (Table 18, Figure 23) reflected the warm, dry, low-level conditions experienced in 2001, resulting in a deepening of macrophyte colonisation (only in areas under the influence of the Ottawa River), a decrease in wetted surface area, an increase in the surface covered by emergent macrophytes and an increase in SAV biomass in three of the four (except the southern) water masses of Lake St. Pierre. These inferred changes suggest that changing water levels alter the inherent character of Lake St. Pierre, since they result in a dramatic shift from a large marshland with high biomass of SAV at low water levels to an open-water body with lesser plant biomass at high levels.

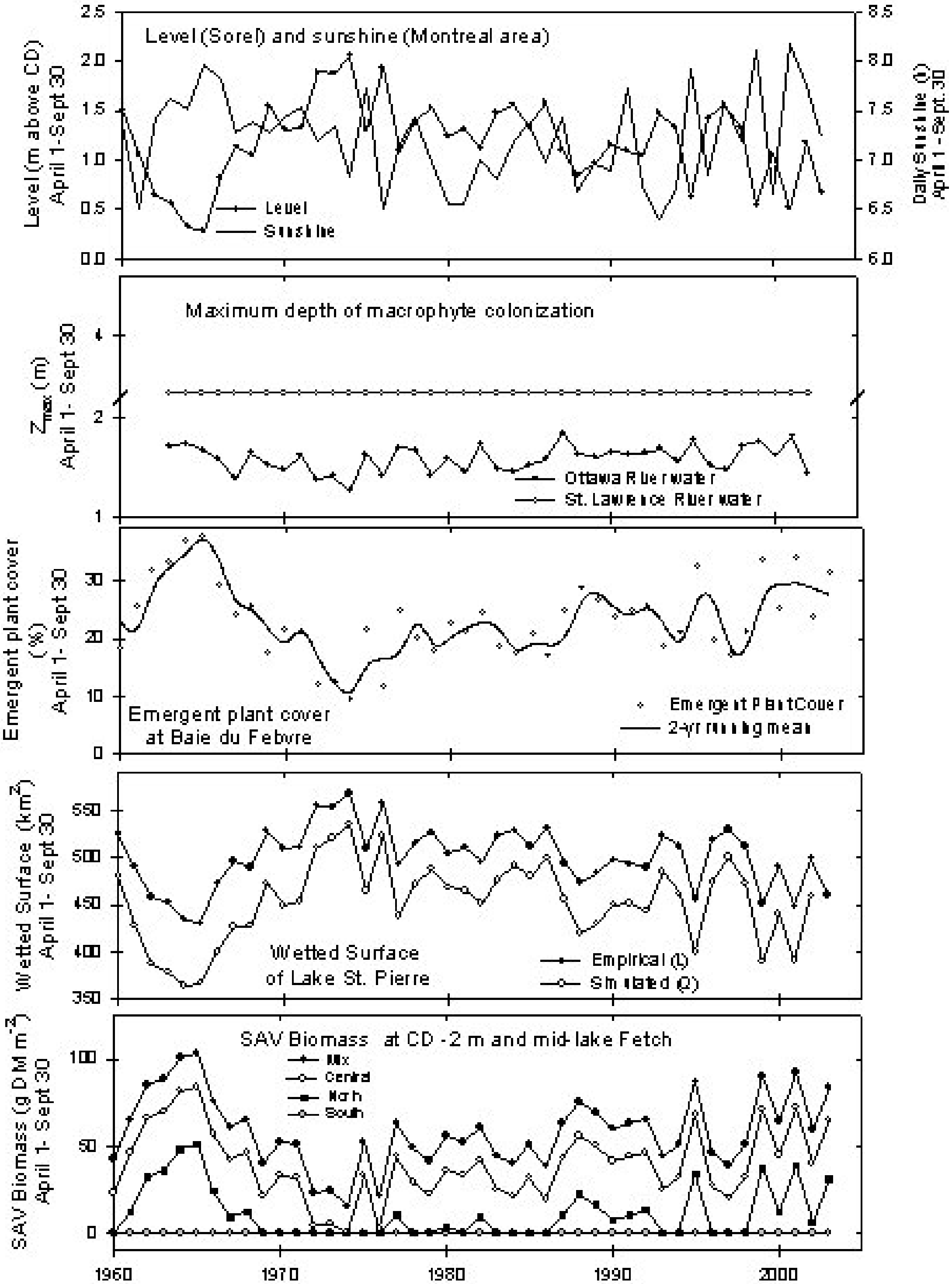

Figure 23 Temporal variations (1960-2003) of biological characteristics of emergent and submerged plant assemblages during the growth season (1 April to 30 September) in Lake St. Pierre, predicted from the equations presented in Table 7. When applicable, values were computed separately for different water masses.

Table 18
Predicted values of the biological characteristics in Lake St. Pierre (1960-2003), for the growing season (1 April to 30 September). Mean values predicted for 2000 and 2001 are indicated for comparison with measured values (Table 15)

Predicted variable (units)	**Water Mass**	**1960-2003 mean min-max**	**2000 Predicted**	**2001 Predicted**
Z_{max}	Ottawa River	1.6 (1.3 - 1.9)	1.6	1.8
	St. Lawrence River	3.5	3.5	3.5
Emergent Plant cover at Baie du Febvre (%)	South	23.3 (9.5 - 37.6)	25.2 (2-yr mean 29.3)	33.9 (2-yr mean 29.5)
Wetted Surface area (km^2) Empirical (L)	*n.a.*	500.5 (430.5 – 567.7)	490.9	448.6
Wetted Surface area (km^2) Simulated (Q)	*n.a.*	452.3 (363.6 – 535.2)	439.8	390.8
Biomass of SAV at a depth of –2m CD and a 26000 m Fetch (g dry mass m^{-2})	North - Ottawa River	11 (0 – 51)	12	39
	Mixed	58 (15 – 103)	64	92
	Central - St. Lawrence River	39 (0 - 84)	45	72
	South – tributaries	0	0	0

DISCUSSION

Relationship between water discharge, level and physical, biological variables

Interannual and seasonal variations of discharge and level have strong effects of the physical properties of St. Lawrence and Ottawa River waters, which are superimposed to the effects of deepening water depth under high flow conditions. The linkage between riverine water level, discharge and water turbidity and colour is well documented for world rivers (Fraser *et al*., 1995). However, for a river of its size (average annual discharge near Montreal > 8000 $m^3 s^{-1}$), the St. Lawrence River carries a remarkably low sediment load (Milliman and Meade 1983), owing to the presence of the Great Lakes upstream of its watershed, which act as a sedimentation basin (Rondeau *et al*., 2000). Relationships with discharge and level were stronger for the Ottawa River waters, which drain a multitude of smaller tributaries flowing over the Precambrian Shield, resulting in the occurrence of waters more coloured, more turbid and richer in sediments than waters originating from Lake Ontario. Under high discharge conditions, these conditions resulted in deeper waters and lower light penetration for both water masses, albeit reduction in light penetration was most pronounced for Ottawa River waters. For both water masses, the correspondence of high water levels with colder than average monthly water temperatures (and vice versa) (Tables 4 and 5) was unexpected and probably resulted from the coincidence, for a given month, of high discharge with wet, overcast conditions and below average air temperatures throughout the Great Lakes-St. Lawrence watershed.

Outside of the main river channel, river clarity, generally slow (< 1 $m s^{-1}$) currents and relatively shallow (< 5 m) waters provide excellent growing conditions for emergent and submerged aquatic vegetation in the St. Lawrence River. Extensive cover of emergent and submerged wetland habitats is an unusual feature for a river of the size of the St. Lawrence, since large rivers are generally very turbid (Fraser *et al*., 1995). Models describing plant distribution and biomass developed in this study all converge on water depth and light availability, emphasizing their importance per se or in combination with others (exposure, fetch)(Tables 6, 7, 9, 13).

Figure 24 represents the combination of the different PI inferring the inter-annual variations of growth conditions (top), emergent plant cover (middle) and submerged plant biomass (low panel) in Lake St. Pierre. As expected from the regression models with physical variables, years of low levels appeared to coincide with conditions that were generally more favourable to SAV growth (markedly above average values in 1963-1966, 1995, 1999, 2001), because of higher illumination and warmer water temperatures than over years of high levels (markedly below average values in 1972-1974, 1976) (Figure 24).

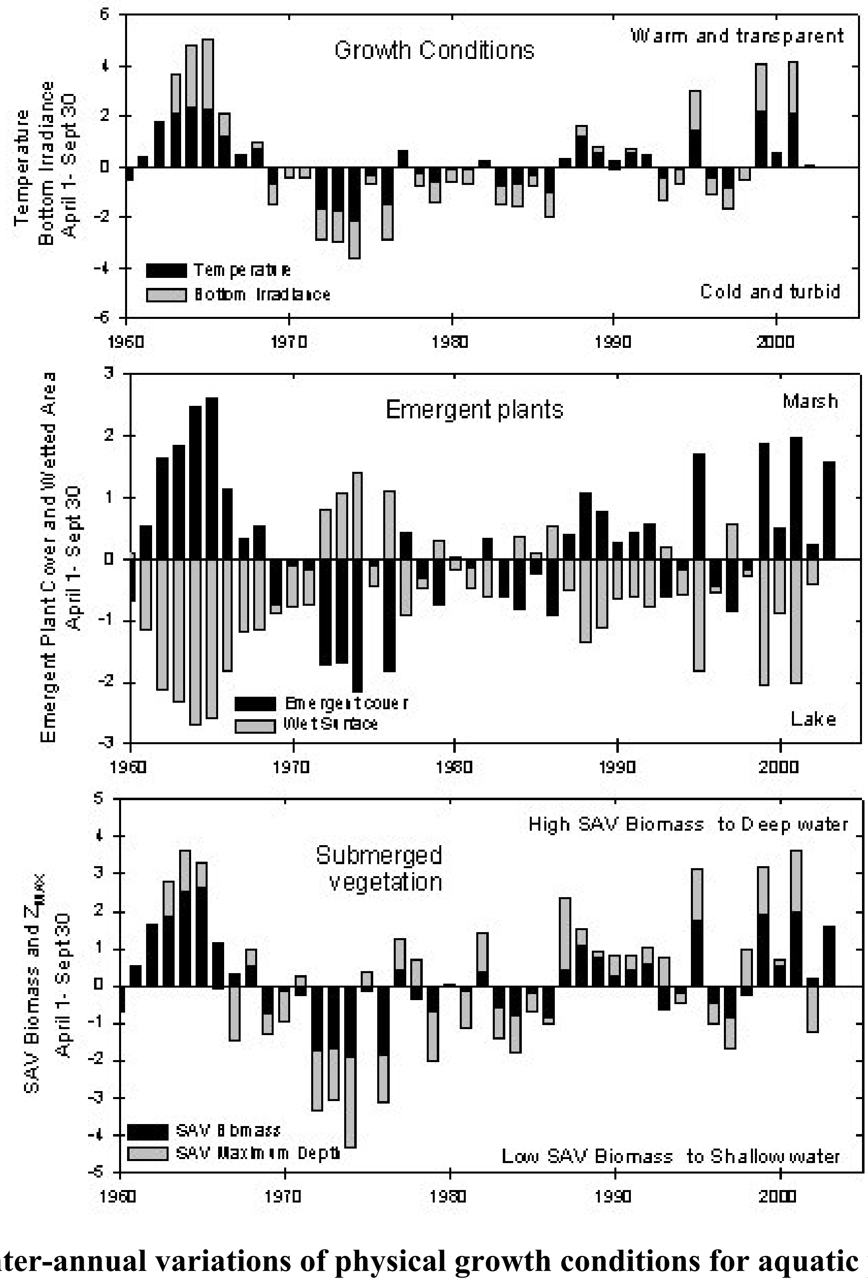

Figure 24 Inter-annual variations of physical growth conditions for aquatic plants (top panel), cover of emergent plants (middle panel) and biomass of submerged aquatic vegetation (lower panel) in Lake St. Pierre, obtained by the transformation (annual value - mean/standard deviation) of variables presented in Figures 22 and 23.

The cover of emergent plants varied inversely with wetted lake surface (Figure 24, middle panel), contrasting dry, low-level periods characterized by a higher than average cover of emergent plants and a lower than average wetted surface (1961-1966, 1995, 1999, 2001) alternating with wet, high-level periods of low emergent plant cover and high wetted lake area (1972-1974, 1976). Lake St. Pierre thus appears to have fluctuated between a marsh-dominated and a more truly lacustrine water body in the past. Whereas the 1960-1980 period was characterised by gradual, temporally autocorrelated changes from one extreme to the other, the last 10 years of the series showed a strong year-to-year variability, which could have considerably shortened the period of emergent plant adaptation to the new water prevailing water level conditions.

Predicted values of biomass and maximum depth of SAV also showed marked inter-annual variations (Figure 24, bottom panel), low-water years corresponding with periods of above-average biomass and propagation to deeper lake areas (1962-1965, 1995, 1999, 2001) and high-water years coinciding with below-average biomass and restriction to shallower lake areas (1972-1974, 1976, 1979).

The three groups of PI exemplified above provide a very coherent picture of the environmental changes that likely have affected Lake St. Pierre over the last 40 years, in spite of the fact that they were calculated from different (and largely independent) regression models. Such good accord between PI reinforces their individual signal and indicates that only a subset could be used to test regulation plans. On the bases of the ease of interpretation and strength (explanatory power) of the linear regressions, equations 6, 7b and 8 (Table 6) could be selected to predict SS, K and Iz /I0 respectively, providing an overall estimation of the fraction of incident surface light intensity reaching the average depth of the river for a given water level condition.

From the standpoint of discharge management at the Moses Saunders dam, the increment of wetted surface area of Lake St. Pierre as a function of a 1000 $m^3 s^{-1}$ discharge increase at Cornwall (equation 10e and 10f, table 9) appears to be the most useful relationship, since it provides a direct link between river flow increment at the source and its repercussion 200 km downstream in Lake St. Pierre. It also underlines the fact that it will generally be *easier* to manage high average level conditions, to periodically recreate environmentally optimal floodplain development for instance, than low levels in Lake St. Pierre.

From an empirical standpoint, the percent cover of emergent vegetation at Baie du Febvre (equation 11) appears to respond very well to changes water levels and is very easily interpreted. Its future improvements could confirm it as one of the most efficient, yet simplest PI for testing regulation plans. In addition, its suitability is confirmed by its particularly good performance with independent validation data sets; the predicted values of all PI were corroborated by the validation exercise, both in terms of their absolute value and in terms of the direction of the anticipated differences between 2000 and 2001. Validation must be used as one of the means to assess the reliability and relative weight of the PI developed by different ETWG components prior to their use for regulation plan assessment.

In addition to the comparison of predicted values with mean values observed in 2000 and 2001, model results were generalized spatially to the surface area of Lake St. Pierre (Figure 17, Table 8). The combination of field data with GIS techniques allows to examine the location and magnitude of changes in area, biomass and types of plant communities, thus facilitating the interpretation of inferred changes. For example, the drop in average water level between 2000 and 2001 increased the surface area of marshes from 86 to 110.9 km^2 and decreased the area of shallow and deep SAV from 157.4 to 132.7 km^2 (Table 8). A fraction of the marshes observed in 2000 was predicted to shift from rushes to annual transition (tall grasses) and barren substrate, altering both biomass and distribution of emergent plant cover, resulting in a 50% increase in emergent plant biomass. These predictions were entirely consistent with field observations and with previously documented changes in emergent vegetation following episodes of low-levels in Boucherville (Hudon, 2002; 2004 in press). In contrast, total biomass of shallow and deep submerged vegetation did not change markedly between years, since the decrease in surface area was compensated by the increase in biomass per m^2 under shallower water conditions.

GIS-based assessment coupled with empirical models derived from field data was shown to be the most efficient way to quantify temporal changes in wetland biomass and distribution (Vis *et al*., 2003), which compared the different techniques (remote sensing, echo-sounding, empirical models derived from field sampling) commonly used to assess the distribution and biomass of emergent and submerged aquatic vegetation. Although remote sensing and echo-sounding provided the most accurate assessment of the surface area covered by emergent and submerged vegetation (respectively) at the time of the survey, results from both techniques require field validation and do not allow to model past or future vegetation changes. Conversely, empirical models based on simultaneous field measurements of environmental conditions and of plant biomass provided a less precise but a more direct assessment of plant biomass over the entire elevation gradient. Since field data acquisition is an essential component of all environmental assessment study (regardless of the technique used), techniques allowing modelling of future conditions provide the best information / effort ratio (Vis *et al*., 2003).

Feedback between SAV and their environment

The specific adaptations of *Vallisneria americana* and *Myriophyllum* spp. to broadly different environmental conditions were previously documented in the laboratory (Titus and Adams, 1979), highlighting the intricate relationships between the morphology of submerged macrophytes and their tolerance to light, current, temperature conditions (Table 1). Results from this study confirm these observations with field data and quantify the magnitude of the response of these two sharply contrasting species, which occupy well-defined ecological niches. Although the two species were associated to broadly different habitats in Boucherville, it appeared that our sampling of the open-lake northern basin of Lake St. Pierre did not comprise sufficiently sheltered areas for this species to thrive; however, very dense *Myriophyllum* spp. beds were observed in the Baie du Febvre area, an area off bounds for sampling owing to Dept. of National Defence safety requirements. Development of predictive relationships describing the feedback between dense SAV beds and physical environmental conditions could nevertheless be useful to model the cumulative impacts of future water level conditions.

SAV species forming a dense sub-surface canopy, such as *Myriophyllum* spp. and *Elodea canadensis*, were very efficient in monopolizing incident light (Figures 20-21).Changes in stem morphology (Figure 18) with distance below the surface likely reflected the intense self-shading under high biomass. In sheltered areas, low water level conditions further accented the vertical gradient of light intensity observed within the leaf canopy, by favouring the piling up of vegetation under the surface. In exposed areas, low water levels increased light intensity near the bottom, through the decrease in water depth and increase in water transparency, without much interference from biomass of *Vallisneria americana*. At the time of maximum biomass, light extinction coefficient within dense *Vallisneria americana* beds were one order of magnitude lower than for *Myriophyllum* spp. beds (Figure 20). This ribbon-like species did not form a thick canopy floating at the surface, although the leaves occasionally reached and floated on the surface. The reduction of light intensity reaching the bottom was observed for both canopy and non canopy-forming species, and fitted single linear relationships regardless of sampling site and of whether the biomass was expressed per unit of surface area or volumetrically (Figure 21).

Our study also demonstrated the indirect effect of high SAV biomass of canopy-forming species on sediment composition, as high SAV biomass tend to slow down water flow and trap fine sediments (Petticrew and Kalff, 1992). Retention by canopy of imported suspended matter and of locally-produced dead plant matter thus improved plant growing conditions, through the accumulation of thick, nitrogen-rich, organic sediment (Table 12, Clarke, 2002). Conversely, the exposed site showed significantly higher sediment compaction and mineral contents (Table 12), which coincided with a 4-fold increase in the fraction of total biomass devoted to anchoring belowground structures (Table 11). At the sheltered site, sediment trapping resulted in an average decrease in K by 13% (from 0.7 to 0.6 m^{-1}) after the passage of water through the dense canopied SAV (Hudon and Sylvestre, 1998).

Next Steps – towards the assessment of regulation plans

The regression models linking physical and biological characteristics described in this study document the Performance Indicators (PI) requested by the Environment Technical Working Group (ETWG) of the Lake Ontario – St. Lawrence Study, assessing the effects of water discharge and level on the environment. These PI will serve as the scientific basis to elaborate new regulation criteria to regulate discharge while accounting for the environment and will be used to assess the environmental suitability of different discharge regulation plans. The items listed below consider some of the technical aspects involved for the future application of PI to Plan Development.

Improving Performance Indicators

The PI presented in this study have been parameterised using the best data available – the potential for improvement is there, in particular for PI relating water quality characteristics to levels and flows, which are steadily monitored by water filtration plants. Furthermore, equations relating water turbidity and colour including year-round data may also be useful to determine critical thresholds and costs incurred for municipal water treatment under different proportions of mixing of waters originating from Lake Ontario and from the Ottawa River (or other tributaries).

For PI related to Lower St. Lawrence River wetlands, improvements will be made to the forecasting of the surface area of distinct types of emergent wetland vegetation (Equation 12, Hudon *et al*., 2003b) and their translation into habitat in Lake St. Pierre. This information will also be useful to improve equation 11, which predicts the total percent cover of emergent wetlands in Baie du Febvre and may yield a finer, seasonally-based indication of the effects of spring and fall levels (Hudon et al. in prep.).

GIS-based assessment of plant production will be completed by inclusion of phytoplankton and periphyton, thus allowing to estimate the relative contribution of the three major compartments of primary producers to total Lake St. Pierre production (Vis, in prep.). This assessment will yield valuable information on the carrying capacity and food chain structure of this highly valuable habitat for fauna.

Additional PI describing the propagation dynamics of aggressive plant species (the common reed, *Phragmites australis*) under different water level conditions are also in preparation (Jetté *et al*., in prep.).

Next steps of Lower St. Lawrence wetlands assessment

Models of emergent plants previously developed (Hudon *et al*., 2003b) will be applied to LSP, in conjunction with assessment of average biomass of major emergent plant assemblages from data base. Emergent and submerged plant biomass assessment will be completed with estimation of annual production of plankton and periphyton, which are most likely to contribute significant amount of carbon to this ecosystem. This will allow calculation of production for the time series 1960-2003 and test of different regulation plans (in year 4). Special efforts should be dedicated to the identification of common PI describing wetland habitat characteristics for Lake Ontario, Upper and Lower St. Lawrence River.

Desirability thresholds

From a habitat diversity standpoint, intermediate amounts of SAV are likely to be most desirable: low SAV abundance corresponds to low habitat complexity and carrying capacity (Jeffries, 1993) whereas SAV proliferation is a generally undesirable outcome since it increases the probability of a nocturnal oxygen deficit (Frodge *et al*., 1990), resulting in decreased habitat suitability for fish (Miranda *et al*., 2000). One of the remaining challenges is thus to define the thresholds defining desirable (to maximise habitat diversity for aquatic fauna) and less desirable biomass of SAV. Keeping in mind the Planning Objective originally defined by members of ETWG (Ensure that diverse habitats are maintained), PI describing global habitat heterogeneity, landscape fragmentation, morphological and structural diversity should also be developed for wetlands.

Scaling up

The problem of generalisation from the study site to the entire Lower St. Lawrence River system was addressed differently according to each PI developed in the present study. PI derived from relationships between physical water quality properties (suspended solids concentrations, light extinction coefficient, colour, turbidity) were specifically associated to a water mass and the region of the river for which data was originally gathered. However, the main stem of the river between Cornwall and Quebec can also be viewed as a continuum, over which a progressive increase in suspended solids and a decrease in transparency occur. Owing to the rapid advection rate in the central navigation channel (about 1 m s^{-1}, 3.6 km h^{-1}), the distance between Cornwall and Quebec (about 375 km) can be covered in as little as 4.3 days. Such rapid advection rate allows for some degree of generalisation of physical properties (such as water temperature, colour, turbidity) to the region located immediately downstream of a sampling point, within the same water mass. This assumption underlined our estimation of K for waters under the influence of St. Lawrence and Ottawa Rivers using measurements made at Varennes and Repentigny and our use of these values to characterise extreme K values in Lake St. Pierre, 60 km (16 hours) downstream. Comparison of the range of predicted (0.8 – 2.6) to measured (0.8 – 3.5) K values in Lake St. Pierre showed the model to be completely accurate for low extinction coefficient values associated to St. Lawrence River waters but to underestimate the turbidity of other water masses under the influence of the Ottawa River and other tributaries.

The anticipated effects of water level variations forecasted for marshes in Lake St. Pierre to the entire River system do not require scaling up per se to be significant in their own right, as this lake represents 76% of all St. Lawrence River marshes between Cornwall and Trois-Rivières (Jean *et al*., 2002). Not only is Lake St. Pierre important in terms of the mere surface area of floodplain, wetlands and beds of submerged aquatic vegetation (about 450 km^2 of wetted surface area), but its habitats are also much less fragmented than Lake St. Louis and hydraulically unaltered than Lake St. Francis.

Defining significant effects

Owing to its size (see above section), its unique environmental characteristics and central importance to fauna and flora, Lake St. Pierre represents the last example of relatively unaltered floodplain and wetlands ecosystem in the St. Lawrence River. These features have been underscored by Lake St. Pierre denomination as a RAMSAR site, a World Biosphere Reserve, a National Wildlife Refuge and identified as a key area in the Joint Habitat Management Plan of Eastern North America. Any demonstrated adverse effects to this ecosystem would thus be significant.

Defining adverse effects

Adverse effects refer to change with respect to a baseline – in this case the range of variability that the Lake St. Pierre ecosystem has sustained over the last 100 years. Any effect that can be demonstrated to alter the diversity, species richness, productivity or carrying capacity of an ecosystem is deemed to be adverse. Alteration is demonstrated when the ecosystem is taken beyond the bounds of past documented variability, or is shown to have a lesser resistance to change and a lesser resilience (capacity to return to its original state). Invasion of exotic and aggressive species (Jetté *et al*., in prep.), reduction in species richness, habitat fragmentation are all examples of adverse effects.

Translating PI into criteria

Results from this study can potentially be translated into regulation criteria, two of which are exemplified below:

Maximise the vertical range of water level between April 1 (high) and Sept 30 (low). At Sorel, the vertical range of water level during the growth period has followed a significant decline over the 1912-1994 period (Hudon, 1997). The vertical range is likely to further decline under chronically low water supply to the basin, which will accentuate the tendency for management to store water in Lake Ontario in the spring (thus decreasing spring peak levels) to release it in the fall (thus rising lower levels). 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 spring rise in water discharge flush out organic matter and fine sediments, thus resetting the river system each year prior to plant growth season. Under unaltered conditions, spring rise in discharge is of major importance since it maintains ecosystems at equilibrium by preventing drying out of river bed through long-term sediment accumulation. Conversely, the progressive decline in water level and periodic drying out of shallow areas allow the germination of annual plant species which maintain species diversity and ensure 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-thawing events, an environmentally-sound management option would be to maintain discharge patterns harmonised with the 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, change the relative importance and timing of Ottawa River and other tributary flow. These changes will bring additional (and unpredictable) challenges to Lake Ontario – St. Lawrence River water management, altering the magnitude and timing of seasonal episodes of high and low water supply.

Cumulative impacts: Managing St. Lawrence River discharge in times of climatic uncertainties

Our study allows to identify the sensitivity and response of SAV beds to major environmental variables potentially impacted by climate change. Low levels are accompanied by a reduction in water depth, increase in water temperature and in the light intensity reaching the bottom, all factors which favour SAV growth and biomass accumulation. Reduction in current speeds is also to be expected, which will likely increase in SAV maximum biomass, reducing exposure to current and favouring sediment accumulation. Under chronic decrease of water levels and discharge, SAV assemblages may shift to high biomass canopy-forming species at the expense of ribbon-leaved species. Change in dominant plant species' architecture could then accelerate alterations to the fluvial ecosystem, through a further reduction in current speed and concurrent increase in sediment accumulation, towards a stagnant, marshy shallow-water system. In conjunction with warmer water temperatures, these cumulative impacts could alter considerably the suitability of underwater habitats for invertebrates and fish, with important consequences for the fluvial ecosystem as a whole.

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IJC Memorandum Number: IJC-3-M00

MEMORANDUM OF UNDERSTANDING
Concerning:

CHANGES IN WETLAND HABITATS PRODUCTIVITY AS A RESPONSE TO WATER LEVEL VARIATIONS IN LAKE SAINT-PIERRE (LOWER ST. LAWRENCE RIVER)

Between the Canadian Section of the International Joint Commission and the Quebec Region of Environment Canada

1. The International Joint Commission of Canada and the United States (hereinafter referred to as "the Commission") is reviewing its Order of Approval for certain works for the development of power in the international rapids section of the St Lawrence River which the Commission issued pursuant to the Boundary Waters Treaty of 1909 between Canada and the United States. The Order of Approval was issued on October 29, 1952 and amended on July 2, 1956.

2. In accordance with the provisions of the Boundary Waters Treaty, Canada and the United States are each paying one-half the cost of the study that is being conducted by the Commission's International Lake Ontario-St Lawrence River Study Board (hereinafter referred to as the «Commission's International Study Board»).

3. Environment Canada – Quebec Region (hereinafter referred to as "EC-QR") has information and resources that can contribute to the work of the Commission's International Study Board.

4. EC-QR undertakes to complete all work described in the Statement of Work to this Memorandum of Understanding on or before March 3, 2004. The attached Statement of Work forms an integral part of this Memorandum of Understanding. EC-QR shall commence work on these projects no later than 1 week from the date of signing of the MOU.

5. The International Joint Commission (hereinafter referred to as "the Commission") will arrange for the government of Canada to pay the following amounts to EC-QR, from funds designated by the Government of Canada for the Commission's Lake Ontario – St. Lawrence River Regulation Study, at the times and on the conditions specified below.

(i) $20,000 within 30 days of signature of this Memorandum of Understanding, upon receipt of an invoice to cover up-front costs and existing expenditures,

(ii) $20,000 upon receipt of an invoice and a progress report (in both hardcopy and electronic format) satisfactory to the Scientific Authority and the Commission on work which has been undertaken by EC-QR based on the attached Statement of Work, by December 15, 2003, and

(iii) $40,000 upon receipt of an invoice and a final report (in both hardcopy and electronic formats) to the complete satisfaction of the Scientific Authority and the Commission pursuant to this Memorandum of Understanding.

The total amount payable pursuant to this Memorandum of Understanding shall not exceed $80,000.

6. The Commission intends to use data and information, which are provided to it or to the Commission's International Study Board pursuant to this Memorandum of Understanding in reviewing its Order of Approval for certain, works for the development of power in the international rapids section of the St. Lawrence River and in fulfilling its responsibilities under the Boundary Waters Treaty.

7. The Commission normally makes information, which it has in its possession available to the public, and it does not constrain the use of information through the exercise of rights in intellectual property.

8. It is the Commission's practice to acknowledge and credit in an appropriate manner the sources from which it obtains information.

_________________ ______________
Murray Clamen Date
Secretary, Canadian Section
International Joint Commission

__________________ ______________
Jacinthe Leclerc Date
Directrice - Centre Saint-Laurent
Direction de la conservation de l'environnement
Environnement Canada

STATEMENT OF WORK

PROJECT TITLE:

Changes in wetland habitats productivity as a response to water level variations in Lake Saint-Pierre (Lower St. Lawrence River)

PROJECT OBJECTIVE:

To model the distribution and annual production of plants biomass for each of the major habitat types, as a function of hydrology.

To assemble the following information in a GIS, which will allow to model the distribution and annual production of plants biomass for each of the major habitat types, as a function of hydrology.

1. The seven major plant associations were identified from the analyses of 4 years of field collections at 15 sites; from the driest to the wettest, those 7 associations are: the *Phalaris-Lythrum* wet meadow, the *Polygonum-Alisma* transition zone, the *Typha-Bolboschoenus* association, the *Eleocharis-Sagittaria* association, the *Schoenoplectus pungens* association, the *Schoenoplectus palustris* association and the submerged plant species association. The occurrence of each association for each individual point (pixel) of the bottom of the Lower St. Lawrence can be predicted from the combined effects of a few hydrological variables (for example, the number of days underwater during the current and the previous growth season, the position of the point with respect to water level during the month of July, the average water depth during the previous growth season and the number of days underwater during the previous 7 days).
2. The biomass of submerged and emergent plant species was measured at a number of sites in the Cornwall-Trois-Rivières sector.
3. The biomass, photosynthetic parameters and productivity of free-floating and attached algae have been measured over season of low and average water level conditions;
4. Monthly variations of water clarity, colour and temperature were modeled as a function of water levels near Montreal;
5. Long-term data series for water level, water temperature and meteorological factors have been assembled and validated.

PROJECT DESCRIPTION

In Year 3 of the LO-SL Study, we are thus in a position to assemble the above information in a GIS, which will allow to model the distribution and annual production of plants biomass for each of the major habitat types, as a function of hydrology.

Habitat distribution and production will be modeled for high, average and low average water level scenarios for spring and summer, using previously identified scenarios. Interpolation between these extremes will allow to derive relationships between water levels and habitat diversity and productivity, from which regulation criteria will be finalized for use of PFEG. The thresholds of the « desirable » range of water level conditions allowing to maximize the diversity of habitats and food sources will thus be identified.

The work remaining to be accomplished includes:

6. A model predicting the biomass of submerged aquatic macrophytes will be derived from a combination of physical/hydrological factors such as water depth, water clarity and exposure to winds and waves.

7. The remote-sensing images obtained for Lower St. Lawrence River from Common Data Needs (Létourneau) must be validated with field data from vegetation surveys obtained from various other projects (desGranges, Jean, Hudon). This will be accomplished via a collaboration with Martin Jean and Guy Létourneau;
8. Digital elevation models (DEM) for the shallow-water bathymetry and the floodplain have been completed by the Common Data Needs TWG; however, much work remains to be done with the assemblage of all individual 3 x 3 km tiles (more than 100 tiles for Lake St. Pierre) together and meshed with the central bathymetric map from the Canadian Coast Guard. This will be accomplished in collaboration with Daniel Rioux (Canadian Meteorological Service);
9. Habitat characteristics, remote sensing images and DEM information (identified in points 7-8 above) will be assembled into a GIS, to assess the wetted area of each habitat categories under current (2002) conditions following a gradient of water level conditions. The model of Hudon et al. 2003 predicting the temporal shifts in the distribution and surface area of wetland categories will be applied to the long-term time series of water levels. These calculations will be done by Martin Deschênes (Centre Saint-Laurent)
10. Assemblage of previously acquired biological and physical information (identified in points 1-6 and 9 above) into a GIS and calculation of overall production for Lake St. Pierre. This will be done in collaboration with Chantal Vis (Centre Saint-Laurent).

Plant associations (habitats) will thus be quantified in terms of their availability (quantity, surface area) but will also consider their diversity (the amount of each plant association) and their quality (value as source of carbon supporting different types of food chains). This will allow to answer to the first planning objective defined for the ENV TWG: “Ensure that all types of native habitats (floodplain, forested and shrubby swamps, wet meadows, shallow and deep marshes, submerged vegetation, mud flats, open water, and fast flowing water) and shoreline features (barrier beaches, sand bars/dunes, gravel/cobble shores, and islands) are represented in sufficient abundance (surface area).”

GEOGRAPHIC SCOPE

This study describes the emergent wetland vegetation found in marshes and wet meadows growing in the transition zone between the open water and the floodplain, ranging roughly from a depth of 1 m to an elevation of 1 m above Chart Datum. This transition zone is strongly affected by water level variations and plant assemblages reflect hydrological conditions prevailing during the current growth season. Since field data was gathered between Cornwall (Lake Saint-François), Lake des Deux-Montagnes (Ottawa River mouth) and Nicolet (Lake Saint-Pierre), this study will allow to generalize the results to all lower St. Lawrence River wetlands. In Year 3 of this project, the modeling effort will focus on Lake Saint-Pierre, which represents the largest wetland area of the Lower St. Lawrence River.

DELIVERABLES AND TARGET DATES:

1. Progress report with the available data (in both hard-copy and electronic formats) no later than November 1, 2003, to the complete satisfaction to the Scientific Authority, to include:

A model predicting the biomass of submerged aquatic vegetation as a function of hydrological and other physical variables.

2. Final report, on or before March 1, 2004 (in both hardcopy and electronic copy) to the complete satisfaction of the Scientific Authority, to include:

Application of the model described by Hudon et al. (2003) to determine the historical changes in the surface area of each category of wetland habitats resulting from long-term variations (1960-2002) of water levels in Lake St. Pierre.

Estimation of total plant production under high, average and low water level conditions identified from the historical series in Lake St. Pierre, to elaborate IS curves between water levels and wetlands production.

Attendance of the Environment Canada - Quebec's representatives at two meetings of the ETWG is required. Integration of work with other ETWG members and modellers will be undertaken by the EC-Quebec representative as required.

Attendance of the EC representative for the Habitat Quantity MOU at all Integration sub-group meetings and undertaking of tasks assigned by the Integration sub-group

Final report will be submitted to the Scientific Authority in the language of choice by the authors; an executive summary in English and French will be provided with the final report. The final report, and any associated appendices, once approved by the Scientific Authority will be forwarded to the Information Management Group for the Study.

The final report shall include a copy of the Statement of Work for the project and an assessment by the researcher on delivery of all deliverables.

CONTACTS:

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