MODELING WETLAND PLANT COMMUNITY RESPONSE TO ASSESS WATER-LEVEL REGULATION SCENARIOS IN THE LAKE ONTARIO – ST. LAWRENCE RIVER BASIN

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Abstract. The International Joint Commission has recently completed a five-year study (2000–2005) to review the operation of structures controlling the flows and levels of the Lake Ontario – St. Lawrence River system. In addition to addressing the multitude of stakeholder interests, the regulation plan review also considers environmental sustainability and integrity of wetlands and various ecosystem components. The present paper outlines the general approach, scientific methodology and applied management considerations of studies quantifying the relationships between hydrology and wetland plant assemblages (% occurrence, surface area) in Lake Ontario and the Upper and Lower St. Lawrence River. Although similar study designs were used across the study region, different methodologies were required that were specifically adapted to suit the important regional differences between the lake and river systems, range in water-level variations, and confounding factors (geomorphic types, exposure, sediment characteristics, downstream gradient of water quality, origin of water masses in the Lower River). Performance indicators (metrics), such as total area of wetland in meadow marsh vegetation type, that link wetland response to water levels will be used to assess the effects of different regulation plans under current and future (climate change) water-supply scenarios.

Keywords: Lake Ontario, plant communities, St. Lawrence River, water level regulation, wetlands

1. Introduction

Water-level fluctuations are a natural phenomenon in the Great Lakes-St. Lawrence River system due to climatic variability (Magnuson et al., 1997; Baedke and Thompson, 2000). The biological communities have, by necessity, evolved to adapt to a range of water depths and water-level changes that occur on several time scales, ranging from wind-driven tides or seiches that can occur several times daily, to seasonal changes each year, to longer episodes (Nilsson and Keddy, 1988; Wilcox, 1995, 2004; Bunn and Arthington, 2002).

The biological effects of water-level fluctuations in a lake or river system are most important in shallow water areas, where even small changes in water levels can...
result in the conversion of an aquatic environment to an environment in which sediments are exposed to the air, or vice versa. The localized effects of this variability are most evident in the relatively immobile plant communities that make up wetlands. The strong link between climate, hydrologic regime and composition and diversity of wetland plant communities has been well-documented for both lake (Wilcox and Meeker, 1991, 1995; Hill et al., 1998) and river (Toner and Keddy, 1997; Ward et al., 1999; Hudon, 1997, 2004, 2005) systems. Field data correlating vegetation to changes in water depth through time allow modeling and prediction of the effects of different water-level-fluctuation patterns on wetlands. Since wetlands represent major habitats for fish, water birds, and mammals, maintenance of diversified (in space and time) and well-connected wetlands also bring inherent benefits for aquatic fauna. The definition of sound, yet applicable environmental objectives is the first step towards sustainable management of natural resources.

Alteration of natural water-level cycles through regulation are known to affect wetland community dynamics, productivity, and function in general (Nilsson and Svedmark, 2002; Keddy, 2002). Although environmental effects of regulation are well documented and raise important concerns, only a small number of studies integrating environmental indices into regulation plans can be found in the published literature (Prowse and Conly, 1996; Millburn et al., 1999; Marttunen et al., 2001; Hellsten et al., 2002). Since unaltered flow conditions represent the most desirable hydrological regime to sustain riparian systems (Petts, 1984; Wilcox and Meeker, 1991; Poff et al., 1997), environmentally-conscious water-level management requires knowledge of how much regulated outflow can deviate from natural conditions without impairing wetland sustainability (Hill et al., 1998; IJC, 1999).

The International Joint Commission (IJC) has recently completed a five-year study (2000–2005) to review the operation of structures controlling the flows and levels of the Lake Ontario – St. Lawrence River system. In addition to addressing the multitude of stakeholder interests, the regulation plan review also includes environmental sustainability, with an emphasis on wetlands. Understanding and quantifying the linkages between hydrology and wetlands in both Lake Ontario and the St. Lawrence River, and assessing the historical changes in wetland surface area and type lend support to the identification of water-level-regulation plans that respect wetland integrity and sustainability. However, since the constraints imposed on wetland habitats by level and flow regulation differ markedly between the lake and river systems, the general study approach needed to be adapted to each unique individual setting. This paper describes the scientific methodologies developed to quantify the response of wetlands to hydrology while accounting for regional differences in hydrology and confounding factors.

In addition to the assessment of regulation impacts on wetlands, results of the studies described in the present paper will serve as input to models used in evaluating
regulation plans proposed by other interest groups. These models also include reference to seasonality of water-level changes as required by fish and wildlife, to the amplitude of water-level fluctuations that result in habitat development, and to the frequency of high and low water-level/flow events that determine cycling of habitat changes and result in habitat diversity. In the IJC Study, such quantitative relationships (metrics) linking various hydrologic to environmental and socio-economic characteristics were designated as “Performance Indicators” (PI). These PI allowed to compare the performance of different alternative regulation plans (in terms of relative gains or losses) with the current regulation plan.

Since releases of water from Lake Ontario and the Upper St. Lawrence River largely dictate conditions below the dam on the Lower St. Lawrence River, regulation-plan review must also account for the regional interdependency to ensure that any regulation-plan changes would not be detrimental to any region. Therefore, lake and river wetland study teams coordinated efforts in their approach to generate comparable results and compatible regulation options. The present study provides an example of the challenges involved in linking environmental objectives, scientific data acquisition and applied management considerations across a large and diversified watershed.

2. General Approach for Wetland Studies

Members of the Environment Technical Working Group (hereafter designated as ETWG) of the IJC study agreed upon the following working hypothesis and environmental objectives, defining the framework of the environmental studies to be carried out by the group members.

2.1. Working Hypothesis

Hydrologic conditions affect the distribution, species composition, and biomass of emergent wetland plant assemblages.

2.2. Environmental Objectives

The overall objective of the environmental studies was to ensure that all types of native habitats (floodplain, forested and shrub 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) were represented in sufficient abundance (surface area) to sustain critical biological populations and communities.

A corollary objective was to maintain hydraulic and spatial connectivity of habitats to ensure that fish and wildlife have access, temporally and spatially, to a sufficient area of all habitat types required to complete their life cycles. Specific
studies were conducted to evaluate amphibian, fish, avian, and muskrat habitat availability.

These principles outline the linkage between hydrology and biological components of the lake and river ecosystems, which may manifest themselves either directly (effect of hydrology on plant and animal species, populations, communities) or indirectly (effect of hydrology on the availability and access to suitable habitats for fauna). Wetlands are an ETWG priority due to their intrinsically important ecosystem components and representation of habitats that support a productive and diverse fauna. Environmental objectives also acknowledged the hierarchical organization of ecosystem components (species, populations, guilds, communities), which may be affected by water-level/flow regimes at different spatial and temporal scales.

2.3. GEOGRAPHICAL SCOPE

The area covered by the Lake Ontario – St. Lawrence River water-level study encompasses four distinct regions (Figure 1), which can be distinguished on the basis of their morphology, hydrologic regimes, and degree of alteration from human interventions, all of which affect wetlands (Table I).

Lake Ontario (region I) is by far the largest of the four regions, extending from Hamilton (to the west) to Kingston, Ontario (to the east). The Upper St. Lawrence River (Kingston to Iroquois dam) was included in this region since it is subjected to a hydrologic regime in phase with that of the lake. The next region downstream (region II) encompasses a 71-km stretch of the river that has been permanently flooded since the beginning of Moses Saunders Dam operations at Cornwall in 1959. The lake that has formed upstream from the dam is now referred to as Lake St. Lawrence and is the region most affected by regulation, since its water levels fluctuate broadly in the short term (hourly, daily, and weekly) according to dam operations. Such high variability in levels contrasts sharply with the downstream Lake St. Francis (region III), where water levels have been largely stabilized since the beginning of the operation of the Beauharnois dam. Finally, the Lower St. Lawrence River (region IV) extends 151 km between Lake St. Louis and the outlet of Lake Saint-Pierre. In addition to the regulated outflow of Lake Ontario, the hydrologic regime of this region is influenced by the Ottawa River and several other largely unregulated tributaries, which increase the seasonal water-level range to >2 m in the downstream direction (Table I).

Wetlands studies described here largely focused on the Lake Ontario – Upper River (region I) and on the Lower St. Lawrence River (region IV), since these were the largest and were considered to have been subjected to less severe hydrologic alteration than the two middle regions. However, complementary information on Lake St. Lawrence wetlands was gathered and analyzed to examine some of the impacts on wetlands and fish habitat in the Akwesasne – St. Regis area (region II). In addition to hydrologic alterations, the four regions are also affected by different
Figure 1. Location of wetland field study sites in the Lake Ontario and St. Lawrence River system. Major segments of the study area comprise (moving downstream) Lake Ontario and the Upper St. Lawrence River (Kingston to Iroquois dam, region I), Lake St. Lawrence (Iroquois dam to Cornwall, Moses-Saunders dam, region II), Lake St. Francis (Moses-Saunders dam to Beauharnois dam, region III), and Lower St. Lawrence River (Beauharnois dam to Trois-Rivières, region IV). The geomorphic type of each wetland study site is indicated in the legend.
### TABLE I


<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Lake Ontario and Upper Lawrence River (region I)</th>
<th>Lake St. Lawrence (region II)</th>
<th>Lake St. Francis (region III)</th>
<th>Lower St. Lawrence (region IV)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geographical limits</td>
<td>Hamilton to Iroquois dam (above dam)</td>
<td>Iroquois dam (below dam)</td>
<td>Moses-Saunders dam (above dam)</td>
<td>Beauharnois dam (below dam)</td>
</tr>
<tr>
<td></td>
<td>412</td>
<td>71</td>
<td>74</td>
<td>to the outlet of Lake Saint-Pierre</td>
</tr>
<tr>
<td>Linear distance (km)</td>
<td>&lt;1 m, seasonal variations</td>
<td>Annual range was reduced</td>
<td>Annual range was reduced</td>
<td>1 m, range increases</td>
</tr>
<tr>
<td></td>
<td>412</td>
<td>from ~2 to 1.2 m, with high</td>
<td>from ~1.5 to 0.3 m, largely</td>
<td>downstream due to seasonal</td>
</tr>
<tr>
<td></td>
<td></td>
<td>short-term (daily peaking,</td>
<td>stabilized</td>
<td>tributary discharge.</td>
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<tr>
<td></td>
<td></td>
<td>weekly ponding) variations</td>
<td></td>
<td>Regulation of discharge</td>
</tr>
<tr>
<td></td>
<td></td>
<td>owing to dam operation</td>
<td></td>
<td>decreases spring levels to</td>
</tr>
<tr>
<td>Major structural modifications to shorelines and regional morphology</td>
<td>Shoreline impingement, erosion and armouring</td>
<td>Ancient Galop, Plat and Long</td>
<td>Erosion (near dam); &gt;80% of</td>
<td>Channel excavation and</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sault Rapids were flooded by</td>
<td>river flow was redirected from</td>
<td>river infilling alter flow</td>
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<tr>
<td></td>
<td></td>
<td>&gt;20 m following impoundment</td>
<td>Coteau, Split Rock and Les</td>
<td>and sedimentation regimes;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>of Lake St. Lawrence for</td>
<td>Cedres Rapids through</td>
<td>shoreline impingement</td>
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<tr>
<td></td>
<td></td>
<td>hydroelectric production,</td>
<td>Beauharnois Canal and</td>
<td>erosion and armouring</td>
</tr>
<tr>
<td></td>
<td></td>
<td>changing rapids into lake</td>
<td>dam</td>
<td></td>
</tr>
</tbody>
</table>

(Continued on next page)
<table>
<thead>
<tr>
<th>Other anthropogenic modification affecting wetlands</th>
<th>Lake Ontario and Upper Lawrence River (region I)</th>
<th>Lake St. Lawrence (region II)</th>
<th>Lake St. Francis (region III)</th>
<th>Lower St. Lawrence (region IV)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total wetland surface (km²)</td>
<td>240</td>
<td>11</td>
<td>25</td>
<td>180</td>
</tr>
<tr>
<td>Wetlands geomorphic types</td>
<td>Open embayment, protected embayment, barrier beach drowned river mouth</td>
<td>Open embayment, protected embayment, barrier beach drowned river mouth, shallow and deep shoals (flooded islands)</td>
<td>Island channel (upstream), exposed shoreline (downstream), sheltered embayment, shallow and deep shoals</td>
<td>Exposed shoreline, sheltered embayment island channel</td>
</tr>
<tr>
<td>General wetlands characteristics</td>
<td>Wetland development varies with slope and exposure, frequent dominance by cattail</td>
<td>Shift from a riverine to a lacustrine marsh system, erosion areas and mud flats common near dam</td>
<td>Limited emergent marshes due to abrupt shoreline transition; shrubby swamps and erosion areas common</td>
<td>Wetland development varies with slope and exposure; vulnerability to exotic species</td>
</tr>
</tbody>
</table>

types and degrees of anthropogenic alterations and degradation of water quality, which act as confounding factors since they also affect wetland surface area and general characteristics (Table I). Such regional differences needed to be accounted for in wetland studies carried out across the basin.

2.4. Hydrologic Regime under Current and Unregulated Conditions

Lake Ontario water levels and outflow to the St. Lawrence River at Cornwall–Massena have been regulated since 1963 using Plan 1958D (with deviations), under the conditions and criteria set out in the “Orders of approval for the regulation of Lake Ontario” of the International Joint Commission (Carpentier, 2003). Over the past century, climatic variability subjected Lake Ontario and the St. Lawrence River to alternating periods of low (1930s, the mid-1960s and the late 1990s) and high (1970s and mid-1980s) water supply. In addition to the effects of regulation, water level conditions have been increasingly modified over the last century by a variety of other human interventions, such as shoreline alteration, channel excavation and ice management. In order to isolate the impact of regulation, water level variations were simulated for the 1900–2000 interval using historical water supplies while maintaining the current channel configuration, structures and ice management regime. These simulated levels allowed us to compare water-level variations under unregulated (grey lines) and the present regulation plan (plan 1958D with deviations, black lines) for Lake Ontario and Lower St. Lawrence River at Sorel (Figure 2).

In Lake Ontario, regulation resulted in stabilization of long-term mean levels, elimination of decadal-scale periods of high levels and reduction of the overall range from >2 m to about 1 m (Figure 2, see also Wilcox and Whillans, 1999). More specifically, regulation reduced the amplitude and frequency of high water-level episodes to control flooding. In the downstream reaches of the Lower St. Lawrence River (Sorel), the effects of regulation were perceptible in the reduction of extreme high and low water level episodes in Sorel (Figure 2), but appeared dampened by the added influence of the Ottawa River and other tributaries. However, the seemingly small effects of regulation derived from simulated levels (Figure 2) markedly contrast with recorded level values (not shown), which show a 0.7 m reduction in overall range between 1912 and 1994 (Hudon, 1997). Such difference between simulated and recorded levels points out to the cumulative effects of regulation with other anthropogenic factors such as channel excavation, shoreline alteration and control of ice jams.

At the watershed scale, although water-level variations from year to year are largely controlled by climatic conditions (Magnuson et al., 1997; Baedke and Thompson, 2000), regulation has modulated the timing and magnitude of levels and flow to suit the needs of the various interest groups, upstream and downstream of Moses-Saunders dam (IJC, 1999). The reduction in the range of Lake Ontario levels was achieved by increasing river discharge during periods of high water supply.
Figure 2. Comparison of water-level variations (1900–2000) in Lake Ontario (top panel) and in Lower St. Lawrence River at Sorel (bottom panel) simulated at a quarter-monthly time step for unregulated (grey line) and current regulation conditions (black lines indicate annual mean and range for Plan 1958D with deviations). All calculations are based on the historic sequence of water supplies to the basin while maintaining constant and using the structures presently in place, the present channel sizes and configurations and the present ice management regime. Water levels (m) are referenced to the International Great Lakes Datum of 1985 (IGLD85); note the difference in vertical scale between graphs. Data source: Environment Canada – Great Lakes – St. Lawrence Regulation Office, Ontario Region, Cornwall, unpublished data.
and by decreasing discharge to store water in the lake during periods of low water supply (Carpentier, 2003), thereby modifying the seasonal timing and increasing the short-term variability of river discharge and levels. This type of regulation induces major differences in the temporal scale of hydrological alterations for Lake Ontario (multi-decadal, long-term) and Lower St. Lawrence River (inter-annual, seasonal, short-term), which needed to be accounted for in the regional wetland studies.

2.5. General Approach and Study Design

The different effects of regulation in the upstream and downstream reaches of the study area prompted our use of different, regionally-adapted methodologies, albeit based on a common approach, to assess linkages between hydrology and wetlands in the Lake Ontario – Upper River and Lower St. Lawrence River regions. In both regions, historical variations in wetland surface area and community types were assessed from aerial photographs and remote sensing images. Several field study sites were selected in which plant surveys were conducted over a range of elevations and hydrologic conditions, serving as the basis for the elaboration of quantitative models linking wetlands in each region to hydrology, while accounting for potentially confounding effects (exposure, geomorphic type, and other factors). These models allowed us to generalize the study findings over broad geographical areas, after independent validation from the aerial photographs, remote sensing images or additional data. Finally, performance indicators (metrics) were developed to assess the response of wetlands to various regulation plans, applied to a 101-yr time series (1900–2000) using either historical, stochastic (wet and dry periods), or climate-change water-supply scenarios. The following two sections describe how the common approach was adapted to suit specific conditions in the Lake Ontario – Upper St. Lawrence River (Section 3) and in the Lower St. Lawrence River (Section 4) region. The technical solutions used at each step are contrasted between regions in Table II.

3. Lake Ontario – Upper River Wetland Studies

3.1. Data Acquisition for Model Development

3.1.1. Selection of Field Study Sites

Thirty-two wetlands were studied in Lake Ontario and the Upper St. Lawrence River. Twenty-five of the study sites are located along the Lake Ontario shoreline, and the remaining seven sites are in the Upper St. Lawrence River (Figure 1). Site selection was based on geomorphic type, wetland distribution, shoreline reaches for which topographic and bathymetric data were available or would be collected, and
| TABLE II  
Comparison of technical approaches taken in Lake Ontario and Lower St. Lawrence River wetland studies |

<table>
<thead>
<tr>
<th>Study Area</th>
<th>Lake Ontario and Upper St. Lawrence River (region I)</th>
<th>Lower St. Lawrence River (region IV)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Selection of study sites</strong></td>
<td>32 sites (16 US+16 CDN), 8 sites ×4 categories (barrier beach, drowned river mouth, open embayment, and protected embayment)</td>
<td>13 sites, upstream-downstream and transversal gradients, fluvial lakes and corridors, exposed and sheltered sites.</td>
</tr>
</tbody>
</table>
| **Inventory of remote sensing and aerial photograph** | Resolution: 1:4,800 to 1:40,000  
| **Field surveys of plant assemblages** | 7 transects per plot, 2 plots per site, transect at specific elevations parallel to the shoreline  
Elevation range: about Lake Ontario chart datum +1.5 m above chart datum  
Sampling frequency: Late summer, one season (2003)  
Plant measurement: Percent cover (× classes) of plant species | 1 transect per site, perpendicular to the shoreline  
Elevation range: about +1 m above to −1 m below chart datum level  
Sampling frequency: Late summer, four consecutive seasons (1999–2002)  
Plant measurement: Relative abundance of each plant species = Percent cover (7 class) × mean height in each of the 630 quadrats |
| **Physical characterization of study sites** | Hydrology: Sampling along elevation contours corresponding to areas last flooded 30, 10, 5 and 1 year ago and last dewatered 2, 4, 38 and 68 years ago | Hydrology: 54 variables (see Section 4.1.5)  
Climate: Mean daily air temperature, precipitations, number of sunshine, drought index  
Environment: fetch from the NE and SW, water mass, water clarity  
Sediment: % sand, % clay, % loam, total P, organic N, % organic contents, pH and grain size distribution [mean, median and standard deviation] |
| **Identification of plant assemblages** | Categories identified on aerial photographs and ground truthing | Cluster analyses based on relative abundance of taxa sample field quadrats |
| **Linkage between plant assemblages and hydrology** | Non-metric Multi-Dimensional Scaling | Canonical Correspondence Analysis Classification and Regression Tree (CART) analysis |
minimization of the influences of other human impacts. Each of the 32 study sites was classified as one of four geomorphic wetland types (barrier beach, drowned river mouth, open embayment, and protected embayment). Although more than one wetland type can occur within a site, the predominant geomorphic type was chosen. The barrier-beach wetlands are protected from wave attack by the presence of a beach that is longitudinal with respect to the lakeshore. The drowned-river-mouth wetlands are situated at the mouth of a tributary flowing into Lake Ontario (or the Upper St. Lawrence River) and are influenced by both the hydrology of the lake and the tributary. Lacking a shielding geomorphic structure, the open embayments are unprotected from wave action. Conversely, the orientation of the protected embayments away from the lake or river provides protection from wave action.

3.1.2. Aerial Photographs and Vegetation Classification
An aerial photograph time series (1938 to 2001) at approximately decadal intervals was used to assess historical changes in wetland vegetation types at the 32 study sites. The photographs varied in type (black and white, color, and color infrared) and scale (between 1:4,800 and 1:40,000), and occurred within the growing season (between April and September) (Table II).

The Ecological Land Classification (ELC) system for Southern Ontario was used to label vegetation types in this study (Lee et al., 1998). This layered classification system contains six nested levels that are organized by spatial scale from large regions down to specific vegetation types, each sub-level further defining the area being studied. Specific class rules for the study were also developed to standardize the classification process and ensure consistency.

3.1.3. Identification of Current Major Wetland Plant Assemblages
Current vegetation patterns within each of the 32 wetlands were identified by photointerpretation and ground-truthing. The resulting vegetation maps were ground-truthed, delineated, digitized, and processed using a geographic information system (GIS) to identify relationships between vegetation types and water levels. Four of the identified vegetation categories were analyzed in detail: meadow marsh (e.g., Carex), cattail (Typha), mixed emergent (e.g., Sagittaria), and floating leaf (e.g., Nymphaea). Area and percent-vegetated cover were calculated for each vegetation category, and the data were summarized for analysis by site and geomorphic type. These plant assemblages were then compared with vegetation survey data from transects (see next section), which were analyzed using summary statistics and ordination/classification procedures.

3.1.4. Field Surveys of Plant Assemblages
Plant community data were collected in July 2003 by sampling along topographic contours that represented different flooding/dewatering histories associated with past lake-level changes. Two transects perpendicular to the shore were established
50 m apart at each of two randomly selected locations along the perimeter of each study wetland. The topographic cross-section along each of these perpendicular transects was surveyed using a laser transit. Since permanent bench marks were generally not available near study sites, the current lake level was used to establish altitudes. Lake level at the recording station nearest the study site was obtained by telephone from the National Oceanographic and Atmospheric Administration or Canadian Hydrographic Service on the morning of the survey. Specific elevations with ecological significance based on the past yearly peak water-level history were located along each transect and were used for vegetation sampling. Since the existing wetland vegetation in the lake developed in response to the history of high lake levels and low lake levels, the selected elevations reflect lake-level history. The elevations (International Great Lakes Datum 1985) used for sampling transects A-G are as follows: A) 75.60 m, last flooded 30 years ago; B) 75.45 m, last flooded 10 years ago; C) 75.25 m, last flooded 5 years ago; D) 75.0 m, last flooded 1 year ago and last dewatered during growing season 2 years ago (variable flooding and dewatering over past 3 years; E) 74.85 m, last dewatered during growing season 4 years ago; F) 74.7 m, last dewatered during growing season 38 years ago; G) 74.25 m, last dewatered during growing season 68 years ago (Table III).

Sampling was conducted in ten 0.5 × 1.0 m quadrats placed randomly along transects that followed the contours for each specific elevation chosen (parallel to the shoreline) and running between the two transects surveyed in perpendicular to the shoreline. The quadrats were placed on the landward side of the contour transect lines. Such placement allowed the quadrats to adhere to the water-level history of each elevation according to the sampling design. In each quadrat, the plant species present were identified, and percent cover estimations were made by visual inspection. Substrate types were also noted and recorded at each quadrat location. In general, the plant communities at elevations that had not been flooded for five or more years (transects A, B, and C) were dominated by sedges and grasses, and those that had not been dewatered for 4–39 years (transects E and F) were dominated by cattails. The intervening transect D that was intermittently flooded and dewatered over a five-year span contained a combination of sedges, grasses, cattails, and other emergent species. Plant communities that had not been dewatered in the growing season for 40 or more years (transect G) were dominated by floating and submersed species (Table III).

3.1.5. Physical Characterization of Study Sites
Bathymetric/topographic data were compiled for each study site; sources included a combination of existing flood damage reduction maps and airborne and boat-based sounding techniques. Elevation point data were seamed together, and detailed study site elevation maps were created within a GIS model framework. In addition, soils were sampled along each of the vegetation survey transects and analyzed for bulk density and percent organic matter.
### TABLE III
Summary of hydrological variables defining wetland plant assemblages in Lake Ontario and Upper St. Lawrence River (region I, determined from pre-defined elevations sampled in the field) and the Lower St. Lawrence River (region IV, variables and thresholds identified from statistical analysis of field data)

<table>
<thead>
<tr>
<th>Wetland Plant Assemblages</th>
<th>Lake Ontario and Upper St. Lawrence River (region I)</th>
<th>Lower St. Lawrence River (region IV)</th>
</tr>
</thead>
</table>
| Meadow marshes and mudflats | - 75.60 m, last flooded 30 years ago;  
                                - 75.45 m, last flooded 10 years ago;  
                                - 75.25 m, last flooded 5 years ago;  | - Elevation above mean water level in July of the current growing season  
                                | - Mean depth during the previous growing season  
                                | - Elevation above or depth below the mean water level in July of the current growing season  
                                | - Number of days flooded over the previous growing season  
                                | - Depth below the mean water level in July of the current growing season  
                                | - Number of days flooded over the previous growing season  
                                | - Standard deviation of daily water depth over the current growing season |
| Emergent marshes           | - 75.0 m, last flooded 1 year ago and last dewatered during growing season 2 years ago (variable flooding and dewatering over past 3 years;  
                                - 74.85 m, last dewatered during growing season 4 years ago;  
                                - 74.7 m, last dewatered during growing season 38 years ago;  
                                - 74.25 m, last dewatered during growing season 68 years ago. |                                                                                  |
| Floating-leaved/submerged vegetation |                                                                                  |                                                                                  |
3.2. Model Development and Application

3.2.1. Linkage Between Plant Assemblages and Hydrology
GIS methodologies were used to generate bathymetric/topographic models for each of the four wetland geomorphic types studied based on the individual digital elevation models. The generalized models were developed by determining the relative areal proportion of each individual wetland that lay above, below, or between selected contour intervals. The resultant models represented all wetlands of each specific type but not any individual site. GIS methodologies allowed the models to be manipulated as required to place contour lines at any desired elevation for purposes of evaluating proposed scenarios.

An algorithm was created to calculate the range of elevations that correspond to specific histories of past flooding and dewatering for any proposed new regulation plans. For each wetland in each of the four geomorphic types, elevation ranges reflecting ecologically significant histories of flooding and dewatering were delineated. Area calculations for each range were averaged by geomorphic type and displayed as a simplified representation of a geomorphic type (e.g., half ring shape to represent open embayments). Results of the model, when integrated with quantitative vegetation data, provide a means to predict and characterize the vegetation response to proposed regulation plans.

Quadrat sampling data that show the past response of plant communities at specific elevations (transects) to changes in lake level were overlaid on the topographic/bathymetric models, which allowed potential distributions of plant communities to be weighted by the area encompassed by various water-depth intervals and by the time intervals during which these water-depth conditions exist. More specifically, proposed regulation plans are assessed to determine ranges of elevation with flooding and dewatering histories corresponding to those assessed in field studies. Those ranges of elevation are then applied to the bathymetric/topographic models to determine percentages of wetland area occupied by the elevation ranges. The percent area determinations are weighted by the number of years (within the total time span of the proposed scenarios) during which each water-level history would apply. The time-weighted wetland area projections are then related to the plant communities found within each elevation range to describe the composition of the projected wetland vegetation. The end result for each scenario tested is a series of relativized, time-weighted predictions of percentage of occurrence of the plant communities identified as growing at elevations with specific water-level histories (from transect data).

3.2.2. Generalization of Model Predictions to a Large Area
A coastal wetland inventory database for Lake Ontario and the Upper St. Lawrence River was created by using existing digital data sets and adding new data generated from photointerpretation of imagery from the entire shoreline. This database was used to extrapolate results from the four wetland geomorphic models to basin-level
estimates. The wetland inventory has over 25,800 hectares of wetlands identified and classified based upon the four wetland types used in the study. Over 90% of the estimated wetland area is located within the eastern portion of the study area. In addition, wetlands occurring within the western basin of Lake Ontario are almost exclusively barrier-beach and drowned-river-mouth wetland types. The distribution of study sites is reflective of this skewed distribution in wetland area and type (Figure 1). Basin-level area estimates for each wetland type were used to area-weight the appropriate individual model results.

3.2.3. Validation of Model Spatial Generalization
The study design for the Lake Ontario /Upper St. Lawrence River portion of this project made use of data with direct ties between plant assemblages and the hydrologic conditions under which they developed, thus requiring no secondary correlation of data to determine applicability. As the generalized models for each wetland geomorphic type were being constructed, plant community data were analyzed for each wetland individually, and grouped data for all wetlands of a geomorphic type were also included in the analyses to determine if a generalized plant assemblage for that geomorphic type compared favorably with individual wetlands. Using both summary statistics and ordinations, the generalized wetland plant assemblages portrayed the expected characteristics and were thus applied to all wetlands of that geomorphic type identified in the wetland inventory.

4. Lower St. Lawrence River Wetland Studies

4.1. DATA ACQUISITION FOR MODEL DEVELOPMENT

4.1.1. Selection of Field Study Sites
In contrast with Lake Ontario, in which geomorphic type and exposure gradients largely determine wetland assemblages, Lower St. Lawrence River wetlands are also subjected to longitudinal gradients of increasing discharge and decreasing water quality resulting from tributaries and human activities along its course. Sites were thus chosen to reflect the complexity of the fluvial system and the various types of hydrologic alteration, shoreline morphology (fluvial corridor and fluvial lakes), exposure (wind, waves and current), origin of water mass, and water quality along the upstream – downstream riverine gradient. Thirteen field study sites distributed over a 225-km-long study area were selected in Lake St. Francis (1 site, region III), Lake des Deux-Montagnes (2 sites, Ottawa River) and the Lower St. Lawrence River (10 sites, region IV) to the outlet of Lake Saint-Pierre (Figure 1, Table I). The upstream sites were chosen as controls for stabilized levels (Lake St. Francis) and to represent the hydrologic regime of the Ottawa River (Lake des Deux-Montagnes), without the influence of regulated Lake Ontario discharge. Four island sites were selected downstream from Montreal to represent the conditions
experienced in the fluvial corridor. In this area, water quality varied widely from site to site depending on the proximity to diffuse or point sources of pollution, as well as exposure to water masses of different origins. The last six sites were located in shallow, gentle-sloping (< 0.01 − 0.8 cm m⁻¹) Lake Saint-Pierre. Here, tributaries draining farmland increase the nutrient loads substantially, which combined with the effects of different water masses and contrasted sheltered (on the south shore) and exposed (on the north shore) conditions.

4.1.2. Remote Sensing Images
Remote sensing images were used as a source of independent data to validate the results of our model predicting wetland plant assemblages from the hydrologic regime (Table II). The distribution and type of wetland plant assemblages were assessed on eight remote sensing images acquired in July-September (1984 to 2002) for which water levels at Sorel ranged from 4.23 to 5.20 m. Beyond the analysis of vegetation cover, the challenge of this procedure was to harmonize the nine wetland plant categories derived from hydrologic models (see Section 4.1.4) with the plant assemblages detected on remote-sensing images of improving definition through time, increasing from 8 (on LANDSAT 1984–1988 images) to 12 (MEIS 1990) and up to 55 plant assemblages (MEIS 2000 and IKONOS 2002). For example, the “meadow marsh” plant assemblage derived from the hydrologic model was identified as either “high marshes” (LANDSAT), as “wet meadows,” or “tall graminea” (MEIS 1990) or as a complex mosaic of plant assemblages dominated by taxa such as Phalaris arundinacea, Leersia ozyoides, Spartina pectinata, Phragmites australis, Lythrum salicaria, Carex spp. (etc.) (on MEIS 2000 and IKONOS 2002 images). Correspondence was most difficult to establish for deep-water, scattered emergent marsh assemblages in which submerged plants coexisted with floating-leaved and low density patches of emergent plant taxa, which resulted in a wide signature range on remote sensing images.

4.1.3. Field Surveys of Plant Assemblages
The effects of inter-annual variability in water levels on wetland plant assemblages was assessed through four consecutive late-summer plant surveys (end of July to early October of 1999 to 2002, Hudon et al., 2005). At a small spatial scale (1–100 m), we assessed the relative abundance of all plant taxa recorded in six to 27 quadrats (surface of 1 × 2 m) at each site along elevations ranging from about 1 m above chart datum to about 1 m below chart datum. This allowed us to sample plant assemblages subjected to a continuous gradient of hydrologic conditions within a single site, ranging from assemblages briefly flooded in the spring to those flooded continually up to a depth of about 50 cm. Species relative abundance was determined by multiplying average plant height (in cm) by median percent cover (0.5, 3, 8, 18, 37.5, 63, and 87.5%) to provide an indication of plant architecture.

At a larger spatial scale (1–10 km), the limits of closed-dense (>50% surface cover) and scattered-open (<50% cover) marshes were surveyed in Lake
Saint-Pierre (2000–2002) by following the inner and outer limit of scattered emergent plants in an airboat, with a continuous (DGPS) position recording. This field assessment was then compared to the emergent plant assemblages detected on remote sensing images as a cross validation (Section 4.2.3).

4.1.4. Identification of Major Wetland Plant Assemblages
Nine major wetland plant assemblages were identified from the clustering of quadrats on the basis of the relative abundance of the most common taxa. In order to reduce the number of rare species (occurring in <1% or <7 quadrats), some species were lumped at the genus level or in groups of similar ecological form (i.e., linear-leaved Potamogeton species). This procedure resulted in the inclusion of 76 taxa (frequency >1%) in multivariate analyses. Annual meadows and mudflat plant assemblages, coincided with a sharp drop in mean annual water levels and were found only during the unusually dry summers of 1999 and 2001. The other wetland classes, corresponding to wet meadow, five types of marshes, and submerged vegetation, occurred over the four years of sampling. Each class was associated with different diagnostic taxa; marsh classes showed a gradient of increasing emergent plant cover (ranging from open, scattered, mixed, dense to closed marshes) (Table IV). Plant assemblages identified for Lower St. Lawrence River wetlands corresponded with the 4 major assemblages identified in Lake Ontario (Table IV), but identified additional sub-categories resulting from the large inter-annual variations of levels.

4.1.5. Physical Characterization of Study Sites and Sampling Seasons
The effects of potentially confounding factors (climate, environmental variables and sediment characteristics) were assessed to isolate the effect of hydrology on river wetland plant assemblages. Major differences in climatic conditions and mean annual water levels were observed over the four sampling seasons (1999–2002). The 1999 and 2001 seasons had higher air temperatures (warmer by 1 to 1.7 degree daily), were more sunny (by about 1 hour of sunshine daily), and had higher drought indices (average water deficit $>47$ mm in comparison with $<40$ mm of rain) than the 2000 and 2002 seasons (April 1 – September 30). Mean daily water levels at Sorel (upstream of Lake Saint-Pierre) over the same period were about 50 cm below (3.95 m in 1999 and 3.91 m 2001) or near (4.48 m in 2000 and 4.56 m in 2002) the 1960–2002 average level (4.48 m; levels are referenced to the International Great Lakes Datum of 1985). Climatic differences and other environmental variables (fetch, water mass, and water clarity) explained about 9.6% of the variance among classes of wetland plants. Sediment characteristics (percent sand, loam and clay, mean, median, and variance in particle diameter, percent of volatile organic contents, organic N, total P, and pH) measured at all sites (in 2000 and 2001 only) explained 11.5% of wetland classes.

Hydrologic conditions were the main factor of our analysis, which tested the hypothesis that the presence of a given class wetland over a given year resulted
### TABLE IV

Description and comparison of major wetland plant assemblages identified and modeled in Lake Ontario, Upper and Lower St. Lawrence River studies.

<table>
<thead>
<tr>
<th>Lake Ontario and Upper St. Lawrence River (region I)</th>
<th>Lower St. Lawrence River (region IV)</th>
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<tbody>
<tr>
<td>4 assemblages</td>
<td>9 assemblages</td>
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</table>

**Meadow marsh:** *Calamagrostis canadensis, Onoclea sensibilis, Cornus sericea, Viburnum spp, Carex spp.*

**Wet meadow:** *Phalaris arundinacea, Lythrum salicaria, Onoclea sensibilis*  
Annual meadow: *Polygonum spp., Urtica dioica, Cyperus spp.* (larger than 10 cm)

**Mudflat:** *Polygonum spp., Leersia oryzoides, filamentous algae*

**Typha dominated emergent marsh:** *Typha angustifolia, Typha x glauca, dead Typha spp.*

**Closed marsh (aggressive vegetation):** *Sparganium eurycarpum, Typha angustifolia, Phragmites australis, Sagittaria latifolia, Butomus umbellatus*

**Mixed emergent marsh:** *Sagittaria latifolia, Sparganium eurycarpum, Typha spp., Hydrocharis morsus-ranae*

**Dense marsh (robust emergents):** *Bolboschoenus fluviatilis, Alisma plantago-aquatica, Potamogeton richardsonii, linear-leaved Potamogeton*

**Mixed marsh (narrow-leaved vegetation):** *Schoenoplectus pungens, Eleocharis palustris, E. acicularis, Pontederia cordata*

**Scattered marsh (tall Scirpus):** *Schoenoplectus lacustris, Myriophyllum spp., Potamogeton richardsonii, Heteranthera dubia*

**Floating-leaved/submerged vegetation:** *Nymphaea odorata, Potamogeton spp., Nuphar variegata, Chara spp.*

**Open marsh (floating-leaved vegetation):** *Nymphaea odorata, Nuphar variegata, Vallisneria americana, Chara sp., Schoenoplectus lacustris*

**Shallow submerged vegetation:** *Myriophyllum spp., linear-leaved Potamogeton*

For each major plant assemblage, diagnostic taxa are indicated in italics.
primarily from the hydrologic conditions experienced during the current and pre-
vious growing seasons. Fifty-four hydrologic variables were calculated for each
of the 630 plant quadrats, including the number of days of flooding, the number
of wet-dry (water-air-water) cycles, quadrat depth (mean and standard deviation),
and quadrat elevation with respect to water level (mean and standard deviation).
Different periods and time intervals were tested to identify the most significant scale
of hydrological variability on plant assemblages over the very short (1 to 8 weeks
before sampling), short (mean monthly levels in May, June, July, and August), and
medium terms (current and past growing seasons).

4.2. MODEL DEVELOPMENT AND APPLICATION

4.2.1. Linkage between Plant Assemblages and Hydrology
All hydrologic variables were calculated for the current growing season (ending
on the day each quadrat was sampled); longer term variables (monthly average,
growing season average) for the previous growing season (1 April–30 September)
were also computed. Once the effects of climatic, environmental, and sedimentary
variables had been removed, a small subset of hydrologic variables explained 24%
of the variance in wetland classes.

The combination of hydrologic variables and the critical thresholds allowing
the best separation of the nine wetland classes were identified using a binary,
hierarchical model (Classification and Regression Trees, CART; Breiman et al.,
1984). The most significant variables derived from this analysis were: 1) elevation of
quadrats with respect to the average water level in July and 2) variability (standard-
deviation) of water depth during the current growing season; 3) average water depth
and 4) the number of days flooded over the previous growth season. The first two
variables discriminated among plant assemblages that were mostly dry (meadows
and barren mudflats) or wet (marshes), whereas the last two allowed to differentiate
between different types of marshes and submerged vegetation (Table III).

4.2.2. Generalization of Model Predictions to the Lake Saint-Pierre Area
The predictions of the model were generalized to the Lake Saint-Pierre area, which
represents over 70% (11,700 ha) of St. Lawrence River marshes (Jean et al., 2002).
Owing to the major ecological value of this area, it was felt that measurable impacts
of water-level regulation to wetlands of this large fluvial lake would be considered
highly significant. 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 less fragmented
than Lake St. Louis and less hydrologically altered than Lake St. Francis.

The surface area and distribution of wetland classes in Lake Saint-Pierre were
predicted from the combination of information derived from a two-dimensional
hydrodynamic simulation model determining the hydrologic regime (Morin and
Bouchard, 2001) experienced over each point (pixel) of lake bottom (Numerical
Elevation Model, EC, 2003). Predicted wetland classes for each pixel were then identified from the combination of hydrologic conditions for the previous and current growing season over the 1961–2002 interval (Hudon et al., 2005), which covers the period over which regulation took place.

4.2.3. Validation of Model Spatial Generalization
The validity of the prediction of spatial distribution of the nine wetland classes (Table IV) in Lake Saint-Pierre was assessed using three methods. First, we compared predicted habitats with remote sensing images for the same years, showing that the wetland assemblages coincided over 58% (1988) to 96% (1987) of the surface area.

Second, we compared the limits of continuous (>50% surface cover, dense and closed marshes) and sparse (<50% cover, scattered and open marshes) emergent plants surveyed in the field (2000–2002) with the limits of equivalent classes derived from the hydrology-based CART model and from remote sensing for the same years. The limits set by the airboat survey coincided generally with the mixed marsh plant assemblage, which represented the median marsh type in terms of plant cover.

Third, we verified the attribution of groups of quadrats derived from the hydrology-based model against the classes previously identified by the cluster analyses based solely on species’ relative abundance, yielding a 71% (range of 24 to 84% depending on class) overall match.

4.2.4. Analysis of Historical Changes in Wetland Plant Assemblages
The distribution of the predicted wetland classes was mapped using a geographic information system (MapInfo version 6.5), which was then used to calculate the surface area of each class for each year (1961–2002). The 42-year sequence of changes in the surface area of wetlands classes was reduced from a nine-descriptor (surface of nine wetland classes) time series to a two-dimensional, state-space diagram. The new factors consisted of simple differences of wetland class areas and were identified by inspection of the first two principal components of the covariance matrix between the surface areas of the nine herbaceous wetland classes. The resulting diagram showed that Lake Saint-Pierre wetlands alternated between three major configurations, dominated by meadows and open marshes with floating-leaved vegetation (in the low-level period of the 1960s), scattered tall Scirpus marshes (during the high-water levels of the late 1970s), with a greater year-to-year variability and the appearance of closed marsh with aggressive emergents in the last decade.

5. Deriving Performance Indicators and Assessing Alternative Regulation Plans for Lake Ontario – Lower St. Lawrence River Wetlands
Several performance indicators (metrics) quantifying the relationships between various wetland characteristics and hydrologic conditions were derived from the above
studies for both regions, allowing a relative assessment of the effect of different regulation plans and water-supply scenarios on wetlands. Performance indicators linking hydrologic to environmental variables were derived from rules-based and regression models for the Lake Ontario and the Lower St. Lawrence River, respectively. The wetland habitat models incorporate seasonal water-level data to predict the annual distribution and abundance of various wetland plant communities. The performance indicators focus on general wetland plant community attributes such as estimated total area of wetland, area of meadow marsh, non-cattail dominated emergent marsh, and open marsh.

Wetland characteristics correspond to the type and magnitude of hydrological alteration experienced in each region. In Lake Ontario and Upper St. Lawrence River (region I), range reduction at the decadal scale resulted in the progressive expansion and colonization of cattail into meadow marsh and once diverse interspersed emergent marsh communities (Wilcox and Ingram, unpublished data). In Lake St. Francis (region III), stabilization of level resulted in colonization of meadows by shrubs (Jean and Bouchard, 1991), reduction of low marsh area (Jean et al., 2002) and historically increasing submerged vegetation (Reavie et al., 1998; Morin and Leclerc, 1998), compounded by other anthropogenic alterations (reduction in traditional fire-setting practices by aboriginal people, changes in land use, nutrient enrichment, shoreline encroachment, erosion, and armouring). In Lower St. Lawrence River wetlands (region IV), discharge regulation and associated channel excavation, ice control, and degradation of water quality resulted in the progressive drying out of wetlands, with a greater incidence of upland vegetation, aggressive or exotic taxa, and plants species indicative of eutrophic conditions (Jean et al., 2002; Lavoie et al., 2003; Hudon, 2004; Hudon et al., 2005).

Studies linking wetlands and hydrology, including ours, underline the importance of natural water level variations (seasonal timing and annual range in level, recurrence of high and low water levels over longer time spans) in sustaining wetland abundance and diversity. For socio-economic interest groups, the current regulation plan (1958D with deviations) represents the status quo option and is the plan against which the anticipated performance of alternative plans will be measured. For wetlands, however, the environmental sustainability of the current plan remains questionable in comparison with non regulated conditions, which must constitute the basic reference conditions for the environment. Allowing Lake Ontario level and discharge to fluctuate in phase with natural variations of water supplies to the basin would increase the range of lake levels while ensuring that discharge to the river follow a more natural pattern.

Both the current and alternative regulation plans must be examined on the basis of their lack of significant adverse effects on wetlands throughout the Lake Ontario – Upper St: Lawrence and Lower St. Lawrence River basin (CEAA, 1992). This general approach is also co-incident with the protection of endangered species (USFWS, 1973; COSEWIC, 2004) and the protection of fish habitat, based on the No Net Loss Guiding Principle (DFO, 1998). From an environmental standpoint,
the selection of an alternative regulation plan to replace the one currently in use should proceed following the precautionary principle, seeking to reduce adverse environmental impacts from regulation. It is imprudent, based on the specific studies designed for this study, to recommend that any “benefits” will accrue to the natural environment based on water-level manipulation. Similarly, environmental “losses” anticipated (modelled) for given habitats or species cannot be traded against “gains” to other ecosystem components or against mitigation measures. The pursuit of environmental benefits and trade off for losses would require a much more comprehensive understanding of cause and effect relationships in the environment than our science now possesses.

6. Future Management Considerations

Historical changes in wetland plant assemblages related to regulation assessed in the studies described here may also be used back-track mapped vegetation types through time to correlate the signature of pre-regulation vegetation. For Lake Ontario, the estimate of the percentage of wetland occupied by the major vegetation types prior to regulation thus can provide generalized targets for wetland plant community assemblages that can be compared against proposed new regulation plans. For the Lower St. Lawrence River, regulation appears to be one factor among numerous others which exert cumulative impacts on wetland assemblages in Lake Saint-Pierre (Hudon et al., 2005). For both lake and river regions, however, wetland monitoring is required to determine the effects of the new regulation plan on natural habitats quantity and quality through time. Such follow-up on model predictions would provide a unique opportunity to put adaptive management in practice, thus ensuring the sustainability of Lake Ontario – St. Lawrence River wetlands under the future regulation plan.

Acknowledgments

This study benefited from the help of many staff members of Environment Canada, Quebec and Ontario Regions, U.S. Geologic Survey, and Eastern Michigan University. We particularly thank J.-P. Amyot, M. Carlson, M. Deschênes, G. Grabas, P. Gagnon, M. Galloway, K. Holmes, M. Jean, K. Kowalski, G. Létourneau, J. Meeker, N. Patterson, C. Plante, D. Rioux, and Y. Xie. Joyce Barkley kindly supplied information on Lake St. Lawrence. Thanks to David Fay for information update on water-level simulations. The constructive comments of A. Talbot, Y. de Lafontaine and three anonymous reviewers are acknowledged with thanks. This study was partially funded by the Lake Ontario–St. Lawrence River Water Level Study of the International Joint Commission.
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