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Modelling submerged macrophytes distribution: evaluation of models transferability in three St. Lawrence River sections

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1 INTRODUCTION

Submerged macrophytes are present in high densities in shallow lake ecosystems and were an important component of the trophic web integrity. They interact and provide habitat of quality (shelter, nesting and feeding site) for zooplankton (Timms & Moss, 1984; Basu et al. 2000), macroinvertebrates (Lorman & Magnuson 1978; Scheffer 1998), fish communities (Werner et al. 1983; Weaver et al. 1997) and water bird populations (Jupp & Spencer 1977; Lauridsen et al. 1993; Noordhuis et al. 2002).

When they are very abundant, submerged macrophytes can modify the flow distribution of the fluvial system during the growing season of plants, affecting water velocity (Wilson & Keddy 1985; Petticrew & Kalff 1992, Chambers & Prepas 1994, Morin et al. 2000; Madsen et al. 2001), absorbing wave's impact (Kobayashi *et al*. 1993, Camfield 1977), reducing sediments resuspension (Petticrew & Kalff 1992; Sand-Jensen 1998; Benoy & Kalff 1999; Madsen et al. 2001; Rooney et al. 2003) and ultimately increasing light penetration in the water mass (Scheffer 1998). In a shallow lake ecosystem, all theses physical changes can strongly modify the fragile trophic web equilibrium.

Submerged aquatic plants are present all along the St. Lawrence River and are particularly abundant in its three fluvial lakes (Lake Saint-François, Lake Saint-Louis and Lake Saint-Pierre). Water level fluctuations can have a significant influence on the spatio-temporal variability of local environmental factors (Wetzel 1983; Crowder & Painter 1991, Howard-Williams *et al.* 1995, Geis 1985) and consequently, on submerged macrophytes distribution and biomass in the St. Lawrence River (Hudon 1997). Submerged macrophytes establishment is influenced by environmental factors like water depth and light penetration (Spence 1982), water velocity and waves (Chambers et al. 1991; Schutten & Davy 2000), bottom slope (Duarte & Kalff 1986), substratum size and sediment characteristics (Barko & Smart 1980, Carignan & Kalff 1980).

Although the identification of environmental factors controlling the spatial distribution of submerged macrophyte species is relatively well known , the use of these environmental factors at the lake or at the river scale to build predictive spatial models are still rare (but see Van den Berg et al. 2003). Therefore, precise knowledge on submerged macrophytes distribution is essential to characterize habitat quality for fauna and to accurately describe hydrodynamics, sedimentation and pollutant transport processes.

Development of predictive tools of plant distribution according to water levels seems to be a key procedure to understand and predict the spatial and temporal variability of submerged macrophytes species. To be useful in environmental management, predictive models should be accurate (high variance explication, high proportion of cases correctly predicted), easy to used and applied (not time and money consuming) and relatively general (high transferability potential between sites) (Levin 1992; Guisan & Zimmerman 2000). Since few years, there is a growing interest in model development framework (Figure 1) and on models evaluation to assess their performance and their predictive power. Some papers compare the ability of statistical tools to to model relationships between habitat and organisms (Manel et al. 1999; Olden & Jackson 2002) when other focus on the importance of model evaluation (Fielding & Bell 1997; Manel et al. 2000) and on proper model validation (Fielding & Bell 1997; Olden et al. 2000; Guisan & Zimmerman 2000). Model validation on new or independent data ("model transferability") is relatively new in habitat selection models and was mainly explored in fish habitat models (Freeman et al. 1997; Leftwich et al. 1997; Mäki-Petäys et al. 2003; Guay et al. 2003; Nykänen & Huusko 2004). Many authors have cautioned against generalizations based on single "snapshot" studies (e.g., Moyle and Baltz 1985; Greenberg et al. 1996).

Large rivers, like the St. Lawrence River, have fluvial lakes located along their courses (Chessman 1984; Allan 1986; Kohler 1993; Thorp et al. 1994) and are especially suitable to evaluate models transferability between sections. In order to respect the essence of a good model, one of the main advantages of this study is that the environmental variables are simulated with 2D numerical models with an appropriate level of precision, allowing prediction on the entire domain and on different water levels, reducing field measurements of these variables (easy of use and application for management purposes). Logistic regression was used to model relationships between submerged macrophytes distribution and habitat variables. Logistic regression is a predictive tool that was extensively tested and has usually given good results (Scheffer et al. 1992; Manel et al. 1999; Hosmer & Lemeshow 2000; Olden & Jackson 2000; Van den Berg 2003). To model submerged macrophyte density, regression trees were used (Breiman et al. 1984; Dea'th & Fabricius 2000).

This complete modelling routine would lead to reliable forecasting of different kind of impacts including climatic changes and water level/discharge management actions on submerged macrophytes, a key component of the fluvial ecosystem.

2 METHODS

Objective: The main objectives of this research are 1) to model the spatial distribution of eight submerged macrophyte species using environmental simulated variables for describing plant habitat distribution in using a complete model routine (Figure 1), 2) to improve the understanding of the controlling environmental factors influencing the distribution of submerged macrophytes species in the St. Lawrence River; 3) to evaluate models transferability among the three St. Lawrence study sections. Logistic regression was used to model plant presence/absence and regression trees were used to model macrophyte densities from field observations, combined with environmental factors data obtained from 2D numerical simulations.

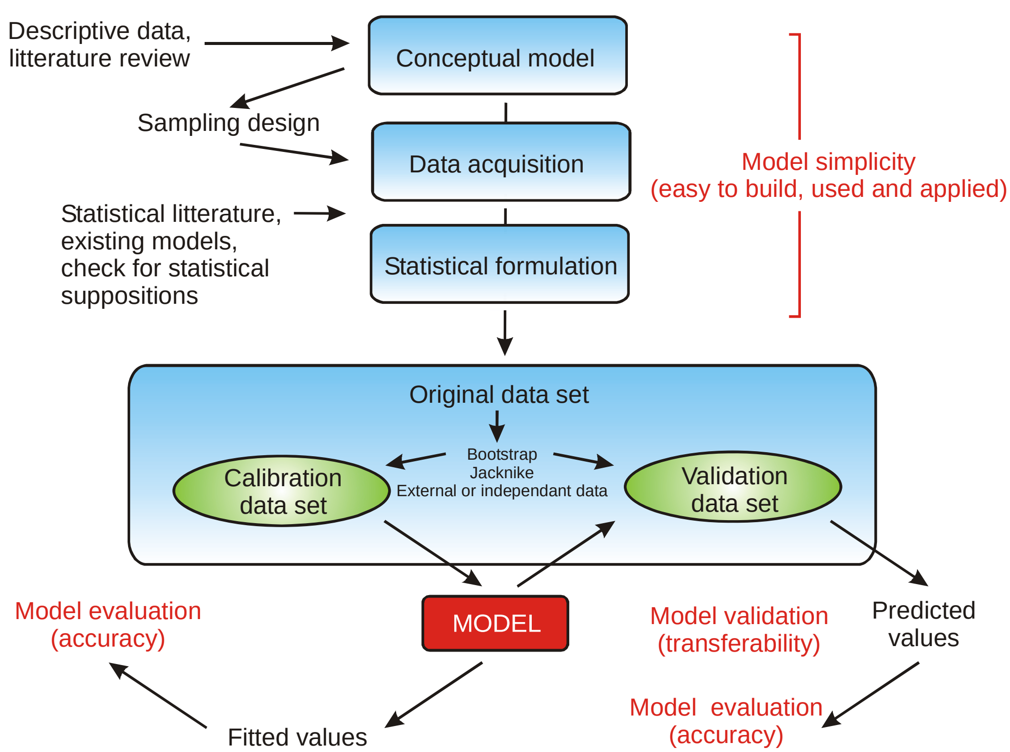


Figure 1. Suggested framework to build adequate habitat selection models (modified from Guisan & Zimmermann 2000).

2.1 Study sites

Sampling was conducted in three sections of the Saint-Lawrence River, Qc (

Figure 2). The first section was the Lake Saint-Pierre (LSP) and it is the largest fluvial lake (315 km^2) along the St. Lawrence River and the last major enlargement (13.1 km width at mean discharge) of the river before the estuary. It is typically shallow (average depth: 3.17 m at mean discharge). Lake Saint-Pierre has a large width/depth ratio and this is responsible for the very limited lateral mixing within the lake's three main water masses (north, central and south respectively) (Frenette et al. 2003). The south water mass is composed of inflows from the Ottawa, Du Loup, and Maskinongé rivers. The central mass is composed of water coming from Great Lakes and included the maritime channel. Finally, the south water mass is composed of inflows from the Richelieu, Saint-François and Yamaska rivers.

The second section was the St. Lawrence fluvial reach (SLFR) and was composed of five archipelagos; the Berthier-Sorel archipelago (upstream of the Lake Saint-Pierre), the Contrecoeur archipelago, the Verchères archipelago, the Thérèse-Varennes archipelago and the Boucherville archipelago (North of Ste-Hélène Island, near the Montréal harbour). This fluvial reach was 85 km in length and covered an area of 230 km^2. The St. Lawrence River in this fluvial reach flows in one water mass. The annual discharge varies between 8775 $m^3 \cdot s^{-1}$ (Varennes) to 10 180 $m^3 \cdot s^{-1}$ (Tracy at the south of aux Foins Island).

Finally, the third section is the Lake Saint-Louis (LSL), located southwest of the island of Montréal at the outlet of Lake des Deux-Montagnes which is divided in two channels (Sainte-Anne and Vaudreuil). Water that flows into Lake Saint-Louis through these channels comes from the Ottawa River. The outflow from the Ottawa River transits through Lake des Deux-Montagnes where it is then channeled into the Mille-Iles and des Prairies Rivers. The other main inflow of Lake Saint-Louis is composed of water from the Great Lakes that transits through the Beauharnois and Les Cèdres power dams situated at the outlet of Lake Saint-François. A third inflow to Lake Saint-Louis is the Châteauguay River which is divided in two outlets at the downstream portion of the lake.

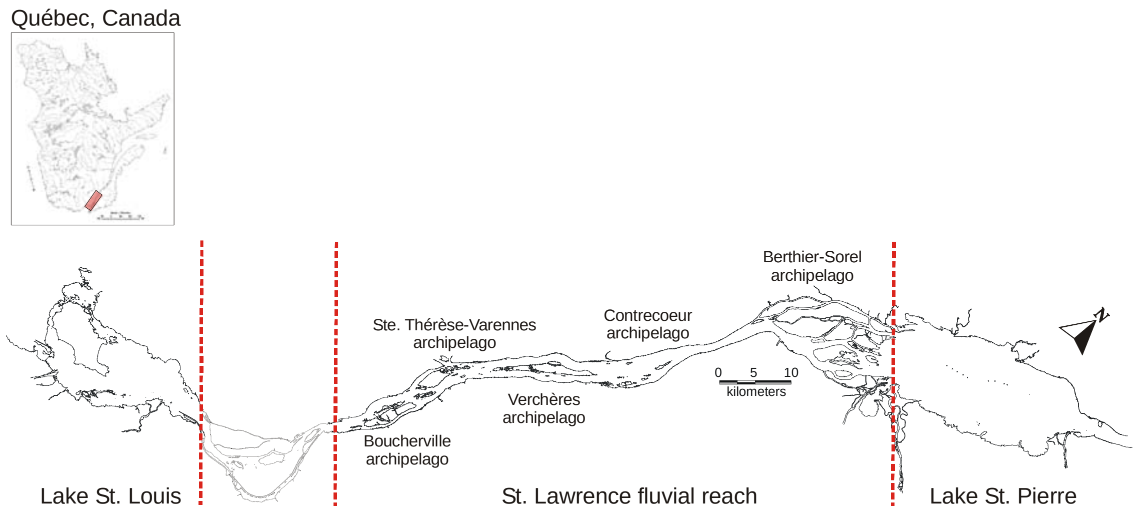


Figure 2. Location of the three study sections (Lake St. Pierre, St. Lawrence Archipelagos and Lake St. Louis) in the St-Lawrence River, Qc.

2.2 Macrophytes sampling

In the LSP, species presence was sampled in 1997 and 2000 during a plant mapping survey (Morin *et al.* 1999). From September 24th to October 3rd, 35 transects were covered in the central and eastern portion of the Lake. In the SLFR, mapping survey was conducted from September 15th to October 10th in 1997. A total of 325 transects were covered (Côté 2003), and finally in the LSL section, the mapping survey was conducted between September 28th and October 8th in 1999. A total of 47 transects were done to cover the entire LSL.

Transects were observed with a Raytheon paper echosounder using a 200 kHz transducer at a 9° angle of penetration and a submersible video camera (Cosmicar HX 3.7 mm). Sites position were measured with real-time differential GPS (dGPS) for horizontal precision of less than 2 m at every second, at every 100 m along transects, positions were marked on the echosounder chart and the plants were identified. The echosounder was used to assess the presence of submerged plants while a submersible video camera was used to identify plant species. Observations on the plant beds with the camera lasted for 1 to 5 minutes and covered 10 to 20 m in distance, to allow avoiding problems associated with patchy distribution of some species assemblages. Video observations were validated with direct sampling, and field samples of plants were identified by Normand Dignard (Marie-Victorin Herbarium, Québec City).

To record a transect position, the dGPS signal is transmitted to a portable computer which uses a GIS software. The point coordinates are recorded in the GIS every 1 m with a “fix” occurring every 50 m that is used to keep track of the paper echosounder. Every time a “fix” point is recorded, a beep is heard and a line is drawn on the echosounder chart. The echosounder is used to map the presence of plants on the river bed. The plants presence is interpreted from the shape of the echosounder signal and validated with underwater camera to identify the species and density for future reference.

Macrophyte assemblages were essentially composed of at least one of the following nine species: *Vallisneria americana* Michx., *Myriophyllum spicatum* L., *Potamogeton richardsonii* (Ar. Benn.) Rydb., *Potamogeton pectinatus* L., *Ceratophyllum demersum* L., *Elodea canadensis* Rich., *Heteranthera dubia* (Jacq.) MacMill., *Nitella sp.* and *Alisma gramineum* Lej.. Observed macrophyte assemblages in the three study sections were dominated by four species: *V. Americana*, *P. richardsonni*, *Nitella* sp. and *M. spicatum*. Other species like *Lemna trisulca* L., *Chara sp*, and *Potamogeton crispus* L. were observed in very few stations.

2.3 Environmental variables production

The IERM grid (Integrated Ecosystem Response Model) covers the St. Lawrence River between Beauharnois and Trois-Rivières without the area comprises between Lachine rapids and Laprairie basin (

Figure 2). The IERM grid has supported the overall hydrodynamic calculations to produce the environmental data set. Distance between grid points varies from 160 m to 20 m depending of field complexity (Figure 3). Environmental variables simulations represent the environmental conditions of periods before and after growing season, which are the initial habitat characteristics allowing plant settlement and development, not those modified by plants during summer. The six following environmental variables were simulated and used to model the distribution of submerged macrophytes; water depth (m), light penetration, the orbital force of waves ($m \cdot s^{-1}$), specific discharge ($m^3 \cdot s^{-1}$) the mean water velocity ($m \cdot s^{-1}$), fine material deposited at bottom ( ) and bottom slope. These six variables were chosen in agreement with the literature on abiotic factors influencing submerged macrophytes distribution.

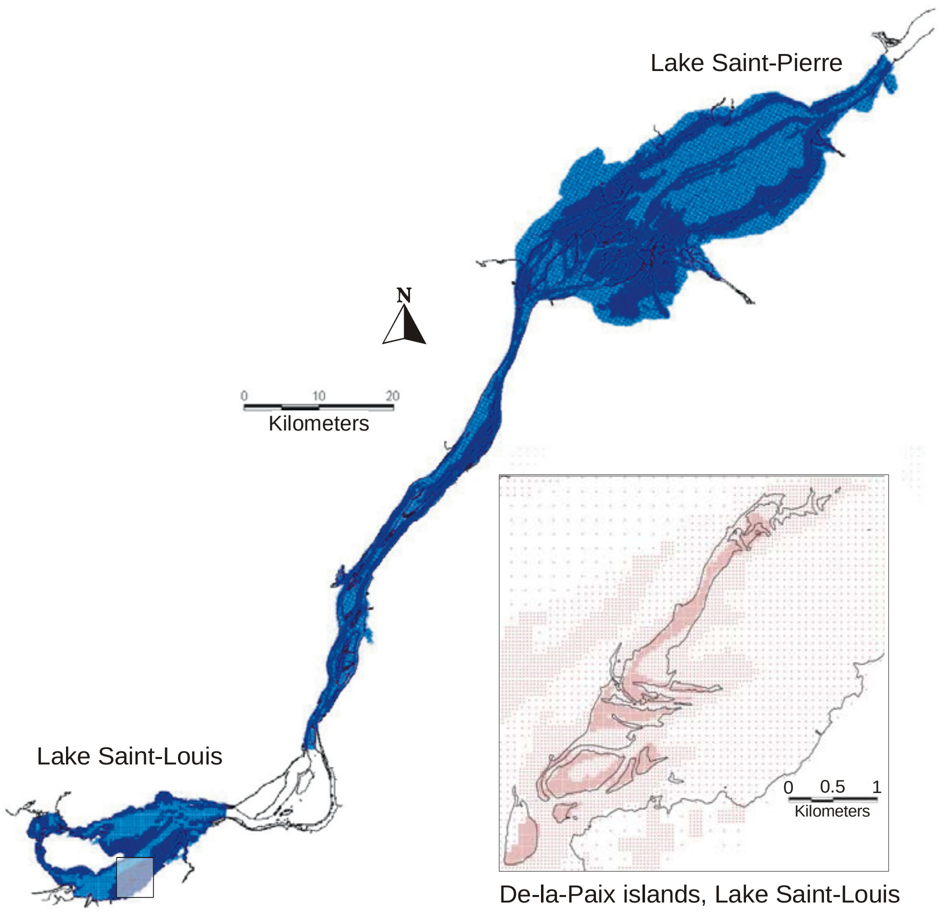


Figure 3. Area covers by IERM grid (Integrated Ecosystem response model) in the St.Lawrence River. Inset: example of IERM grids points density and distribution in the de la Paix Islands, lake Saint-Louis, Québec.

2.3.1 Numerical Terrain Model (NTM): Topography

To produce environmental variables (estimated and/or simulated), we needed topographic information. For this aim, the NTM (Numerical Terrain Model) containing bathymetric and topographic information was built. Bathymetric information was provided from soundings of the Canadian Hydrographic Survey (CHS), Meteorological Service of Canada (MSC) and the Canadian Coast Guard (CGC). A total of 866 527 bathymetric points were available in the study section. These measures have a mean density of about one point every 30 to 50 m. The topographic information was provided by an airborne laser survey (LIDAR; Light & Detection Ranging). The density of the soundings determines the precision limit of the whole data model.

2.3.2 Water levels calculation and projection

Water levels fluctuations are important in the study area. Indeed, between 1967 and 2001, at Sorel measurement station, water levels fluctuations had reached 5 m in amplitude. Although it is possible to know water levels variation at each measurement station, the topographic and hydrodynamic complexities of the St. Lawrence River limit the extrapolation of water levels values at measurements stations to points between these two stations. To solve this problem, and to know water levels fluctuations at each point of the IERM grid, 2D hydrodynamic models were used. 2D hydrodynamic models give the local influence of topography, substratum and water velocity on water levels. The overall water conditions simulations of St. Lawrence River may allow us to know water levels fluctuations at any point of the grid in the study area. Eight reference scenarios were produced to represent the overall water conditions of the St. Lawrence River from Montréal to Trois-Rivières (see Morin & Bouchard (2000) for further information on scenarios definition). However, theses eight reference scenarios correspond to mean conditions of water levels and did not take into account the water levels fluctuations caused by tributaries discharge variations at a finer scale. This additional complexity is not quantified in hydrodynamic simulations and should be considered to calculate water levels at each point of the grid. One-dimensional relations between sampling stations and hydrodynamic simulations were used to integrate more adequately the water levels fluctuations caused by tributaries discharge variations. Water levels projection on the IERM grid was based on a combination of punctual one-dimensional relations (Fan & Fay 2002) and local water levels from hydrodynamic simulations for each reference scenarios (Morin & Bouchard 2000). This procedure use linear interpolation between stations used by Fan & Fay (2002) and points of the IERM grid. The methodology used for water levels calculation, water levels projection and linear interpolation between water levels at measurement stations is similar to those used in Turgeon et al. (2004). The water depth (m) at each point of the

IERM grid was derived from topographic data minus the water level at each point of the grid.

2.3.3 Hydrodynamics models (water velocity and currents)

Currents and water levels were calculated with a 2D hydrodynamic model (horizontal). The HYDROSIM model (Heniche et al. 1999) uses a discretisation of the shallow water equations solved by the finite elements method. The model applies the conservative form of the quantity of movement from the Saint-Venant equations and takes into account the local friction caused by substratum. Vertically integrated, the model had produced reliable predictions of mean velocity of the water column, water level, and specific discharge for a wide range of hydrological conditions. The element used is a 6 nodes triangle called T6L (Triangle with 6 nodes and an internal linear interpolation scheme) where specific flows are evaluated on each node while levels are calculated at the summit nodes. 2D hydrodynamic model for the area between Montréal Port and Trois-Rivières contains 166 217 nodes and 81 322 elements while the grid of the lake Saint-Louis contains 76 236 nodes and 37 369 elements. Water velocities validation was done with Doppler (ADCP) data measured during four events. The approach by reference events was used to determine simulated conditions. Theses conditions cover the overall water conditions of St. Lawrence River; Morin & Bouchard (2000) for the area between Port of Montréal and Trois-Rivières and Morin et al. (2003) for the area of the lake Saint-Louis. This simulation has been validated with water levels and velocity measurements (for more detail on hydrodynamic validation see Morin *et al* 2000).

This simulation had provided water levels required to calculate water depth, water velocity and values of diffusion potential and shear stress for the transport-diffusion model (see “Sedimentation of fine particules” section). The mean flow velocity (vertically integrated) was selected as the variable representing the influence of currents.

2.3.4 Waves effects on submerged macrophytes

The HISWA model has been designed to model the growth and transformation of wind waves in shallow water environments (Holthuijsen *et al.* 1989, Booij *et al*. 1993). It simulates in 2D (horizontally), wave propagation including refraction and shoaling, growth due to wind action, as well as dissipation by bottom friction and breaking. This model calculates various parameters such as wave energy, frequency, height and direction of waves on a regular square grid. This model used a regular grid with squared elements (elements size varied between 25 to 50 m). Each node of the grid supports the water velocity (X and Y), the water level, wind intensities and directions and topography, according to the scenario chosen.

The simulation of natural waves was characterized by the intensity and the direction of wind. Winds data came from Environnement Canada stations and the directions and wind intensities were recorded hourly. Two stations (Nicolet; 7025442 from 1992 to 1999 and Trois-Rivières; 701HE63 from 1991 to 1999) were retained in the lake Saint-Pierre area, one station (Saint-Hubert; 7027320 from 1993 to 1999) in the area between Sorel and Port of Montréal and finally one station (Dorval; YUL71627 from 1993 to 1999) in the lake Saint-Louis area. Wind intensities were divided in four classes: low winds (0-9 $km \cdot h^{-1}$), moderate winds (10-24 $km \cdot h^{-1}$), heavy winds (25-44 $km \cdot h^{-1}$), and extreme winds (45-60 $km \cdot h^{-1}$) and for each wind intensity, frequency analysis was reduced in 16 directions. A total of 64 simulations were produced according to scenarios. For each scenario, theses simulations were combined in order to obtain a mean intensity of wave's energy for the growing season.

The orbital near-bottom velocity generated by waves seems to be the best index of stress on plants. This variable is generally used in sedimentation models to assess grain stability on the bottom (Van Rijn 1989, Signell *et al.* 2000).

2.3.5 Sedimentation of fine particles

Dispersion and accumulation patterns of suspended matters were simulated once computer-generated hydrodynamic data was available using DISPERIM. This is a 2D (horizontal) eulerian transport-diffusion model that was solved with a finite element formulation (Secretan *et al.* 2000). Among other water quality processes, it allows to simulate transportation of suspended matter and its possible deposition on the bottom.

Sedimentation simulation is a function of the ratio of a selected threshold related to the critical shear stress of the substratum grain size and the local shear-stress. Calculation is done with a triangular element of three nodes (T3), where residual concentrations and local deposition velocities are evaluated. Basic information for DISPERSIM includes water depth, flow diffusivity, velocity and shear stresses simulated with hydrodynamic and wave models.

Threshold for allowing fine particles sedimentation was fixed to 0.3 Pa for current induced shear stress, which corresponds to the theoretical stability limit of medium sized sand grains (0.6 mm) (Van Rijn 1989). For wave induced near-bottom velocity, the threshold was established at 0.24 $m \cdot s^{-1}$, which corresponds to medium grain size stability (0.6 mm) with waves of a period of about 3 sec (Komar and Miller 1975). This value is slightly higher than the 0.15 $m \cdot s^{-1}$ used by Signell *et al.* (2000) as a value for resuspension of fine mud (mm?). The calculations were carried out on the Global TIN considering a steady state (non-transient) regime, with the hydrodynamic simulation presented earlier (7500 $m^3 s^{-1}$). The suspended load was injected at the upstream boundary of the Global TIN. The upstream concentration was imposed to a value of 5 mg l^{-1}, which is similar to measured local values, and the maximum settling velocity was parameterized at 0.05 mm/s. This settling velocity is similar to typical suspended load in river estuaries (Van Rijn 1989) and it corresponds to a particle with an equivalent diameter of 10 µm (Droppo & Ongley 1991, Teisson 1991, Ongley *et al*. 1981).

The variable used represents the local accumulation on the bottom of the materials injected upstream and transported as suspended load over the entire domain. It is obtained by multiplying the local concentrations and deposition velocities as calculated with DISPERSIM.

2.3.6 Light intensity on the bottom

As described earlier, DISPERSIM allows calculating the local concentration of suspended matter. The same simulation used for estimating the accumulation of fine particles on the bottom, is used for describing the spatial distribution of suspended load concentration.

Considering the ratio of incidental light reaching the bottom is a function of depth and local concentration of suspended matter. It is calculated with the following function:

[1] $$I_z = I_0 \, e^{-KZ}$$

Where I_0 is the intensity of light at the surface, K is the local extinction coefficient and Z is the depth. The extinction coefficient was considered to vary linearly with the concentration of suspended matter. It was roughly calibrated with Secchi disk depth (S), measured in Lake Saint-François at four locations (S = 6.0 to 10.6 m), and with a simple relation between K and S: $K=1.46/S$. According to this relation, values of K for these four locations would vary from 0.13 to 0.24 m^{-1}. This relation represents slightly smaller values of K (0.28 and 0.33 m^{-1}), than those measured in near shore areas of Lake Saint-François (Hudon & Lalonde 1999). The variable used in the HDB is the calculated ratio of incidental light reaching the bottom, considering a value of one for the incidental light (I_0).

2.4 Macrophytes assemblage characterization

To determine the potential environmental gradient influencing the submerged macrophytes distribution, a Canonical Correspondence Analysis was performed (CCA with CANOCO 4.5; Jongman et *al*. 1987; Ter Braak 1986, 1987), on calibration points for the three study sections. Statistical significance of environmental components was evaluated by a series of Monte Carlo permutations (Verdonschot & Ter Braak 1994). This species-habitat characterization allows us to understand the significance of variables selected in models according to study sections.

2.5 Models development

2.5.1 Logistic regression (LR) - Presence/absence

We used logistic regression to model the presence of eight species of macrophytes in Lake Saint-Pierre, St. Lawrence archipelagos and Lake Saint-Louis. This statistical technique was already used to model submerged macrophytes presence in lakes and have gave good results (Scheffer et al. 1992; Van den Berg et al. 1999; Van den Berg et al. 2003; Morin et al. *submit manuscript*). LR represents the probability of occurrence as a function of a linear combination of habitat variables, which can include single variables as well as higher-order terms (squares, interactions):

$$p = \frac{e^{\beta_0 + \sum_{i=1}^{k} \beta_i x_i}}{1 + e^{\beta_0 + \sum_{i=1}^{k} \beta_i x_i}}$$

where β_0 is a constant, the β_i are regression coefficients associated with the *k* predictors, and *e* is the base of natural logarithms.

We used program SYSTAT, v.10.2, to build LR models. Squared variables interactions between single variables were included as potential predictors. All variables were *z*-standardized prior to calculating products of variables, to remove non-essential collinearity in quadratic terms. A stepwise procedure, forward selection with a nominal cut-off p = 0.10, was used to determine which variables should be retained in the final models. Once variable selection was completed, models were screened for collinearity by examining the tolerance (1-VIF) of individual variables (Tabachnick & Fidell 1989). Tolerances of environmental variables were greater than 0.25 for all final LR models.

2.5.2 Regression trees (RT) - Density

We used regression trees (SYSTAT 10.0 and Rpart in S-PLUS) to model macrophytes density. Rpart (library available in S-PLUS) uses the binary recursive partitioning algorithm developed by Breiman et al. (1984), which is the best-known, most dependable, and most thoroughly tested one available (Lim et al. 2000).

Beginning with the entire data set (the “root node” at the top of the tree), the algorithm examines all possible splits for each possible value of the predictor variables, and selects the candidate split that maximizes the homogeneity within the two resulting subgroups (nodes) with respect to the response variable.

The impurity of a node in a RT is defined as the total sum of squares of the response variable values about the node mean, and each split minimizes the total sums of squares within the two nodes formed by the split. Equivalently, this maximizes the between nodes sums of squares.

As trees grow by successive splits, misclassification error rates decline. Rpart penalizes models by use of a cost-complexity parameter each time a new split occurs, to obtain the optimal tree size that balances the number of terminal nodes with the misclassification error rate (Atkinson & Therneau 2000). A 10-fold cross-validation was used to estimate prediction error. Final tree size was determined by the 1-SE rule, which favours the largest tree for which the cross-validated error falls within one standard error of the minimum relative error determined by cross-validation (Atkinson & Therneau 2000; De'ath & Fabricius 2000; Feldesman 2002). Given that the selected tree size will vary under repeated cross-validation, 50 sets of 10-fold cross-validation were run and the most frequently occurring tree size was chosen (De'ath & Fabricius 2000).

2.5.3 Models validation and evaluation of transferability

In logistic regression models (LR), we have made internal and external validation. For the internal validation, we used 10% of data set to validate LR models on the same study sections. To validate LR models between sections (external validation), a crossover field tests were used to validate models and assess transferability. This partitioning technique works as follow: models developed and calibrated with data from LSP were used to predict presence or absence on the basis of habitat features from LSL and SLFR and so on, yielding a total of nine validation trials for each species.

To evaluate model accuracy, the following measures were obtained from confusion matrices: correct classification rate (CCR; percentage of all cases correctly predicted), sensitivity (percentage of true positives correctly predicted), and specificity (percentage of true negatives correctly predicted). Cohen's kappa (κ, proportion of specific agreement range: -1 to 1), an additional statistical measure, was calculated from the confusion matrices to assess whether model performance differed from expectations based on chance alone (Fielding and Bell 1997, Manel et al. 2001). A value of zero indicates no difference from random prediction.

In many applications of LR models, a threshold of $p = 0.5$ is used for predicting presence. However with the use of LR, the correct classification rate, sensitivity, and specificity, may be highly sensitive to choice of prediction threshold and to the effect of varying prevalence (Fielding and Bell 1997; Manel et al. 1999; Hosmer and Lemeshow 2000). Therefore, the Sensitivity vs Specificity graph (which show how sensitivity and specificity vary as the decision threshold is changed) was used to evaluate predictive ability over all decision thresholds (Fielding & Bell 1997). The optimal decision threshold (ODT) was chosen to equalize the costs of misclassifying species as present (sensitivity) or absent (specificity) (Fielding and Bell 1997).

3 RESULTS

3.1 Characterization of study sites and macrophytes assemblage

The three study sections differed in their environmental characteristics and seem to form a gradient of environmental conditions encounters in a fluvial dynamic system (Table 1). LSP and LSL had more similar environmental characteristics than those of the SLFR but the three sections were significantly different for all environmental variables (ANOVA p-value > 0.001 and **p-value >0.05*). LSP is a very large fluvial shallow lake and seems to be more affected by waves than two others St. Lawrence River sections (LSL and SLFR) for a comparable sampling period. The SLFR was characterized by higher water velocities, higher specific discharge, more marked slope and was further similar to a river dynamic than a shallow lake dynamic. LSL is situated between LSP and SLFR concerning their environmental characteristics.

Table 1. Mean ± SD of simulated habitat variables on calibration points used to build RL models according to study sites.

Variables	Lake Saint-Pierre	Lake Saint-Louis	Fluvial reach
Depth (m)*	4.707 ± 3.645	5.125 ± 3.723	5.019 ± 3.814
Velocity ($m \cdot s^{-1}$)	0.361 ± 0.139	0.243 ± 0.198	0.511 ± 0.236
Specific flow ($m^2 \cdot s^{-1}$)	2.011 ± 2.135	1.475 ± 1.697	3.219 ± 3.446
Index of light penetration	0.131 ± 0.161	0.146 ± 0.246	0.162 ± 0.212
Slope (degrees)	0.853 ± 1.496	1.250 ± 1.514	2.289 ± 2.368
Fine matters deposited on bottom	0.010 ± 0.024	0.013 ± 0.012	0.003 ± 0.009
Wave effect 10 km/h spring ($m \cdot s^{-1}$)	0.062 ± 0.053	0.037 ± 0.052	0.021 ± 0.028
Wave effect 17 km/h spring ($m \cdot s^{-1}$)	0.139 ± 0.092	0.082 ± 0.084	0.055 ± 0.061
Wave effect 35 km/h spring ($m \cdot s^{-1}$)	0.318 ± 0.145	0.200 ± 0.133	0.157 ± 0.124
Wave effect 45 km/h spring ($m \cdot s^{-1}$)	0.407 ± 0.169	0.271 ± 0.153	0.220 ± 0.154
Wave effect 10 km/h autumn ($m \cdot s^{-1}$)	0.070 ± 0.064	0.037 ± 0.053	0.022 ± 0.031
Wave effect 17 km/h autumn ($m \cdot s^{-1}$)	0.144 ± 0.096	0.083 ± 0.085	0.058 ± 0.066
Wave effect 35 km/h autumn ($m \cdot s^{-1}$)	0.312 ± 0.145	0.202 ± 0.135	0.162 ± 0.129
Wave effect 45 km/h autumn ($m \cdot s^{-1}$)	0.394 ± 0.167	0.272 ± 0.161	0.205 ± 0.153
N (number of samples)	1135	979	5027

To characterize submerged macrophytes assemblage, CCA results suggest that macrophytes differed in their habitat distribution according to species and according to the St. Lawrence sections. The Figure 4 illustrate the macrophytes distribution for all sections pooled, where axis 1, characterised by water velocity and light penetration explain 71.8% of the system variation and axis 2, characterised by wave effects, organic matter deposited on bottom and field slope, explain 23.0 %. Macrophyte assemblage seems to differ slightly between the three study sections (Figure 5); however, similar relationships were observed between macrophytes distribution and environmental variables and more markedly between both lakes.

In Figure 4, where all sections were pooled, *Vallisneria americana* (N=2126) seems to tolerate high water velocity and lower light availability, compared to other species, except *Potamogeton pectinatus* (N=130) who was found in extreme conditions of water velocity, low light penetration and marked slope. Three species, *Alisma gramineum* (N=198), *Nitella sp.* (N=50) and *Potamogeton richardosonii* (N=766), seems to better tolerate mechanical effects of waves but theses species were found in different values of light penetration and velocities. *Alisma gramineum* necessitate higher light availability than both other species. *Myriophyllum spicatum* (N=562) and *Heteranthera dubia* (N=550) were found in similar environments (short Chi-square distance between points) and were strongly dependent of high light penetration. *Ceratophyllum demersum* (N=42) and *Elodea Canadensis* (N=307) seem to be strongly dependent of high light penetration and were associated with marked field slope.

If we observe macrophytes assemblage according to St. Lawrence sections, in Lake St. Pierre (figure 5 a) and in Lake St. Louis (figure 5 b), *Vallisneria americana* was associated with mean values for all variables (near the diagram centroid). In archipelagos (figure 5 c), this specie was associated with higher water velocity than in lakes. For *Potamogeton richardsonii* the same pattern may be observed for Lake St. Pierre and Lake St. Louis and this specie distribution was very close to *Vallisneria americana* in both lakes (figure 5 a and b) but seems less tolerant to high water velocity. In archipelagos, *Potamogeton* *richardsonii* was associated with high wave effects and an accumulation of organic matters in bottom (figure 5 c).

Myriophyllum spicatum was associated differently according to sections (figure 5 a,b,c). In Lake St. Pierre, this specie was related to mean values for all variables except for wave exposure where specie was found with intermediate wave effect (figure 5 a). In Lake St. Louis, *Myriophyllum spicatum* seems to be strongly associated with *Potamogeton richardsonnii* with mean environmental variable values (figure 5 b). In archipelagos, *Myriophyllum spicatum* was associated with high light penetration and low water velocities (figure 5 c).

In Lake St. Pierre and Archipelagos, *Ceratophyllum demersum* was strongly associated with light penetration and negatively associated with water velocities (figure 5 a, b). In three sections, this specie seems related positively to accumulation of organic matter on bottom (figure 5 a, b, c).

Distributions of *Heteranthera dubia, Alisma gramineum, Elodea canadensis* and *Nitella* sp. differ strongly according to sections (figure 5). However, some tendencies may emerge; *Heteranthera dubia* was negatively associated with high water velocities, *Alisma gramineum* was negatively associated with slope, in both lakes, *Elodea canadensis* was negatively associated with light penetration and *Nitella* sp. (few occurrences) was associated with wave effects in Lake St. Louis and Archipelagos.

Potamogeton pectinatus was not represented in Lake St.Pierre (N = 9) but was associated with extremes values of water velocity in Lake St. Louis and in archipelagos (figure 5 b,c). This specie seems tolerant to low light penetration and react differently to wave exposure in Lake St. Louis and archipelagos. In Lake St. Louis, *Potamogeton pectinatus* was found where wave exposure was relatively high but in archipelagos, this specie was associated with low wave effects.

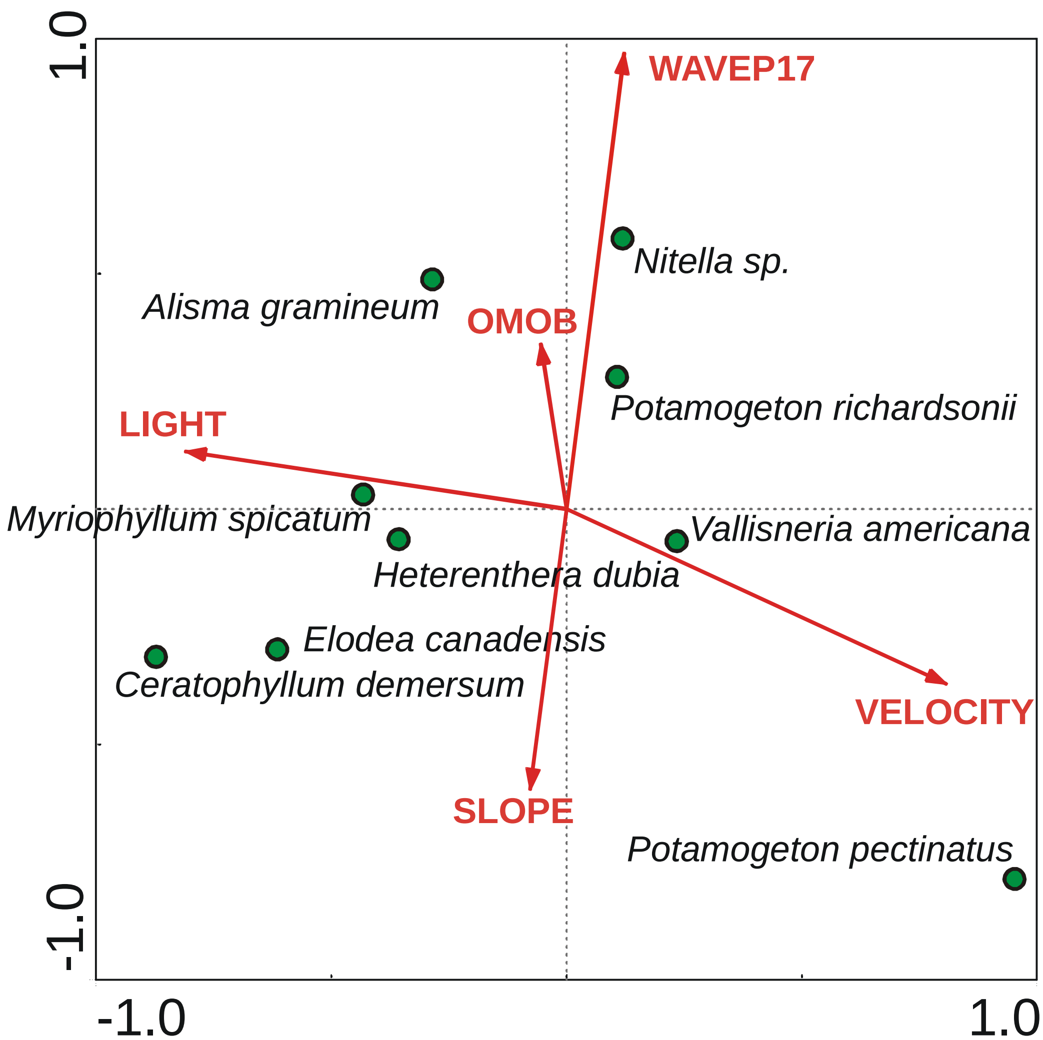


Figure 4. CCA diagram results showing relationships between macrophyte species (points) and environmental variables (arrows). CCA diagram (axis 1 et axis 2) explained 94.8% of variance proportion of macrophytes presence/absence in the St. Lawrence River. Both first eigenvalues were 0.156 and 0.050 et the third and fourth respectively were 0.008 and 0.004.

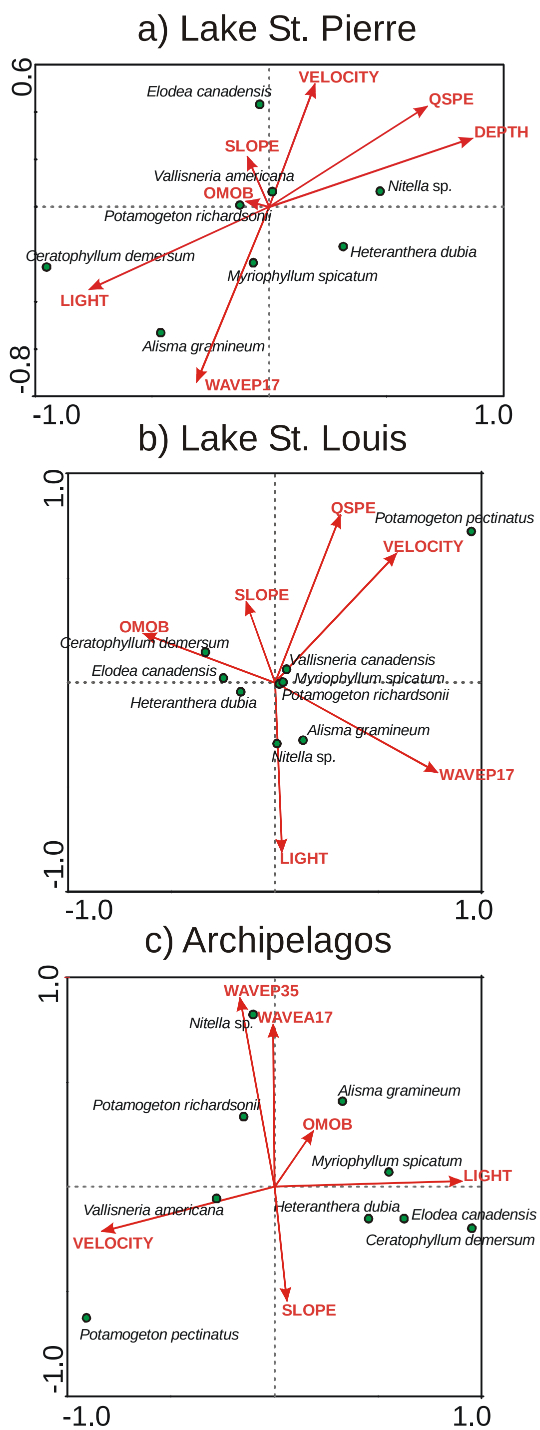


Figure 5. CCA diagram results showing relationships between macrophytes species (points) and environmental variables (arrows) according to study sites. a) CCA diagram of Lake St.Pierre (axis 1 et axis 2) explained 89.2% of proportion of the variance of presence/absence macrophytes in the St.Lawrence River. Both first eigenvalues were 0.113 and 0.059; b) CCA diagram of Lake St.Louis (axis 1 et axis 2) explained 80.8% of proportion of the variance of presence/absence macrophytes in the St.Lawrence River. Both first eigenvalues were 0.051 and 0.032; c) CCA diagram of St.Lawrence archipelagos (axis 1 et axis 2) explained 93.0 % of proportion of the variance of presence/absence macrophytes in the St.Lawrence River. Both first eigenvalues were 0.227 and 0.046.

3.2 Presence/absence models for macrophyte species

Logistic regression (LR) models were simple and varied slightly between the three study sections according to macrophyte species (Table 2, Table 3 and Table 4). The McFadden Rho^2 (goodnest-of-fit measure) was high and range from 0.1796 to 0.5759. On the basis of twelve abiotic variables used in model calibration, only seven variables were retained following forward stepwise selection (acceptation threshold > 0.1). All variables retained were associated with a p-value < 0.05 and all LR models were globally significant with p-value < 0.001. Prevalence of environmental variables was higher than 0.3 for all LR models. Light penetration and water velocity seemed to strongly influence the establishment of macrophytes assemblage in the three study sections and both variables were found in almost all LR macrophyte models. Since some variables are strongly multicollinear, in particular the variables associated with waves effects (spring and autumn with various wind velocities), it is impossible to study their effects simultaneously in a logistic regression model. Usually, only one waves variable can be used to predict the presence of the macrophyte species and model with the higher R^2 was chosen.

In LR models, the number and kind of variables involved differ between sections. Models were simpler and more parcimonious in Lake St. Pierre than in the other sections, globally including five variables to explain presence of 5 submerged macrophyte species (Table 2). In Lake St. Pierre, wave effect (for both season and for all wind velocities) and accumulation of organic matter in bottom seem to have no direct effect on submerged macrophyte distribution. No model at all includes theses variables to predict the presence of submerged macrophytes. The specific flow was only used to predict the presence of *Potamogeton richardsonii* and *Heteranthera dubia* in Lake St. Pierre but was not used in Lake St. Louis and in archipelagos. In archipelago, wave effect seems to have an influence on submerged macrophyte presence because these variables were implicated for both seasons and for three wind velocity (Table 4).

In calibration trials, with the use of optimal decision threshold, the correct classification rate (CCR) was high for all LR submerged macrophyte models, ranging from 75.7% to

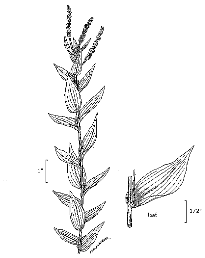
95.3%. Specificity and sensitivity of models were equivalent to CCR because we use the Optimum Decision Threshold derived from Sensibility vs Specificity curves. Cohen's Kappa values varied from very good model (0.6886) to poor model (0.0807). In validation trials (model evaluation on 10% of data set not used in calibration trials), CCR were good varying from 78.2% to 93.1%, specificity varying from 50.0% to 100.0%, and sensitivity range from 54.5% to 98.2%. Cohen's Kappa values range from 00682 to 0.7942.

3.2.1 *Vallisneria americana*

V. americana was the more abundant specie in the three study sections. In Lake St. Pierre, logistic regression model of *V. americana* was calibrated on 315 presences. In this section, LR retained three variables: water velocity (single and quadratic terms), light penetration (single and quadratic terms) and field slope (table 2). In Lake St. Louis, LR model was calibrated on 319 points and LR retained two variables: water velocity and light penetration (single and quadratic terms) (table 3). In the St. Lawrence archipelagos (Berthier-Sorel, Verchères-Contrecoeur and Ste. Thérèse-Boucherville), LR model was calibrated on 1528 points and retained two variables: light penetration (single and quadratic terms) and wave effect (in spring with wind velocity of 17 $km \cdot h^{-1}$) (table 4). *V. americana* predicted distribution from RL models (with the use of the optimum decision thresholds) cover a large portion of the St. Lawrence River (figure 6 a) from Lake St. Pierre to Lake St. Louis.

In calibration trials, correct classification rate (CCR) of LR models for *V. americana* was high, ranging from 77.9% and 85.8% with the use of the optimum decision threshold. Cohen's Kappa values were also high, ranging from 0.5165 to 0.6886 indicating that RL models were robust and differ of what would be expected by chance alone. In validation trials (model evaluation on 10% of data set), model accuracy was also high; CCR: 79.2% to 91.2%; sensitivity: 76.1% to 87.2%; specificity: 80.7% to 93.1% and Cohen's Kappa: 0.5491 to 0.7942. Theses results suggest that LR model for *V. americana*, for the three different sections of the St. Lawrence River, were very good, markedly in both lakes.

3.2.2 *Potamogeton richardsonii*



In Lake St. Pierre, logistic regression model of *P. richardonii* was calibrated on 196 presences. In this section, LR retained only one variable: specific flow (table 2). In Lake St. Louis, LR model was calibrated on 135 points and LR retained three variables: water velocity, light penetration (single and quadratic terms) and wave effects in spring with 17 km · h^{-1} wind velocity (table 3). In the St. Lawrence archipelagos, LR model was calibrated on 435 points and retained three variables: water velocity (single and quadratic terms), light penetration (single and quadratic terms) and wave effect (in spring with wind velocity of 35 km · h^{-1}) (table 4). *P. richardsonii* predicted distribution from RL models (with the use of the optimum decision thresholds) cover also a large portion of the St. Lawrence River but less larger than that of *V. americana* (figure 6 b).

In calibration trials, correct classification rate (CCR) of LR models for *P. richardsonii* was high, ranging from 78.1% and 87.8% with the use of the optimum decision threshold. Cohen's Kappa values were good, ranging from 0.2895 to 0.6399 indicating that RL models were robust and differ of what would be expected by chance alone. However, RL model for *P. richardsonii* in St. Lawrence archipelagos was under the 0.4 limit threshold, indicating a good model. In validation trials (model evaluation on 10% of data set), model accuracy was also high; CCR: 79.0% to 89.3%; sensitivity: 81.3% to 94.7%; specificity: 78.2% to 88.1% and Cohen's Kappa: 0.3120 to 0.7000. Theses results suggest that LR model for *P. richardsonii*, for the three different sections of the St. Lawrence River, were good, markedly in Lake St. Pierre where only one variable (specific flow) gave high model accuracy.

3.2.3 *Myriophyllum spicatum*

In Lake St. Pierre, logistic regression model of *M. spicatum* was calibrated on 29 presences. In this section, LR retained two variables: water velocity and light penetration (table 2). In Lake St. Louis, LR model was calibrated on 124 points and LR retained two variables: light penetration (single and quadratic terms) and organic matter deposited on bottom (single and quadratic terms) (table 3). In the St. Lawrence archipelagos, LR model was calibrated on 409 points and retained four variables: water velocity, light penetration, wave effect (in autumn with wind velocity of 10 km · h^{-1}) and accumulation of organic matter on bottom (table 4).

In calibration trials, correct classification rate (CCR) of LR models for *M. spicatum* was high, ranging from 81.3% and 86.3% with the use of the optimum decision threshold. Cohen's Kappa values were good, ranging from 0.2090 to 0.4288 indicating that RL models differ of what would be expected by chance alone. In validation trials (model evaluation on 10% of data set), model accuracy was also high; CCR: 81.0% to 84.5%; sensitivity: 70.0% to 100.0%; specificity: 82.5% to 84.0% and Cohen's Kappa: 0.2342 to 0.3742. Theses results suggest that LR model for *M. spicatum*, were better in Lake St. Pierre and archipelagos than in lake St. Louis. In validation trials, Cohen's Kappa values were all under the threshold of 0.4 suggesting good model.

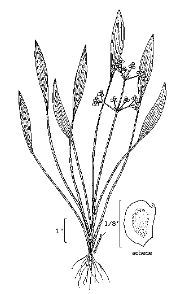
3.2.4 Heteranthera dubia

In Lake St. Pierre, logistic regression model of *H. dubia* was calibrated on 74 presences. In this section, LR retained one variable: water velocity (single and quadratic terms) (table 2). In Lake St. Louis, LR model was calibrated on 117 points and LR retained three variables: water velocity, light penetration (single and quadratic terms) and field slope (table 3). In the St. Lawrence archipelagos, LR model was calibrated on 359 points and retained three variables: water velocity, light penetration (single and quadratic terms) and accumulation of organic matter on bottom (table 4).

In calibration trials, correct classification rate (CCR) of LR models for *H. dubia* was high, ranging from 76.4% and 81.2% with the use of the optimum decision threshold. Cohen's Kappa values were good, ranging from 0.2120 to 0.3946 indicating that RL models differ of what would be expected by chance alone. In validation trials (model evaluation on 10% of data set), model accuracy was also high; CCR: 79.5% to 80.6%; sensitivity: 69.1% to

100.0%; specificity: 80.2% to 80.5% and Cohen's Kappa: 0.1359 to 0.3728. Theses results suggest that LR models for *H. dubia* were good but Cohen's Kappa values were under the threshold of 0.4 suggesting good model in calibration and validation trials.

3.2.5 *Alisma gramineum*



In Lake St. Pierre, logistic regression model of *A. gramineum* was calibrated on 29 presences. In this section, LR retained one variable: specific discharge (single term) (table 2). In Lake St. Louis, LR model was calibrated on 58 points and LR retained one variable: light penetration (single and quadratic terms) (table 3). In the St. Lawrence archipelagos, LR model was calibrated on 111 points and retained three variables: water velocity, light penetration and wave effect (in autumn with wind velocity of 17 $km \cdot h^{-1}$) (table 4).

In calibration trials, correct classification rate (CCR) of LR models for *A. gramineum* was high, ranging from 80.7% and 95.3% with the use of the optimum decision threshold. Cohen's Kappa values were good, ranging from 0.1218 to 0.4899 indicating that RL models differ of what would be expected by chance alone. In validation trials (model evaluation on 10% of data set), model accuracy was also good; CCR: 79.2% to 93.1%; sensitivity: 50.0% to 100.0%; specificity: 78.8% to 92.2% and Cohen's Kappa: 0.1317 to 0.3176. Theses results suggest that LR models for *A. gramineum* were good but Cohen's Kappa values were under the threshold of 0.4 suggesting good model in calibration and validation trials.

3.2.6 *Elodea canadensis*

E. canadensis was present in Lake St. Louis and in archipelagos but not in appreciably quantity in Lake St. Pierre. In Lake St. Louis, LR model was calibrated on 57 points and LR retained two variables: water velocity and light penetration (single and quadratic terms) (table 3). In the St. Lawrence archipelagos, LR model was calibrated on 250 points and retained three variables: water velocity, light penetration (single and quadratic terms) and wave effect (in spring with wind velocity of 17 km · h^{-1} for single and quadratic terms) (table 4).

In calibration trials, correct classification rate (CCR) of LR models for *E. canadensis* ranging from 79.6% and 84.0% with the use of the optimum decision threshold. Cohen's Kappa values were ranged from 0.1875 to 0.2597 indicating that RL models differ of what would be expected by chance alone. In validation trials (model evaluation on 10% of data set), model accuracy was good; CCR: 79.6% to 81.5%; sensitivity: 54.5% to 85.2%; specificity: 81.3% to 81.6% and Cohen's Kappa: 0.1834 to 0.2597.

3.2.7 *Potamogeton pectinatus*

P. pectinatus was in appreciably density only in archipelagos and was present on 112 calibration points. In this section, LR retained three variables: water velocity (single and quadratic terms), light penetration (single and quadratic terms) and wave effect in single and quadratic terms (in spring with wind velocity of 17 km · h^{-1}) (table 4).

In calibration trials, correct classification rate (CCR) of LR models for *P. pectinatus* was good (78.5%) with the use of the optimum decision threshold. Cohen's Kappa values were relatively low (0.1039) indicating that RL model differ of what would be expected by chance alone but was not a good model. In validation trials (model evaluation on 10% of data set), model accuracy was good; CCR: 79.5%; sensitivity: 60.0%; specificity: 79.9% and Cohen's Kappa: 0.0682. Theses results suggest that LR model for *P. pectinatus* had lower predictive power that for other submerged macrophyte species. Cohen's Kappa value indicates that LR model was at the limit of a random distribution.

3.2.8 *Ceratophyllum demersum*

C. demersum was also in appreciably density only in archipelagos and was present on 42 calibration points. In this section, LR retained two variables: water velocity and light penetration (table 4).

In calibration trials, correct classification rate (CCR) of LR models for *C. demersum* was good (86.4%) with the use of the optimum decision threshold. Cohen's Kappa values were relatively low (0.0807) indicating that RL model differ of what would be expected by chance alone but was a poor model. In validation trials (model evaluation on 10% of data set), model accuracy remained high; CCR: 85.3%; sensitivity: 90.0%; specificity: 85.2% and Cohen's Kappa: 0.1608 Theses results suggest that LR model for *C. demersum* had low predictive power.

Table 2. Coefficients of logistic regression models for submerged macrophyte species in Lake Saint-Pierre. Coefficients are given only for terms retained by the stepwise selection procedure ($p < 0.10$). All models were globally significant at $p < 0.001$.

Regression terms	Estimated coefficients				
	Vallisneria americana	*Potamogeton richardsonii*	*Myriophyllum spicatum*	*Heteranthera dubia*	*Alisma gramineum*
Constant	-3.9928	-3.9146	-5.6414	-4.5521	-11.5276
Depth	-	-	-	-	-
Depth · Depth	-	-	-	-	-
Velocity	-0.8352	-	-1.3389	-5.1145	-
Velocity · Velocity	0.6397	-	-	-2.0191	-
Specific discharge	-	-3.6768	-	-	-6.8649
Spec. discharge · Spec. discharge	-	-	-	-	-
Index of light penetration	6.8032	-	1.5314	-	-
Light · Light	-2.7008	-	-	-	-
Slope	-0.8797	-	-	-	-
Slope · Slope	-	-	-	-	-
McFadden Rho^2	0.5759	0.4776	0.2604	0.2207	0.5381
Optimum DecisionThreshold	0.341	0.224	0.047	0.124	0.105
Calibration Total classification rate	86.6%	87.8%	86.3%	76.4%	95.3%
Sensitivity	86.7%	87.8%	86.3%	76.4%	96.6%
Specificity	86.6%	87.9%	86.2%	75.7%	95.2%
Kappa ($p < 0.05$)	0.6886	0.6399	0.2092	0.2120	0.4899
Prevalence	(315/1135)	(196/1135)	(29/1135)	(74/1135)	(29/1135)
Validation Total classification rate	91.2%	89.3%	84.5%	80.6%	93.1%
Sensitivity	87.1%	94.7%	100.0%	100.0%	50.0%
Specificity	93.1%	88.1%	84.0%	80.2%	92.2%
Kappa ($p < 0.1$)	0.7942	0.7000	0.2342	0.1359	0.1743
Prevalence	(31/103)	(19/103)	(3/103)	(2/103)	(2/103)

Table 3. Coefficients of logistic regression models for submerged macrophyte species in Lake Saint-Louis. Coefficients are given only for terms retained by the stepwise selection procedure ($p < 0.10$). All models were globally significant at $p < 0.0001$.

Regression terms	Estimated coefficients					
	Vallisneria americana	*Potamogeton richardsonii*	*Myriophyllum spicatum*	*Heteranthera dubia*	*Elodea canadensis*	*Alisma gramineum*
Constant	-0.9021	-2.5123	-2.3685	-2.7766	-3.3057	-5.3091
Velocity	-0.7562	-0.7364	-	-1.1090	-1.0081	-
Velocity · Velocity	-	-	-	-	-	-
Index of light penetration	2.9123	1.1618	3.4920	1.9930	1.4465	4.9420
Light · Light	-0.9954	-0.5461	-1.2404	-0.7955	-0.6162	-1.3986
Wave spring 17 km/h	-	0.8515	-	-	-	-
Wave_S17 km/h · Wave_S17 km/h	-	-	-	-	-	-
Fine material deposited on bottom	-	-	0.6513	-	-	-
FMD · FMD	-	-	-0.6207	-	-	-
Slope	-	-	-	-0.4116	-	-
Slope · Slope	-	-	-	-	-	-
McFadden Rho^2	0.4870	0.2822	0.3370	0.3188	0.2086	0.3255
Optimum DecisionThreshold	0.380	0.199	0.186	0.112	0.065	0.121
CalibrationTotal classification rate	85.8%	79.6%	81.3%	80.3%	75.7%	83.4%
Sensitivity	85.9%	80.0%	82.2%	79.4%	75.4%	86.2%
Specificity	85.6%	79.5%	81.2%	80.4%	75.7%	83.2%
Kappa statistic	0.6872	0.4092	0.4288	0.3946	0.1875	0.3172
Prevalence	(319/979)	(135/979)	(124/979)	(117/979)	(57/979)	(58/979)
Validation Total classification rate	85.3%	79.8%	81.0%	98.2%	79.6%	83.4%
Sensitivity	82.0%	81.3%	70.0%	75.0%	54.5%	100.0%
Specificity	86.7%	79.6%	82.5%	81.5%	81.6%	82.6%
Kappa statistic	0.6650	0.3473	0.3728	0.3728	0.1834	0.3176
Prevalence	(50/163)	(16/163)	(37/163)	(35/163)	(11/163)	(8/163)

Table 4. Coefficients of logistic regression models for submerged macrophyte species in St. Lawrence archipelagos. Coefficients are given only for terms retained by the stepwise selection procedure ($p < 0.10$). All models were globally significant at $p < 0.0001$.

Regression terms		Estimated coefficients							
		Vallisneria americana	*Potamogeton richardsonii*	*Myriophyllum spicatum*	*Heteranthera dubia*	*Potamogeton pectinatus*	*Elodea canadensis*	*Alisma Gramineum*	*Ceratophyllum demersum*
Constant		-0.9548	-3.5804	-4.9585	-4.5895	-3.1142	-5.5945	-6.4024	-8.0636
Velocity		-	-0.1174	-1.1004	-0.9841	0.9876	-1.2181	-0.3689	-2.2751
Velocity · Velocity		-	0.4885	-	-	-	-	-	-
Index of light penetration		1.8821	1.6492	1.8307	2.8860	1.5290	3.2897	1.5856	1.0712
Light · Light		-1.1986	-1.0808	-	-0.7677	-1.1800	-0.8357	-	-
Wave autumn 10 km/h		-	-	0.5418	-	-	-	-	-
Wave spring 17 km/h		0.9594	-	-	-	0.8272	0.8286	-	-
Wave S17 · Wave S17 km/h		-	-	-	-	-1.1449	-0.7474	-	-
Wave autumn 17 km/h		-	-	-	-	-	-	0.5465	-
Wave A17 · Wave A17 km/h		-	-	-	-	-	-	0.4454	-
Wave spring 35 km/h		-	1.1061	-	-	-	-	-	-
Fine material deposited on bottom		-	-	-0.1853	-0.2299	-	-	-	-
McFadden Rho^2		0.3414	0.2602	0.3932	0.3065	0.1796	0.3521	0.2995	0.3121
Optimum DecisionThreshold		0.398	0.117	0.115	0.111	0.031	0.073	0.023	0.011
Calibration	Total classification rate	77.9%	78.1%	84.9%	81.2%	78.5%	84.0%	80.7%	86.4%
Sensitivity		77.9%	78.1%	84.9%	81.2%	78.5%	84.0%	81.1%	86.4%
Specificity		77.9%	78.4%	84.8%	81.1%	78.6%	84.0%	80.7%	87.5%
Kappa		0.5165	0.2895	0.4090	0.3052	0.1039	0.2867	0.1218	0.0807
Prevalence		(1528/5027)	(435/5027)	(409/5027)	(359/5027)	(112/5027)	(250/5027)	(111/5027)	(42/5027)
Validation	Total classification rate	79.2%	79.0%	82.8%	79.5%	79.5%	81.5%	79.2%	85.3%
Sensitivity		76.1%	87.8%	84.1%	69.1%	60.0%	85.2%	91.7%	90.0%
Specificity		80.7%	78.2%	82.7%	80.5%	79.9%	81.3%	78.8%	85.2%
Kappa		0.5491	0.3120	0.3742	0.2633	0.0682	0.2597	0.1317	0.1608
Prevalence		(176/523)	(41/523)	(44/523)	(42/523)	(10/523)	(27/523)	(8/523)	(10/523)

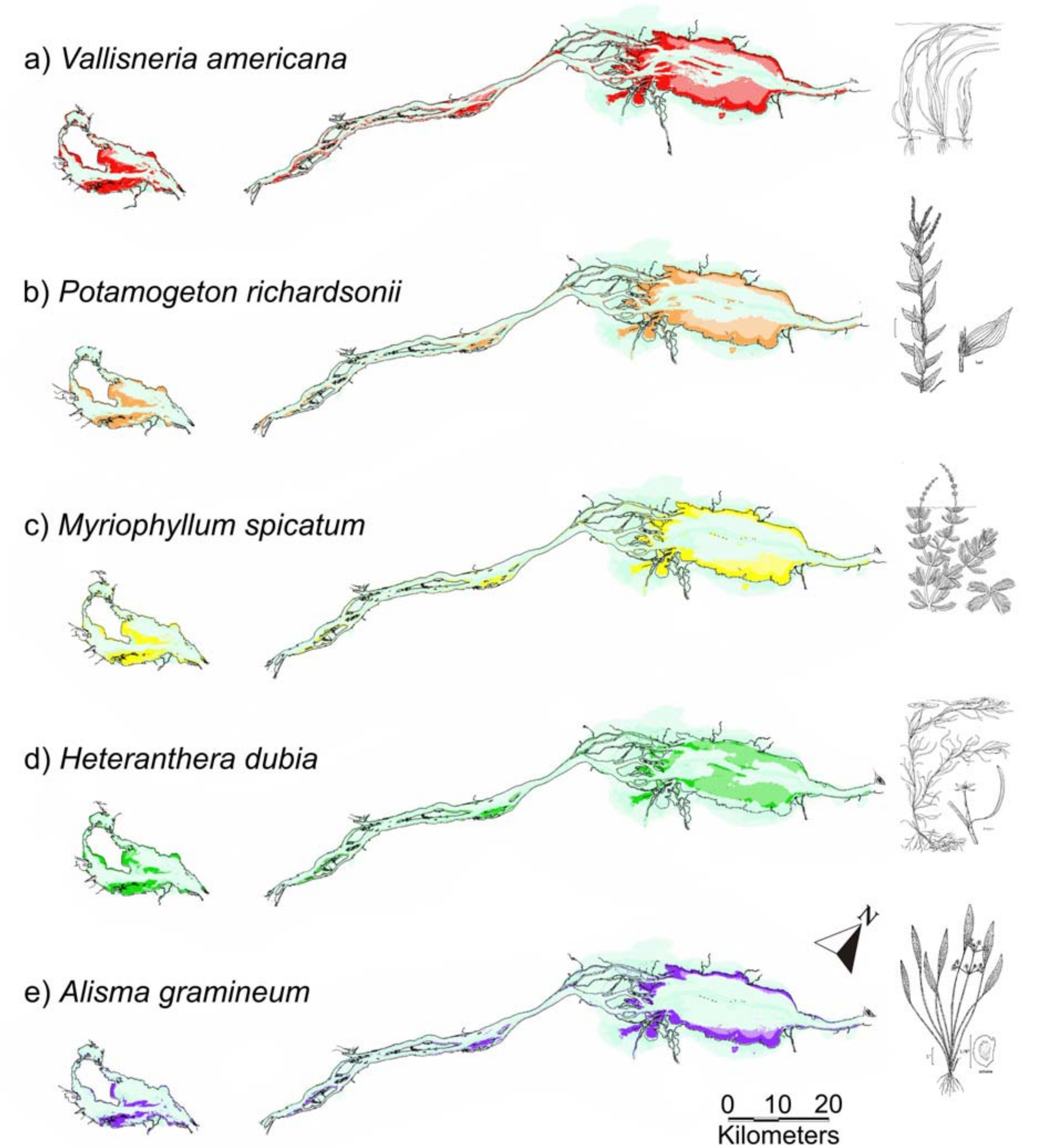


Figure 6. Submerged macrophytes distribution predicted by RL models with the use of Optimum Decision Thresholds. Models build on each sections were projected on the entire MIRE grid for 1997. a) predicted distribution of *Vallisneria americana* with the following optimum decision thresholds (ODT); LSP = 0.341, ARC = 0.398, LSL = 0.380; b) predicted distribution of *Potamogeton richardsonii* with the following ODT; LSP = 0.224, ARC = 0.117, LSL = 0.199; c) predicted distribution of *Myriophyllum spicatum* with the following ODT; LSP = 0.047, ARC = 0.115, LSL = 0.186; d) predicted distribution of *Heteranthera dubia* with the following ODT; LSP = 0.124, ARC = 0.111, LSL = 0.112; e) predicted distribution of *Alisma gramineum* with the following ODT; LSP = 0.105, ARC = 0.023, LSL = 0.121.

3.3 Transferability of presence/absence models

To evaluate the transferability potential of presence/absence models (LR) we used cross-over field test among the three St. Lawrence sections (Fielding & Bell 1997; Guay et al. 2003). Transferability potential was evaluated only for species present in the three study sections: *Vallisneria americana, Potamogeton richardsonii, Myriophyllum spicatum, Heteranthera dubia* and *Alisma gramineum*. Despite the different environmental characteristics between the three study sections, LR models seem relatively general (i.e. good model transferability among sections), and models accuracy varied slightly between St. Lawrence River sections. Models calibrated on LSL data seem to have a better transferability potential, i.e. accuracy measures were less variables than for the two other sections.

For *V. americana,* model transferability was very good among sections (Figure 7). On LSP data set (validation section), models calibrated on Lake St. Louis gave high values of CCR, sensitivity, specificity and Cohen's Kappa (κ). However, model calibrated on St. Lawrence Archipelagos have a lower transferability potential on Lake St. Pierre data set. CCR and sensitivity were under 60% and κ value was under the threshold of 0.4 (good model indicator, Titus et al. 1984) (figure 7 a). On the Lake St. Louis data set (validation section), models calibrated on Lake St. Pierre and Archipelagos gave high values of CCR, sensitivity, specificity and κ (figure 7 b). On the St. Lawrence Archipelago data set (validation section), models calibrated on Lake St. Pierre and Lake St. Louis (calibration section) gave high values of CCR, sensitivity and specificity. However, model build on Lake St.Pierre have a κ value lower than 0.4 (figure 7 c). For *V. americana,* model transferability were high among sections, but model transferability between Lake St. Pierre and St. Lawrence archipelagos was lower.

For *P. richardsonii,* model transferability was good between sections (figure 8) but was more variable than for *V. americana* (figure 7). On Lake St. Pierre data set, models calibrated on Lake St. Louis gave high values of CCR, specificity and κ but lower value of sensitivity. However, model calibrated on St. Lawrence Archipelagos have a lower transferability potential on Lake St. Pierre data set. CCR and specificity were under 60% and κ value was under the threshold of 0.4 (figure 8 a). On Lake St. Louis data set, models calibrated on Lake St. Pierre and Archipelagos gave high values of CCR, sensitivity and specificity but κ values were under 0.4 (figure 8 b). On Archipelago data set, models build on Lake St. Pierre and Lake St. Louis (calibration section) gave high values if CCR and specificity but lower values of sensitivity. κ values were also under 0.4 but differ of what would be expected by chance (figure 8 c). For *Potamogeton richardsonii,* model accuracy and transferability were good, but model build on Lake St. Pierre as well gave lower results on archipelagos and vice versa .

For *Myriophyllum spicatum,* model transferability was good between sections (figure 9). On Lake St. Pierre data set (validation section), models build on Lake St. Louis and on Archipelagos (calibration section) gave high values if CCR, specificity, sensitivity but low κ values (under 0.4) (figure 9 a). On Lake St. Louis data set (validation section), models build on Lake St. Pierre and Archipelagos (calibration section) gave high values of CCR, sensitivity, specificity and κ (figure 9 b). On Archipelago data set (validation section), models build on Lake St. Pierre and Lake St. Louis (calibration section) gave high values if CCR, specificity and sensitivity and high κ values (figure 9 c). However, Lake St. Louis model applied on Archipelagos gave lower value of κ (under 0.4).

For *Heteranthera dubia,* model transferability was relatively good between sections (figure 10). On Lake St. Pierre data set (validation section), models build on Lake St. Louis and on Archipelagos (calibration section) gave high values if CCR and specificity but low value of sensitivity for model build in archipelagos. κ values were under 0.4 (figure 10 a). On Lake St. Louis data set (validation section), models build on Archipelagos (calibration section) gave high values of CCR, sensitivity, specificity and κ. Moreover, κ value was at the limit of being random distribution (figure 10 b). On Archipelago data set (validation section), models build on Lake St. Pierre and Lake St. Louis (calibration section) gave high values of CCR and specificity but low values of sensitivity. κ values were under 0.4 (figure 10 c).

For *Alisma gramineum,* model transferability was good between sections; however we have some problems with κ values (figure 11). On Lake St. Pierre data set (validation section), models build on Lake St. Louis and on Archipelagos (calibration section) gave high values if CCR, specificity, sensitivity but low κ values (under 0.4) (figure 11 a). On Lake St. Louis data set (validation section), models build on Lake St. Pierre and Archipelagos (calibration section) gave high values of CCR, sensitivity, specificity and κ under 0.4 (figure 11 b). On Archipelago data set (validation section), model builds on Lake St. Louis (calibration section) gave high values if CCR, specificity and sensitivity but low κ value. Model builds on Lake St. Pierre gave low sensitivity and κ values (figure 11 c).

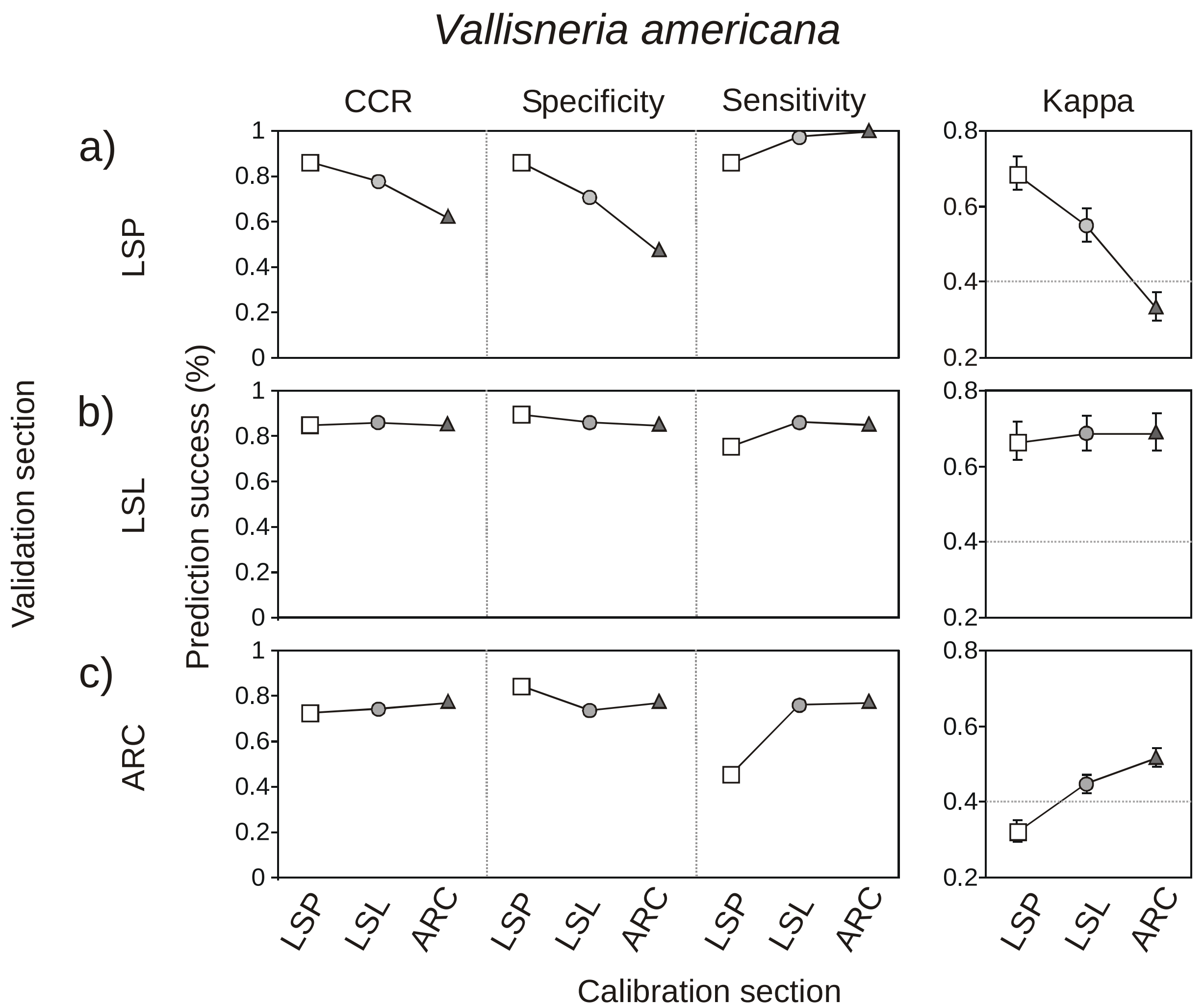


Figure 7. Comparison of models evaluation and transferability potential among St. Lawrence sections with cross-over field test for *Vallisneria americana*; a) model accuracy (CCR, sensitivity and specificity) in validation trials on Lake St. Pierre data set from calibration models of Lake St. Pierre (□), Lake St. Louis (●) and Archipelagos (▲); b) model accuracy in validation trials on Lake St. Louis data set from calibration models of Lake St. Pierre, Lake St. Louis and Archipelagos c) model accuracy in validation trials on Archipelagos data set from calibration models of Lake St. Pierre, Lake St. Louis and Archipelagos.

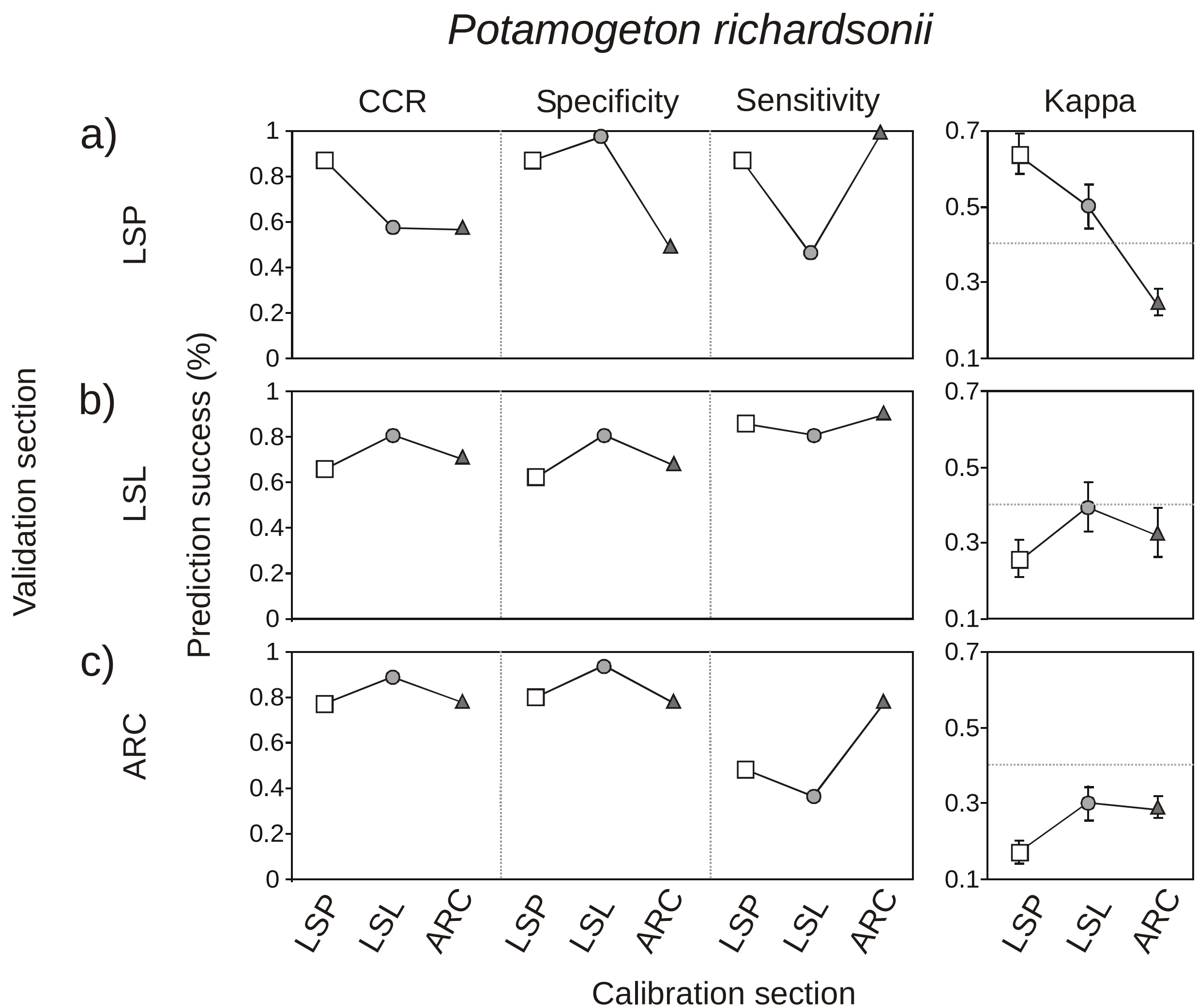


Figure 8. Comparison of models evaluation and transferability potential among St. Lawrence sections with cross-over field test for *Potamogeton richardsonii*; a) model accuracy (CCR, sensitivity and specificity) in validation trials on Lake St. Pierre data set from calibration models of Lake St. Pierre (□), Lake St. Louis (●) and Archipelagos (▲); b) model accuracy in validation trials on Lake St. Louis data set from calibration models of Lake St. Pierre, Lake St. Louis and Archipelagos c) model accuracy in validation trials on Archipelagos data set from calibration models of Lake St. Pierre, Lake St. Louis and Archipelagos.

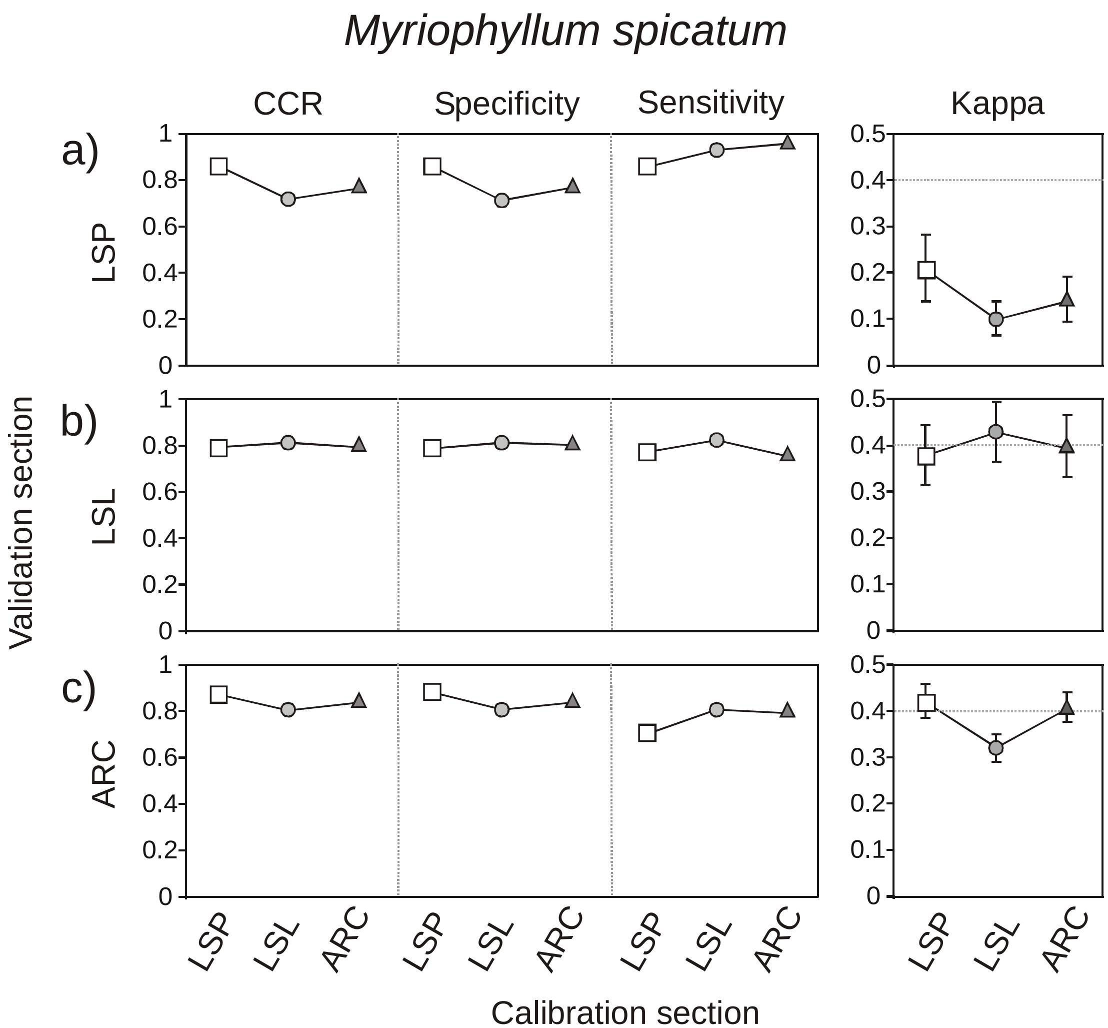


Figure 9. Comparison of models evaluation and transferability potential among St. Lawrence sections with cross-over field test for *Myriophyllum spicatum*; a) model accuracy (CCR, sensitivity and specificity) in validation trials on Lake St. Pierre data set from calibration models of Lake St. Pierre (□), Lake St. Louis (●) and Archipelagos (▲); b) model accuracy in validation trials on Lake St. Louis data set from calibration models of Lake St. Pierre, Lake St. Louis and Archipelagos c) model accuracy in validation trials on Archipelagos data set from calibration models of Lake St. Pierre, Lake St. Louis and Archipelagos.

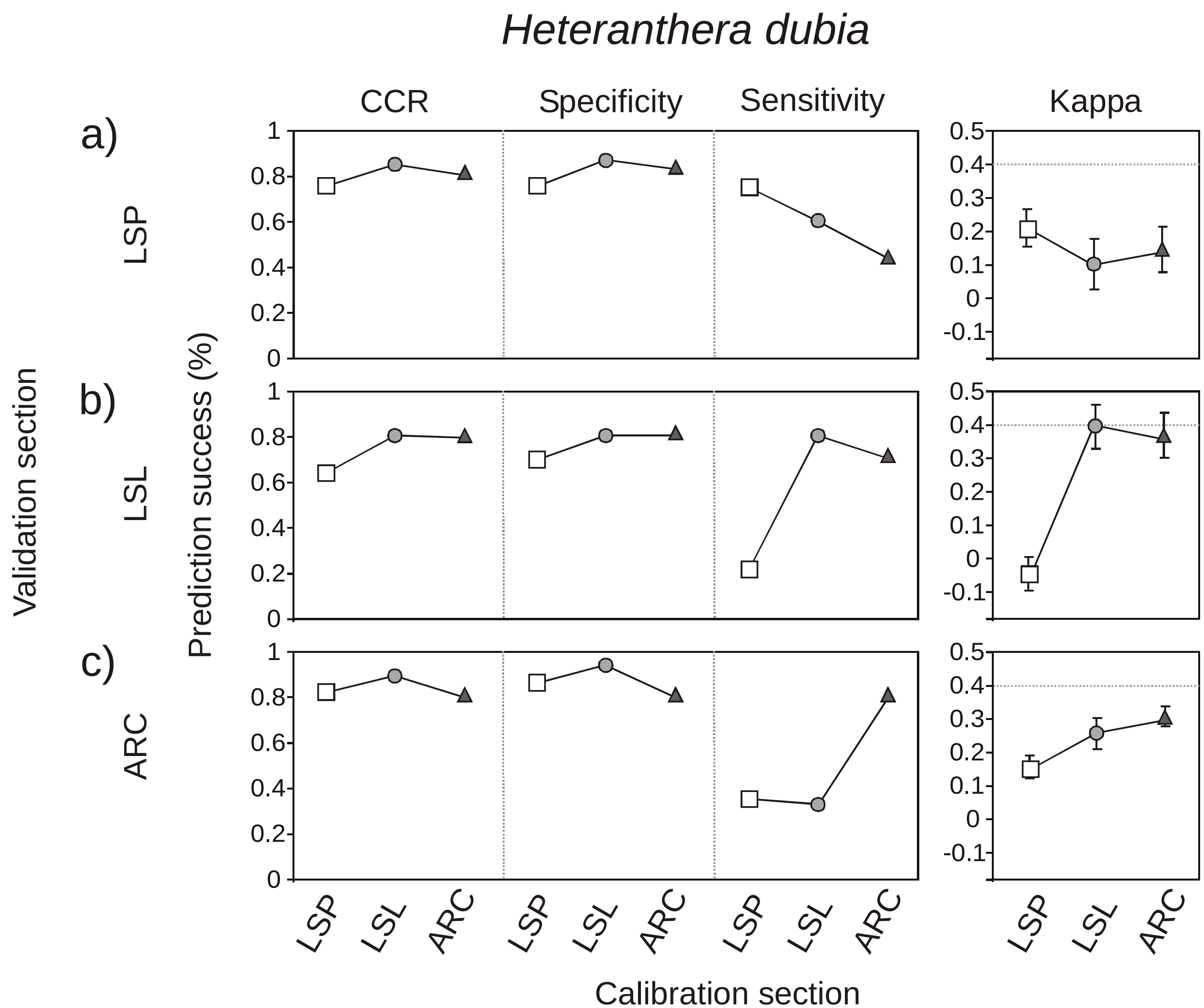


Figure 10. Comparison of models evaluation and transferability potential among St. Lawrence sections with cross-over field test for *Heteranthera dubia*; a) model accuracy (CCR, sensitivity and specificity) in validation trials on Lake St. Pierre data set from calibration models of Lake St. Pierre (□), Lake St. Louis (●) and Archipelagos (▲); b) model accuracy in validation trials on Lake St. Louis data set from calibration models of Lake St. Pierre, Lake St. Louis and Archipelagos c) model accuracy in validation trials on Archipelagos data set from calibration models of Lake St. Pierre, Lake St. Louis and Archipelagos.

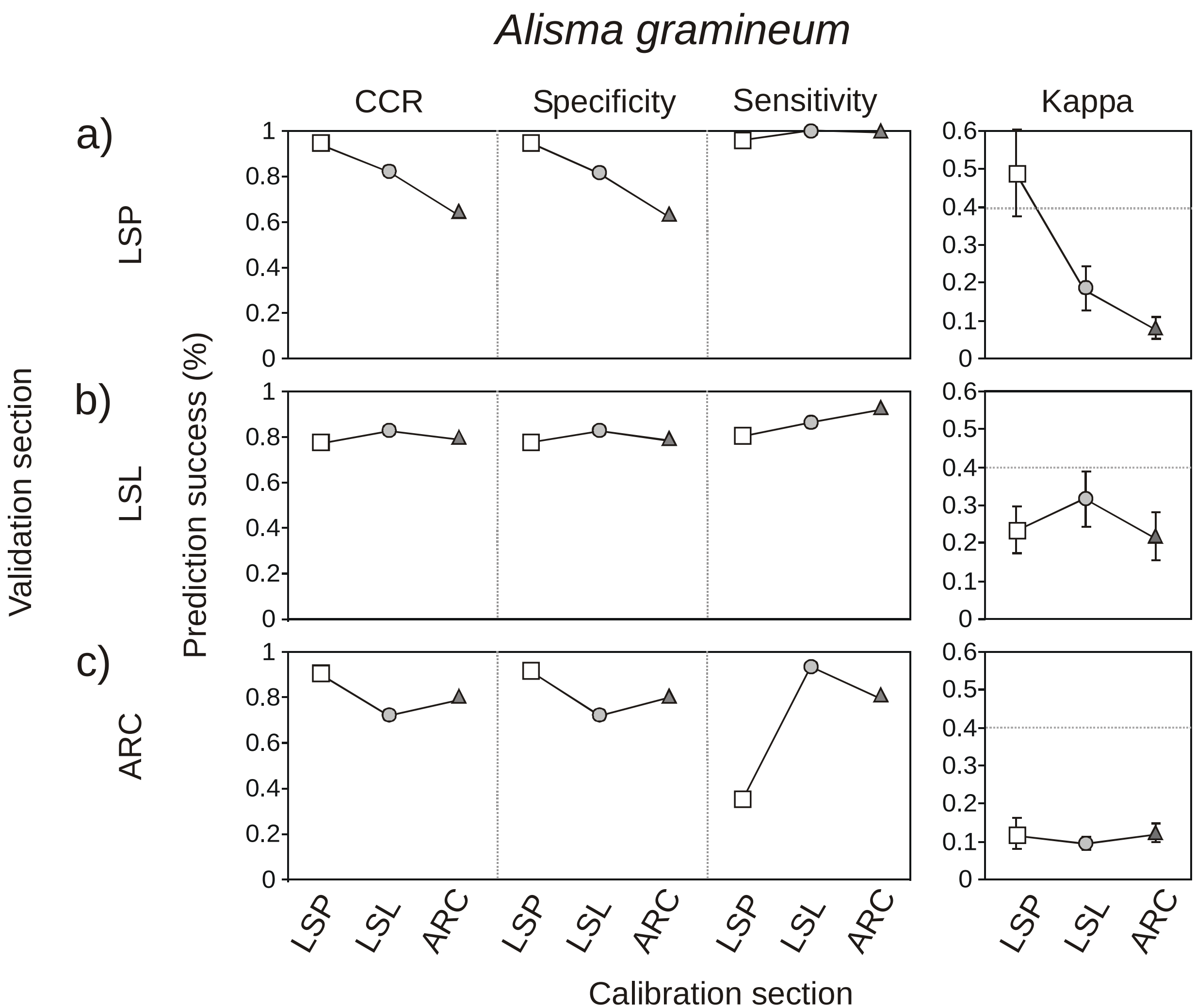


Figure 11. Comparison of models evaluation and transferability potential among St. Lawrence sections with cross-over field test for *Alisma gramineum*; a) model accuracy (CCR, sensitivity and specificity) in validation trials on Lake St. Pierre data set from calibration models of Lake St. Pierre (□), Lake St. Louis (●) and Archipelagos (▲); b) model accuracy in validation trials on Lake St. Louis data set from calibration models of Lake St. Pierre, Lake St. Louis and Archipelagos c) model accuracy in validation trials on Archipelagos data set from calibration models of Lake St. Pierre, Lake St. Louis and Archipelagos.

3.4 Macrophytes density models

With the use of Regression tree (RT), we build very simple model to predict submerged macrophyte density in the three study sections of the St. Lawrence River. RT models were very parsimonious and use only three environmental variables to predict submerged macrophytes densities: water depth (m), light penetration index and water velocity ($cm \cdot s^{-1}$) (figure 12).

In Lake St. Pierre, medium to high submerged macrophyte densities were associated with shallow water (< 3.0139 m) and very high to high densities were present in shallow water when water velocities are low (< 0.2459 $cm \cdot s^{-1}$). RT model explained 53.86% of the variation of the system (Proportionnal reduction in error (PRE) values on branch of the tree figure 12 a). In Lake St. Louis, medium to high macrophyte densities were associated with light penetration higher than 0.0437 but light penetration have to be lower than 0.1705 to observed high to very high macrophytes densities (figure 12 b). RT model in Lake St. Louis explained 52.38% of system variation. In St. Lawrence fluvial reach, medium to high macrophyte densities were associated with shallow water (< 3.63 m) (figure 12 c) and RT model explained 34.05 % of the variation of the system. SLFR model have only two densities classes compare to LSL and LSP model which have three densities classes.

In Lake St. Pierre and in the St. Lawrence fluvial reach, similar values of water depth (< 3.01 and < 3.63 m) seem to be associated with high submerged macrophytes densities (Figure 12). The index of light penetration was strongly correlated with water depth explaining the good transferability potential of the Lake St. Louis model, between sections despite the use of different environmental variables. Transferability of density models was relatively good between sections (Figure 13, Figure 14 and

Figure 15).

The concordance between predicted densities and observed densities in the LSP was good as illustrated on Figure 13a. Model transferability between LSL and LSP was also good (Figure 13b); high densities and low densities to absence were correctly predicted, however, model calibrated on LSL tend to overestimated the medium to high densities in the middle of the LSP. Model transferability between SLFR was less accurate (Figure 13c); low densities to absence class was correctly predicted, however SLFR model was limited to predict medium to high densities. This class seems to be correctly predicted, however, it is impossible to have information about very high densities because this class was absent or very scarce in the SLFR.

The concordance between predicted densities and observed densities in the LSL was good excepted at the right of the central island where densities were underestimated as illustrated on Figure 14b. Model transferability between LSP and LSL was also good (Figure 14a). The general density pattern was correctly predicted, however, model calibrated on LSP tend to overestimated high macrophytes densities in the extreme left of the Lake St. Louis and reproduce the same density underestimation at the right of the central island just as LSL model. Model transferability between SLFR was relatively good considering the mismatch between density classes (Figure 14c). The low density to absence class was correctly predicted. SLFR model tend to overestimate the macrophytes density at the extreme left of the central island as LSP model.

The concordance between predicted densities and observed densities in the SLFA was good as illustrated on Figure 13c. Model transferability between LSL and LSP was also good (Figure 13b); high densities and low densities to absence were correctly predicted, however, model calibrated on LSL tend to overestimated the medium to high densities in the middle of the LSP. Model transferability between SLFR was less accurate (Figure 13c); low densities to absence class was correctly predicted, however SLFR model was limited to predict medium to high densities. This class seems to be correctly predicted, however, it is impossible to have information about very high densities because this class was absent or very scarce in the SLFR.

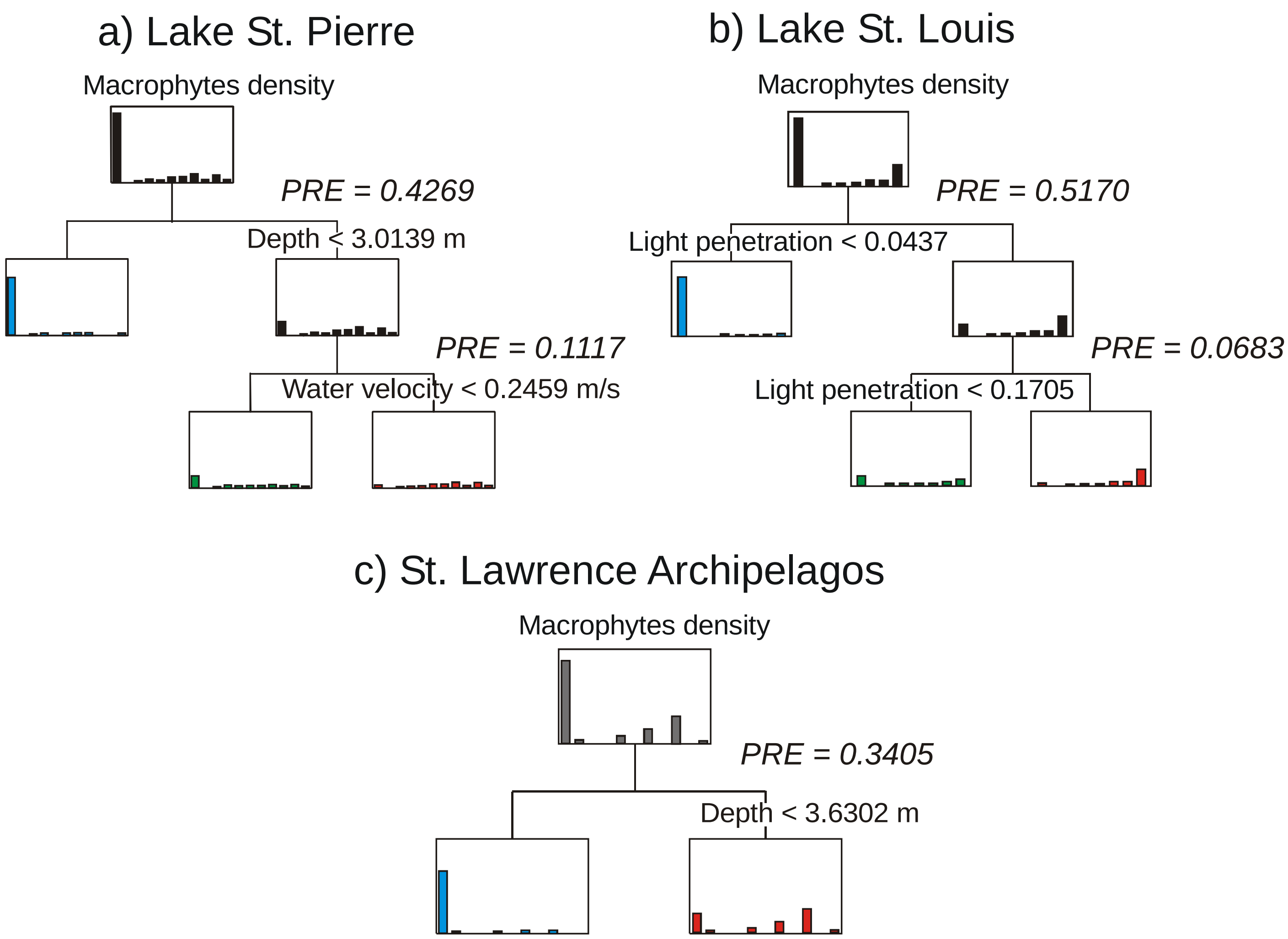


Figure 12. Regression tree models for predicting the density of submerged macrophytes in three sections of St. Lawrence River. Vertical bars represent the density frequency at each node. Splitting rules and PRE (proportional reduction in error) values are given on the branches of the trees.

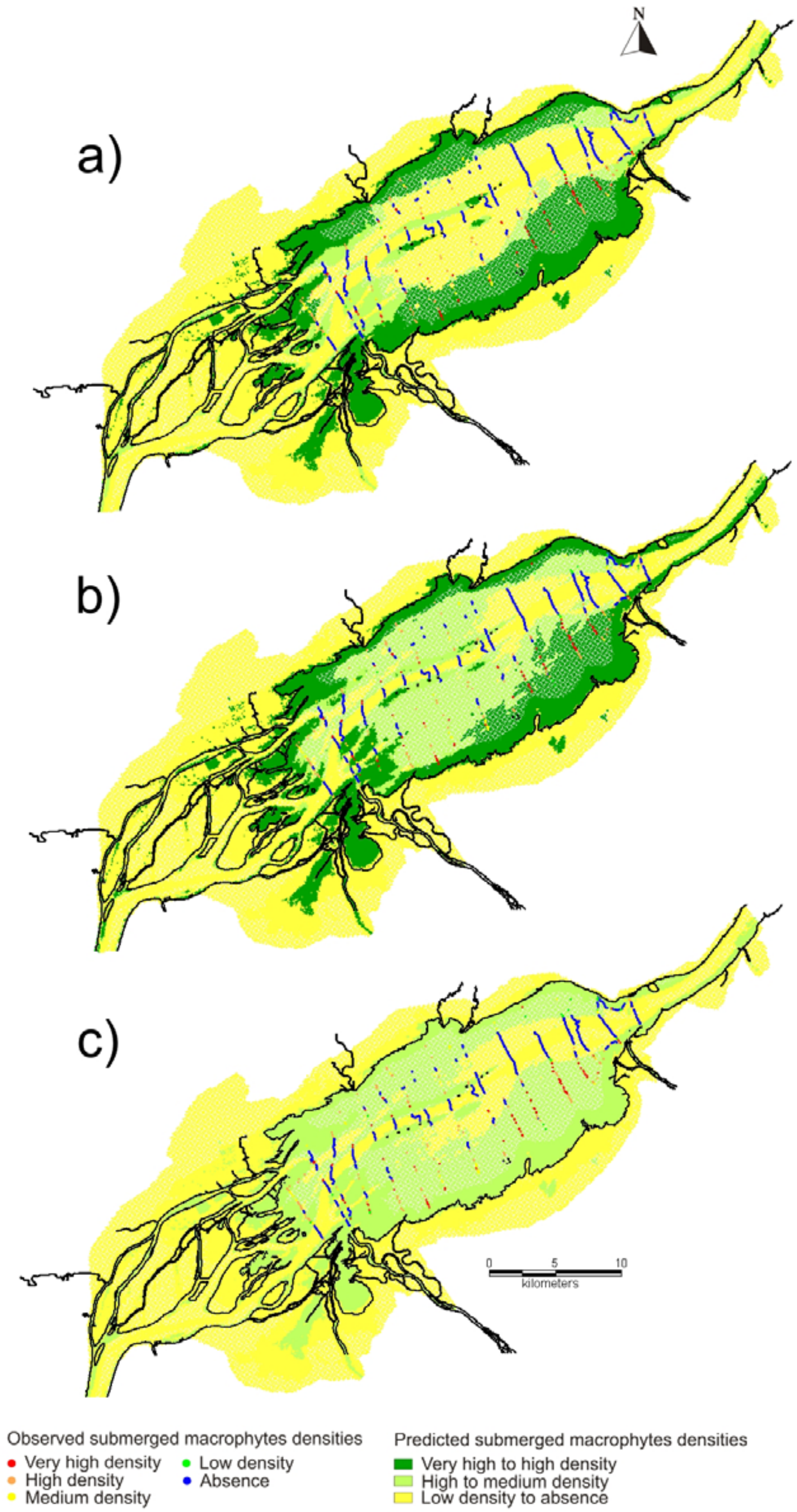


Figure 13. Transferability of regression trees models; a) model calibrated in Lake St. Pierre and applied on Lake St. Pierre data, b) model calibrated in Lake St. Louis applied on Lake St. Pierre data and c) model calibrated in the St. Lawrence fluvial reach and applied on Lake St. Pierre data.

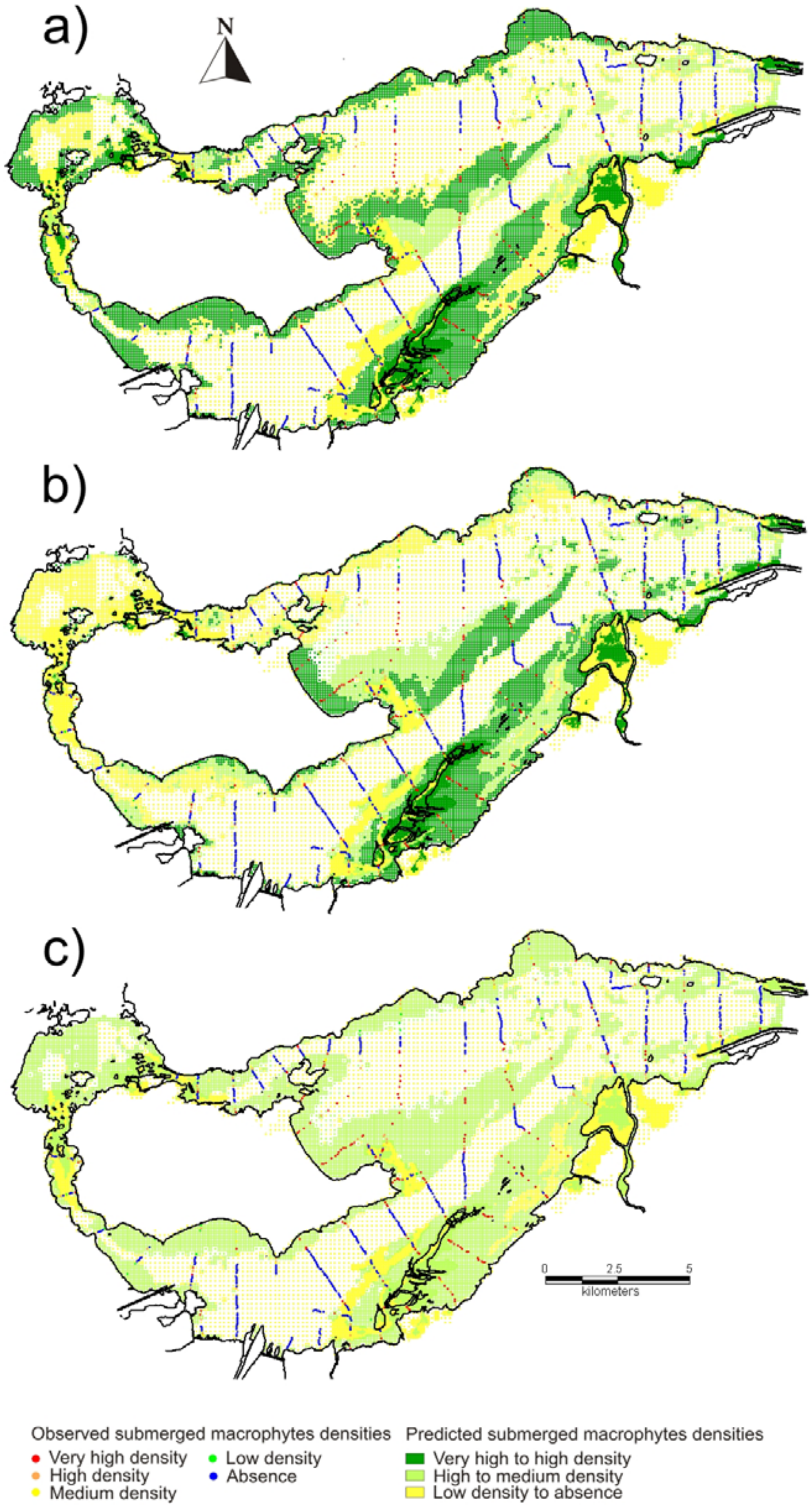


Figure 14. Transferability of regression trees models; a) model calibrated in Lake St. Pierre and applied on Lake St.Louis data, b) model calibrated in Lake St. Louis applied on Lake St. Louis data and c) model calibrated in the St. Lawrence fluvial reach and applied on Lake St. Louis data.

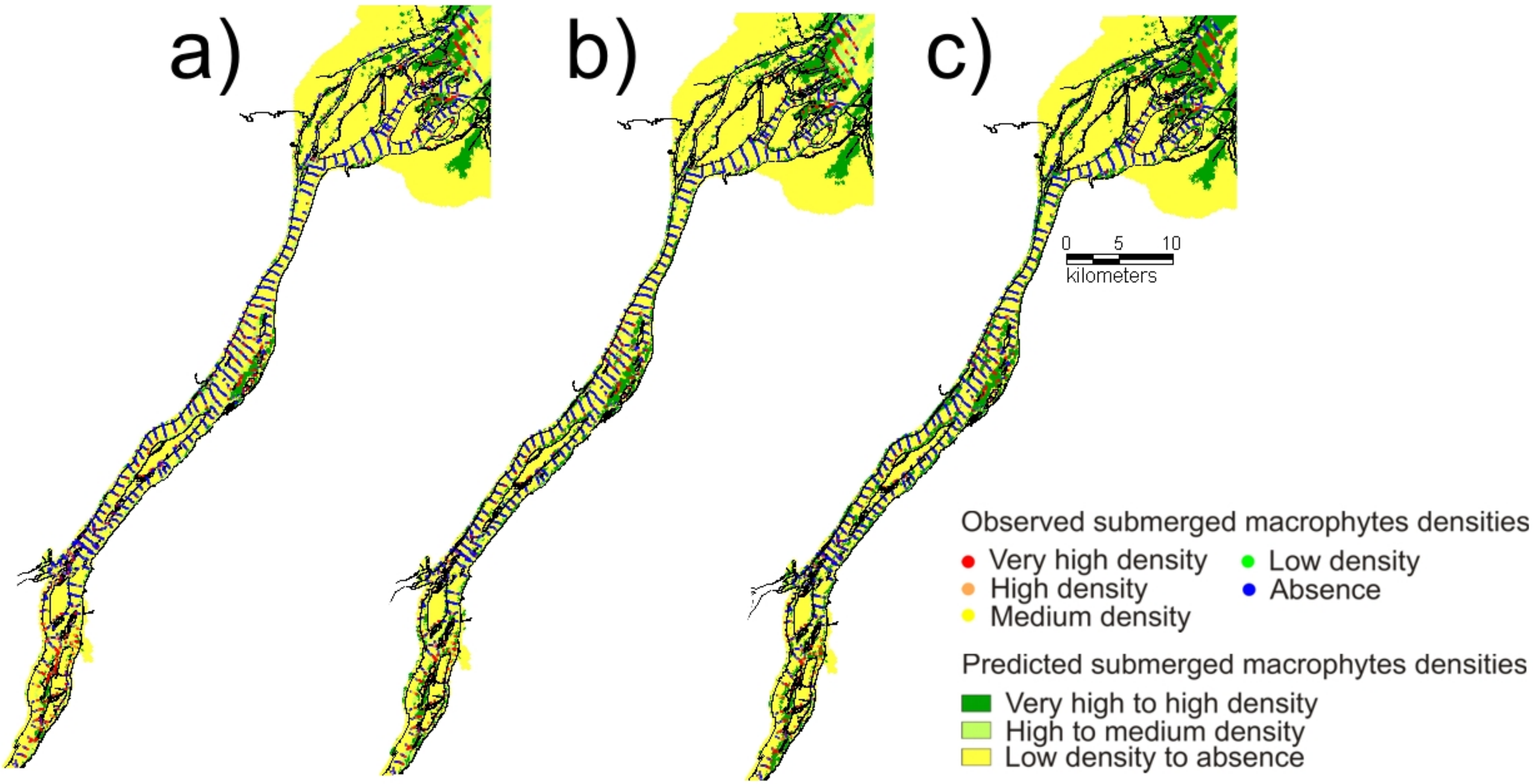


Figure 15. Transferability of regression trees models; a) model calibrated in Lake St. Pierre and applied on St. Lawrence fluvial reach data, b) model calibrated in Lake St. Louis applied on St. Lawrence fluvial reach data and c) model calibrated in the St. Lawrence fluvial reach and applied on St. Lawrence fluvial reach data.

4 DISCUSSION

4.1 LR and RT models: biological interpretation of variables

The main advantage of our study is that the relevant variables are simulated, allowing prediction on the entire domain and reducing field measurements of these variables. Moreover, theses variables can be simulated for different water regimes and discharges to have an overview of submerged macrophytes dynamics over years. The use of nine simulated environmental variables (index of light penetration, water velocity, waves effect (in spring with wind velocity of 17 and 35 $km \cdot h^{-1}$ and in autumn with wind velocity of 10 and 17 $km \cdot h^{-1}$) specific discharge, fine organic matter deposited on bottom and field slope) seem to significantly explain the distribution of the eight submerged macrophyte species.

In other studies, light penetration and water depth were identified as the most important factors explaining submerged macrophytes abundance and distribution (Barko et al. 1982; Scheffer et al. 1992; Rea et al. 1998; Van den Berg 2003). However, in our study, water depth and index of light penetration are strongly correlated, causing tolerance problems during modelling process. Theses variables can't be expressed simultaneously in the LR models. However, this doesn't cause major problem because light penetration index explained a higher proportion of system variation compare to water depth. *V. americana* seems to be tolerant to lower light penetration (figure 6 a). Indeed, this specie was found in large range of water depth and light penetration ranging from 1% to 84% of light intensity (Hudon et al. 2000).

Water movement has long been acknowledged as one of the prime factors regulating the growth and distribution of submerged macrophytes (Chambers et al. 1991; Schutten & Davy 2000). In our study, water velocity seems to strongly influence the occurrence of submerged macrophytes in the three study sections. Except for *Potamogeton pectinatus*, overall species were negatively associated with high water velocity. Our results were similar with those of Chambers et al. (1991) where submerged macrophytes were associated strongly with water velocity but not with specific discharge (or flow). These results may suggest that macrophytes responded to localized change in water velocity rather than river-wide change.

Waves have complex impact on submerged macrophytes that depends on season and intensity of wind velocity. Wave exposure seems important for St. Lawrence Archipelagos and for Lake St. Louis but wasn't seems to influence submerged macrophytes distribution in Lake St. Pierre. In Scheffer et al. (1992), *Potamogeton pectinatus* was also found in waves exposed zones. Apparently, positive effects correlated with exposure overrule negative effects associated with uprooting and stem break. One possible effect is that wave action partly removes the periphyton layer from plants. Periphyton can reduce the light level at the leave surface by as much as 80% and also reduce the diffusion between water and plant (Sand-Jensen and Borum 1984; Sand-Jensen and Revsbech 1987; Scheffer et al. 1992). It is also possibly associated with direct effect of wave action on propagules or other perennial structures.

Slope have been suggested to be a major factor controlling the physical characteristics of the sediments by affecting sediment stability, deposition of fine nutrient-rich materials and wave action in the littoral (Hakanson 1977; Duarte & Kalff 1986). However, in our study, this variable seems to have a weak influence on submerged macrophytes distribution. Slope was significant for *Vallisneria americana* (LSP) and for *Heteranthera dubia* (LSL). Maybe the slope influence was incorporated and has confounding effects with other variables like wave effects and fine material deposited on bottom.

4.2 LR and RT models: accuracy and evaluation

Logistic regression seems to be a useful tool to predict spatial distribution of submerged macrophyte species (Scheffer et al. 1992; Van den Berg et al. 1999; Van den Berg et al. 2003; Morin et al. *submit manuscript*). The overall model accuracy in calibration trials was good and varied slightly, from 76.4% to 95.3%, between species and sections. LR models were simple, involving few variables to explain species distribution. The use of optimal decision threshold (ODT) in predicted probabilities from LR results accounts for low specie prevalence (Fielding & Bell 1997) and can detect more accurately the predicted presence of specie. When applied on new data (Jacknife partition with 10% of the original data base), LR models accuracy remained good for almost all models and differ of what would be expected by chance alone (CCR; ranging from 79.0% to 98.2%, sensitivity; ranging from 50.0% to 100.0%, specificity; ranging from 78.2% to 93.1 and Cohen's Kappa (κ); ranging from 0.0682 to 0.7942).

Regression trees models had produced very parsimonious model to predict submerged macrophytes densities and had explained a large part of the system variation (PRE) in the three sections. Despite their simplicity, RT models seem to have a high concordance with the observed densities of submerged macrophytes (Figure 13, Figure 14 and

Figure 15).

4.3 Models transferability

An important and essential way to validate habitat selection models is to evaluate his transferability potential on other independent sections or rivers. This step in the model building routine is relatively new to evaluate model performance, and was mainly experienced on fish habitat models (see Freeman et al. 1997; Lamouroux et al. 1999; Mäki-Petäys et al 2002; Guay et al. 2003). Submerged macrophytes distributions differ between species and differ according to study sections (figure 4, figure 5 and Figure 6). Lake St. Pierre, St. Lawrence Archipelagos and Lake St. Louis were different in their environmental characteristics (table 1), and seems to represent a gradient of environmental conditions found in St. Lawrence River from Cornwall (Ontario) to Trois-Rivières (Québec). Despite the fact that LR models slightly differ between the three study sections, it is interesting to observe that models accuracy remains high when calibration models were applied on others validation sections (figure 7, figure 8, figure 9, figure 10 and figure 11). Our results indicate that it may be possible to use LR models build on three different sections of St. Lawrence River to assess submerged macrophyte distribution pattern on another independent section (figure 7, figure 8, figure 9, figure 10 and figure 11). Theses results suggest that models were robust and the transferability potential was high among the three study sections. Globally, models developed on Lake St. Pierre were less transferable on St. Lawrence Archipelagos than on Lake St. Louis and vice versa. Models build on Lake St. Louis seems to be more transferable in both other sections, ie. Models were less variables and performance measures were relatively high (figure 7, figure 8, figure 9, figure 10 and figure 11).

4.4 Further developments

It would be interesting to integrate and simulate water temperature in the entire domain. This variable seems to have an influence on submerged macrophytes development and growth (Spencer et al. 2000). The direct importance of temperature for the growth of submerged macrophytes is supported by experimental work (Barko & Smart 1981; Barko et al. 1982; Barko et al. 1986; Spencer et al. 2000). This information could refine: 1) the timing when it would be useful to integrate submerged macrophyte influence on simulated water velocity in the St. Lawrence River and 2) the interactions with submerged macrophytes and other biotic components (fish and waterfowl production).

As several species, are influenced by current conditions that are typical of spring and fall, it is probable that the occurrence of ice during winter, which considerably modifies the flow pattern, will influence the accumulation of fine particles. These conditions might have an effect on plant distribution and should eventually be considered.

CONCLUSION

- 2D hydrodynamics simulated variables, logistic regression (LR) and regression trees (RT) models can be useful tools to predict the probability of presence and the density of submerged macrophyte species in the study portion of the St. Lawrence River.

- The nine simulated variables used to model submerged macrophytes distribution and density seems associated differently with species according to sections.

- Models produced in this study were simple, accurate and transferable between three different sections of the St. Lawrence River. Model transferability vary according to species.

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