Response of wetlands to the extreme low-water levels recorded in 1931 and 1999 in the St. Lawrence River (Quebec, Canada)

Article · December 2002

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Report submitted to the International Joint Commission

Lake Ontario-St. Lawrence Study

Technical Working Group on the Environment - Habitat Quality

November 28 2002

Abstract: The effects of a one-metre drop in average water levels in 1999 on species composition and biomass was documented for a St. Lawrence River wetland and compared with a similar episode in 1931 (Marie-Victorin 1943). Both 1931 and 1999 coincided with waters warmer by 2 to 3 ^{o}C than the previous 10-year period. Wetland vegetation was also markedly, and similarly, modified : dry meadows and marshy areas became invaded by *Phalaris arundinacea*, various Graminea and other facultative annual wetland plant species. Shallow waters previously colonized by submerged species became a dry, barren zone colonized by annual terrestrial plants (*Polygonum* spp.); waterlogged mudflats allowed for the germination and extensive flowering of *Alisma gramineum*. Average water levels generated an overall smaller total aboveground plant biomass, which provided a continuous cover across the riparian zone whereas low water levels supported a spatially-discontinuous plant biomass, which was richer in terrestrial material. Abundant species shifted from *Equisetum* spp, *Butomus umbellatus, Najas flexilis* and *Chara* (in the 1930's) to *Typha angustifolia*, *Lythrum salicaria, Potamogeton* spp. and filamentous algae (in the 1990's) suggesting the additional effects of nutrient enrichment, exotic species and shoreline alteration. These observations highlight the manifold effects of water-level variations on St. Lawrence River wetlands and faunal habitats, resulting from natural hydrologic variability, climate change and/or human intervention.

Résumé : Les effets sur la composition spécifique et la biomasse des milieux humides d'une baisse de 1 m du niveau moyen du Saint-Laurent à l'été 1999 ont été comparés avec un épisode semblable documenté en 1931 (Marie-Victorin 1943). En 1931 et en 1999, la température de l'eau était plus élevée de 2 à 3 °C qu'au cours des 10 années précédentes. La végétation des milieux humides affichait aussi des changements importants, mais similaires : les prairies humides et les marais furent envahies par by *Phalaris arundinacea*, diverses Graminées et d'autres espèces facultatives des milieux humides. Les eaux peu profondes colonisées précédemment par des plantes submergées sont devenues des vasières asséchées et nues, colonisée par des plantes annuelles terrestres (*Polygonum* spp.); la vase humide a permis la germination et la floraison massive d'*Alisma gramineum*. Les niveaux moyens correspondaient à de plus faibles biomasses aériennes de plantes terrestres et aquatiques, qui procuraient un couvert continu sur toute la zone de rivage tandis que les bas niveau généraient un couvert littoral discontinu, comportant une biomasse végétale terrestre plus élevée. Les espèces les plus abondantes sont passées de *Equisetum* spp, *Butomus umbellatus, Najas flexilis* et *Chara* sp. (dans les années '30) à *Typha angustifolia*, *Lythrum salicaria, Potamogeton* spp. et aux algues filamenteuses (dans les années '90), suggérant des effets additionnels de l'eutrophisation, des espèces exotiques et de l'altération des rives. Ces observations soulignent les nombreux effets du niveau d'eau sur les milieux humides et les habitats fauniques du Saint-Laurent, résultant de la variabilité hydrologique naturelle, des changements climatiques et/ou des interventions humaines.

Introduction

Wetlands occupy the shoreline fringe of the transition zone between dry land and purely aquatic systems; as such, the persistence and diversity of this ecosystem is intimately linked to water-level variations. In temperate latitudes, wetland ecosystems have evolved around predictable seasonal conditions related to the timing, frequency, and amplitude of water-level changes, all of which are increasingly threatened by human-induced climatic changes and management interventions (Mortsch 1998).

The effects of various hydrologic characteristics on the composition and biomass of riverine wetland species are well documented (Hudon 1997; Poff et al. 1997; Toner and Keddy 1997; Jansson et al. 2000); water depth produces known variations in wetland plant morphology (Marie-Victorin 1935), the seasonal range in levels/flows induces shoreline plant zonation (Tessier et al. 1984), influences riparian plant succession (Auble et al. 1994; Shafroth et al. 2002), and determines species richness (Keddy and Reznicek 1986; Nilsson et al. 1988; Nilsson and Keddy 1988). In addition, interactions between and combinations of hydrological variables such as water depth/light intensity, litter removal by spring flood and the fertility/exposure gradient produced by waves and flowing water were shown to control wetland vegetation in the Ottawa (Day et al. 1988) and St. Lawrence rivers (Hudon et al. 2002).

The regulation of large rivers for flood control, commercial navigation and hydroelectricity production modifies riverine flow patterns by reducing the amplitude and the duration of spring runoff and raising minimum levels in late summer (Puckridge et al. 1998). How the alteration of large river discharge is manifested, however, is largely determined by the natural variability of the water supply to the watershed — which, in the case of the Great Lakes–St. Lawrence River, responds at the continental scale. Flow management in eastern North America is likely to become severely constrained in the future, as climate change scenarios come into play; in the North American Midwest, predicted increases in air temperature, precipitation declines and higher evaporation will reduce the overall water supply (NRC 2002; Mortsch and Quinn 1996). Under such conditions, the regional demands for Great Lakes water and the regulation of downstream flow are likely to increase, further altering hydrologic conditions and water availability for natural ecosystem components.

Since 1960, the discharge of the St. Lawrence River has been regulated to optimize hydroelectricity production, control flooding of riverfront property, and maintain water levels for commercial ship traffic. Regulation has decreased the natural range of water-level variations by about 1 m downstream of Montreal (Fig. 1), cropping the extreme flooding episodes and raising the summer low flows. Although regulation causes only minor variations in comparison with natural, climate-induced inter-annual variability in discharge, human intervention can either amplify or reduce the effects of extreme high and low levels on wetlands and thus must be accounted into the cumulative effects imposed by human actions on natural ecosystems.

Episodes of extreme low-water conditions during the growing season (April 1–September 30) were observed in the 1930s (1931, 1935, 1936), the 1960s (1962-1965) and the late-1990s (1995, 1999, 2001) (Fig. 1). During the summer of 1931, levels near Montreal reached the record-low values of 1860, generating sufficiently conspicuous changes in wetland vegetation to be documented by Marie-Victorin (1943). The present study compares the low-water episodes of 1931 and 1999 with average water-level conditions prevailing in the years preceding these events. We then examine in more details the recent wetland species composition, zonation and seasonal changes in biomass at a range of elevation, in order to identify the different mechanisms by which water level variations affect wetland plants. This analysis provides information on the numerous alterations inflicted upon the St. Lawrence ecosystems to date, and offer some insight into possible future changes to wetlands resulting from the cumulative effects of regulation, climate variability and climate change.

Material and Methods

Description of the Study Area

The study site is located on the St. Lawrence River, at the western (upstream) tip of the Tailhandier flats (Boucherville Islands). It is the largest wetland (154 ha) in the Greater Montreal area, and is located 1 km across from the Port of Montreal. This wetland has been protected from direct human intervention since 1998, through a 20-year lease between the Montreal Port Authority and the Canadian Wildlife Service. This natural habitat, supporting populations of fish, waterfowl, muskrat, beaver and deer, is in sharp contrast to the adjacent, heavily-urbanized

Montreal area (population 2.5 million). In the 1930s, most of the Montreal area was given over to agriculture; urbanized areas covered only 135 km^2 (27%) of the island of Montreal in 1932, whereas they monopolized 334 km^2 (73 %) in 1989 (Fig. 2 A, B).

The Boucherville wetland is characteristic of the low-lying islands of the St. Lawrence Lowlands, a flat landscape of clay deposits intersected with moraine landforms. Bottom sediments generally consist of fine silt and sand, with a locally variable organic component, lying on glacial deposits of marine clay. Emergent marsh vegetation colonizes the shallow (< 2 m) shelf around islands and shoals, which drops sharply along a steep slope to deeper waters (Hudon 1997; Hudon and Lalonde 1999).

Low water-level conditions were also observed in 1931 at the Boucherville Islands, along the south shore of Longueuil, and at nearby Ile au Vert (Ile Plate) (Fig. 2 C) (Marie-Victorin 1943). This area was significantly altered by major construction projects in the 1960s, including the excavation of Montreal Harbour, the St. Lawrence Seaway and the Louis-Hippolyte Lafontaine tunnel. Dredged spoil was used to shield the nearby shoreline, build-up jetties and islands, fill in wetlands and develop highways and urban areas along the Longueuil–Boucherville shoreline (Fig. 2 C, D). Such alterations in the bathymetry and shoreline profile most likely intensified the passage of water in the harbour area, with a concomitant reduction in flow through the channels between the Boucherville Islands. Accordingly, the reduction in water circulation and progressive drying-up of the inner channel has increased the surface area of emergent wetlands from about 180 ha in 1931 to about 315 ha in 1996-2000. The 1996 videography (October 17, 1996: 0.81 m above chart datum) of Boucherville islands shows the extensive development of emergent plants in the longitudinal channel (originally called «Chenal du courant» – Channel of the current) in comparison with the wide open water channel seen in the 1931 aerial photographs (May 6, 1931: 1.14 m above chart datum) (Fig. 2 C, D); such difference cannot be accounted solely by differences in seasonal water levels (30 cm) and in the development of emergent vegetation.

The low water levels of 1931 coincided with the well-documented «dust bowl» drought period that reduced water levels in the Great Lakes and threatened agriculture in the Prairies (Rosenzweig and Hillel 1993). In 1999, low water-level conditions in the St. Lawrence coincided with a 10% reduction in precipitation and increasing evaporation resulting from a 1–2°C increase in air temperature in the Great Lakes watershed since 1998. Such changes are on the same order of magnitude as those anticipated in the 2 x CO_2 warming climate scenario (Mortsch and Quinn 1996) and could result in a higher frequency of episodes of low levels in the St. Lawrence (NRC 2002).

Physical and climatological measurements

Daily water-level measurements and historical values for the Port of Montreal's Jetty No. 1 (gauging station No. 15520, 5.564 m above sea level), located 1 km across the river from the study site, were obtained from Fisheries and Oceans Canada (2002). Water level values were adjusted to navigation charts (hereafter referred to as Chart Datum reference level, or CD) by subtracting station elevation from original data, which were referenced to sea level according to the International Great Lakes Datum of 1985 (IGLD85). The elevation of each sample was measured at collection time using water depth for underwater samples or a surveyor's level referenced to the current daily water level for samples above the water line; the elevation of individual samples was then calculated with respect to CD levels using daily reported level values. Monthly average water temperature data for the 1921–1999 period were obtained from the Charles-J. Des Baillets water filtration plant (City of Montreal, LaSalle). Daily sunshine and precipitation data were obtained from Environment Canada (2002).

The efficiency of four species of emergent macrophytes at monopolizing incident light was quantified by measuring the fraction of incident light (I_0) remaining at different heights above the ground within a dense, monospecific cluster of each species, using an aerial probe and data logger (LI-COR SA-LI188B and Li-1000).

Assessment of temporal changes in wetland plant composition and biomass

To facilitate the comparisons of species composition reported in 1931 and 1999 low-level and previous average-level years, the wetland was divided among five elevation zones (strata), corresponding to different immersion regimes. Under average water level conditions, these elevations coincided with the sequence of wet meadow, marsh and increasingly deep open water; under extremely low water levels (1931 and 1999), the same elevation sequence coincided with dry meadow, wet meadow, a dry/waterlogged barren mud zone and shallow open water. In the dry 1999 summer, the two uppermost strata were flooded only in the spring (+1 to +0.51 m CD and +0.50 to 0 m CD); the next stratum down was a transition zone which was emerged or submerged at a daily-weekly frequency (0 to -0.24 m CD) whereas the lowermost two zones were constantly wet, albeit under very shallow (-0.25 to -0.50 m CD) to shallow waters (-0.51 to -1 m CD).

The comparison between years of low and average water-levels in the Boucherville wetland was further investigated by quantifying seasonal changes in above- and belowground biomass for each stratum. A total of 197 vegetation quadrats from 13 fortnightly visits to the Boucherville wetland (May 6 to October 20, 1999) were used to characterize seasonal changes in biomass at each elevation stratum. Maximum summer biomass (Aug. 3-Sept. 3) estimates derived from these low water-level quadrats were contrasted with 93 quadrats sampled in 1993-1994 (average water-level conditions) at Boucherville and three neighbouring wetlands (Pointe aux Trembles, Île aux Cerfeuils and Verchères), using the same sampling method (Hudon 1997).

Plant biomass was collected at 1- to 5-m intervals, depending on the slope, along a permanent transect line located perpendicular to the shoreline, running from the upper dry grounds to a water depth of about 1 m. Samples were collected at defined field points located so as to cover the small-scale changes occurring across the elevation gradient; for a given field elevation point, successive fortnightly samples were distanced laterally from the previous ones by about 25 cm. Plant biomass was assessed by collecting all plant matter (above- and belowground structures) in 25-cm x 25-cm quadrats placed at permanent markers at recorded intervals along a transect line (in shallow water). Vegetation growing in the quadrats was collected by hand, using a shovel or a knife to loosen sediments and dislodge roots. Only the most commonly encountered species were accounted for in the present study, since biomass was sampled in small-sized quadrats; the effects of water-level variations on overall species diversity will be documented in a future paper. Emergent plant biomass was characterized separately for obligatory (*Schoenoplectus, Sagittaria, Butomus, Typha,* etc.) and facultative (*Polygonum, Lythrum, Phalaris*) wetland taxa (Reed 1988; Gauthier 1997). Species were identified and designated according to the nomenclature used in Marie-Victorin (1935, 3rd ed. 1995).

Aboveground parts were identified and processed separately for each species, while underground parts and litter were treated as separate groups in each quadrat. Periphyton, loose detritus and sediment were carefully washed off plant matter, which was subsequently dried to a constant mass (at 105^{o}C) and weighed (0.001 g), leading to calculations of biomass of macrophyte dry mass per m^2 (g DM m^{-2}).

Comparisons between low and average water-level conditions were made on the basis of individual species biomass and total aboveground biomass by vegetation group (emergent, submerged vascular plants, algae, litter) and belowground biomass. Differences in biomass between average and low water-level conditions were tested using ANOVA (SAS Institute) on transformed biomass data ($\log_{10} + 1$), to ensure the homogeneity of variances between groups.

Results

Environmental conditions

The summer of 1999 (April 1 to September 30) was characterized by extremely low water levels and unusually dry and sunny weather conditions, relative to the previous ten-year period (Table 1). The 1999 season was about 10% sunnier, warmer and drier than previous years (Environment Canada 2002, Table 1). The same held true for the 1931 season, with the exception of accumulated monthly precipitation, which was higher by almost 10 mm in 1931 than in the 1921–1930 interval.

During the growing season (April 1–September 30), average St. Lawrence River water levels for the 1989–1998 period (1.03 m above CD) were nearly 1 m higher than in 1999 (0.18) (Fig. 3a). A difference of about 1 m was also observed between 1931 (0.53 m above CD) and the intervening ten years (1.55 m above CD). The record-low values reported in the summer of 1931 were therefore about 35 cm higher than summer 1999 levels, although this includes an uncertainty related to historical changes in datum and measurement methods.

Between-year disparities in weather conditions and water levels further generated interannual differences in water temperature; low water years coincided with warmer waters by 2 to 3^{o}C on a monthly average basis (Table 1, Fig. 3b). The combination of low water levels and a sunny and dry climate resulted in conditions that differed consistently from the previous ten-year average conditions for wetland plants, allowing us to observe the response of wetland biomass and species composition to climatic and level variations.

Effect of water levels on major species composition

In comparing changes observed in the extremely low water periods of 1931 and 1999, we were able to distinguish between compositional changes that can be attributed to low water levels and changes due to other environmental causes. This exercise revealed major similarities and also some differences in major species composition under average (before 1931 and before 1999) and low (1931 and 1999) level conditions; for the sake of clarity, the observations of Marie-Victorin and our own were organized according to the elevation gradient of major riparian vegetation strata (Table 2): shrubs, meadow, marsh and open water.

Under the low water levels experienced in 1931 and 1999, the species composition of all strata, except the upper shrubby zone, were markedly, and similarly, modified. Dry meadows and marshy areas became invaded by *Phalaris arundinacea*, various grasses and other facultative annual wetland plant species. Very shallow open waters previously colonized by submerged species became a dry, barren zone colonized by annual terrestrial plants (*Polygonum* spp.), whereas waterlogged mudflats allowed for the germination and extensive flowering of *Alisma gramineum*. Open water areas subjected to lower water depths exhibited changes in species biomass.

If the species mentioned by Marie-Victorin (1943) are taken as commonly occurring, the comparison of major species composition between 1931 and 1999 reveals the lesser abundance of *Equisetum* spp., *Strophostyles helveola, Sagittaria heterophylla, Najas flexilis, Callitriche hermaphroditica* and the increased occurrence of *Phragmites australis, Vallisneria americana, Potamogeton* spp., as well as filamentous algae, in recent years.

The similarities between our results and the general pattern observed in 1931 suggests that a closer examination of the overall zonation of wetland plant biomass and of its short-term seasonal changes would yield general information on the response mechanisms of this community under changing water levels.

Effect of water levels on vertical zonation of biomass

Under average water levels (CD + 1 m), the vertical zonation and species composition in St. Lawrence River wetlands reproduced the usual pattern, including wet meadows, emergent marshes and submerged vegetation (Fig. 4a), as previously documented in numerous ecosystems. Under low water levels, all land located at elevations above chart datum level were beyond the water, and elevations down to 1 m below were submerged under < 1 m of water (Fig. 4b).

Between-year variations in water levels resulted in differences in the vertical distribution of biomass of primary producers along the elevation gradient, both in terms of quantity and quality of organic matter (Fig. 4), thus generating extremely different conditions for aquatic fauna. Under low water levels, the total aboveground biomass was nearly twice the amount recorded under average levels, and followed a different distribution along the littoral zone. At average levels, biomass decreased progressively as depth increased along the littoral area, whereas biomass was discontinuous under low water levels. In addition, important differences in quality and composition could be discerned; under average levels, the more «terrestrial», cellulose-rich (litter and emergents) fraction represented 69% of the total aboveground biomass, whereas it rose to 82% under low levels. Conversely, the more «aquatic», easily degraded and palatable (submerged plants and algae) fraction dropped from 31% to 18% with low water levels (Table 3). Average water levels supported an overall smaller total biomass, which provided a continuous cover across the riparian zone and a greater quantity of food for obligatory aquatic organisms. Low water levels supported a spatially-discontinuous plant biomass, which was more abundant in cellulose-rich material and thus more palatable to terrestrial detritivores than under average water levels.

Effect of water levels on seasonal variations in plant biomass at different elevations

The fortnightly changes in species dominance and biomass were documented for each elevation stratum during a season characterized by low water levels (Fig. 5, 6, 7). For each stratum, the maximum summer (late July–early September) biomass of each major plant group (emergents, submerged, macroalgae, litter) was compared to years of average and low water levels (Table 3) as well as average maximum biomass of major species (Table 4).

Shallow marsh turned into dry meadow (+1 to +0.51 m CD). At this elevation, obligatory wetland plants growing in shallow (10-30 cm) water under average water levels spent the entire summer of 1999 under dry conditions.

From the beginning of the growing season until September, families of perennial (Graminea) and annual (Renonculacea, Lythracea, Compositae, Polygonaceae) facultative wetland plants formed the bulk (> 50%) of total aboveground biomass. On May 20, biomass was dominated by *Phalaris arundinacea* and *Eleocharis smallii*, together with a variety of Graminea, Compositae and *Schoenoplectus* spp. By June 1, *Bolboschoenus fluviatilis* dominated the biomass of all samples, with other unidentified emergent species. After an initial high value of 1.2 kg m^{-2} of dead litter at the beginning of May, the amount of dead organic litter dropped to 0.75 kg m^{-2} (± s.d. =0.14, N = 12) for the remainder of the sampling season. A wide variety of additional species could be identified at mid-June*: Scutellaria* sp.*, Leersia oryzoides, Butomus umbellatus, Equisetum* sp.*,* and *Lythrum salicaria*, with a sharp rise in aboveground biomass (from 0.05 to 0.7 kg dry m^{-2}) during that two-week interval. Wetland vegetation at this elevation range exhibited the highest summer biomass (0.7 ± 0.20 kg DM m^{-2}, N = 10) of all groups, dominated by a very dense cover of *Phalaris arundinacea* (38% of 69 samples) with a common occurrence of *Lythrum salicaria* (either as small germlings or adult plants)(54%), *Bolboschoenus fluviatilis* (46%) and *Leersia oryzoides* (20%) (Fig. 5a). Between June 15 and the end of October, belowground biomass remained high (2.6 ± 0.45 kg DM m^{-2}, N = 10) and the average ratio of green aboveground to belowground biomass equaled 4 (± s.d. = 1.4, N = 10), indicating the presence of a thick root network to capture soil moisture. Towards the end of the growing season (September to late October), however, after annual plant species had completed their life cycles, the aboveground biomass of obligatory wetland plants (*Alisma, Butomus, Sagittaria, Schoenoplectus, Typha, Eleocharis, Sparganium*) increased and became dominant (> 50% of total aboveground biomass).

Deep marsh turned into a wet meadow (+0.50 to 0 m CD). Under average water level conditions, Boucherville and other wetlands in the Montreal area were dominated by obligatory wetland species such as *Sparganium eurycarpum, Bolboschoenus fluviatilis, Schoenoplectus* spp.*, Butomus umbellatus* and *Sagittaria latifolia*, which occupied the elevations between +1 m and 0 m above CD, coinciding with water depths < 1 m. Submerged plants (*Myriophyllum* spp. *Elodea canadensis*, *Ceratophyllum demersum*) grew in the shallow waters amongst the rooted emergent macrophytes. Submerged plants formed a thick canopy, reaching the surface in waters 1–3 m deep, with an undergrowth of *Vallisneria americana* near the bottom.

Under low water levels (CD), the water's edge regressed by about 70 m horizontally, coinciding with a 1-m drop in elevation, turning shallow marshland into a dry meadow (+1 m to +0.5 m CD) and deep marshland into a wet meadow (+0.5 m to 0 m CD). Vegetation growing at this elevation range was characteristic of deep (0.5 to 1 m) marsh under average water levels and was mostly dry, sometimes waterlogged, with brief periods of shallow water (2 cm) incursions during the summer of 1999. A reduction in the average water level from +1 to 0 m CD in 1999 resulted in the complete desiccation of emergent vegetation that had previously grown in soil waterlogged to a 1-m depth (Fig. 4b). Dried-out shallow marshes fostered the proliferation of several grass species (*Phalaris arundinacea, Phragmites australis, Leerzia oryzoides*) among the previously dominant wetland species (*Schoenoplectus* spp.*, Butomus umbellatus, Sparganium eurycarpum*). Under low water-level conditions, the biomass of *Phalaris arundinacea, Lythrum salicaria* and *Typha angustifolia* was 3 to 15 (*L. salicaria*) times higher than under average level conditions (Table 4).

Although the aboveground biomass of this group did not differ significantly from that of plants found at higher elevations, lower belowground biomass (1.5 ± 0.50 kg DM m^{-2}, N = 13), a lower below- to aboveground biomass ratio (2.4 ± 1.4, N = 10), and substantial differences in species composition and seasonal biomass patterns could be discerned. Throughout the sampling period, species occurring the most frequently were *Polygonum* spp. (62% of 47 samples), *Typha angustifolia* (55%) and *Bolboschoenus fluviatilis* (30%); *Lythrum salicaria* (either small germlings or adult plants) was observed in 9% of samples. This stratum supported the highest number of facultative and obligatory species, owing to its emergent, yet waterlogged soil conditions, devoid of the thick cover of space- and light-monopolizing *Phalaris* (Fig. 5b).

Leaves of emergent vegetation too small to identify were found on May 6, suggesting that seasonal growth begins around May 1. Early spring sampling (May–June) revealed a high biomass of decaying belowground structures at the outer edge of the band of emergent plants, which was commonly dominated by *Sagittaria* under average water levels. This was attributed to the effect of frost, as water levels were below this elevation throughout the previous (1998–99) winter. On May 20, biomass was dominated by *Schoenoplectus* spp.; samples located nearest the edge of the water, however, were exclusively composed of dead plant material. On June 1, this stratum supported *Eleocharis smallii*, *Bolboschoenus fluviatilis* and *Typha angustifolia*, with a bare zone of water-logged, anoxic mud at the edge of the water. No clear dominance could be assessed two weeks later (June 17), at which time all previously observed obligatory emergents coexisted in small amounts, with *Butomus umbellatus*, *Equisetum fluviatile* and *Polygonum* spp. Dead litter increased progressively throughout the summer with a maximum in mid-July of near 1 kg DM m^{-2}. Similarly, at this same elevation, a sharp rise in aboveground biomass (from 0.05 to 0.5 kg DM m^{-2}) was observed in the first three weeks of June. However, in contrast to the dry meadow, the assemblage was constantly dominated by obligatory wetland species, which always represented > 50% of total aboveground biomass, despite this stratum remaining almost constantly dry throughout the season. By the end of August (Aug. 24), small *Populus deltoides* grew at the lower edge of this zone, in the dry but open area.

Brief periods under water resulted in the appearance of submerged plants, followed by an decrease in annual species biomass and an increase in litter; however, these changes were short-lived as more terrestrial (annual) species resumed growing after the return to dry conditions. Exposure to light was high since annuals grew near the fringe of large, readily-established obligatory emergents. Facultative wetland plant species also colonized the exposed soil in between obligatory wetland species, using the light and space available between the scattered stems. Major differences were measured in the effectiveness of wetland plant species to monopolize incident light according to their particular morphology (Table 5). Plant morphology and biomass had a marked effect on light attenuation and ground level illumination. Emergent plants with linear leaves and unramified stems such as *Schoenoplectus lacustris* exhibited lower extinction coefficients per unit of biomass than *Typha angustifolia* and graminoid plants supporting a well developed inflorescence at their apex. Germlings from the seed bank were thus exposed to 32% of incident light among stems of *Schoenoplectus lacustris,* 7% among *Typha,* and < 1% of incident light among graminea. Such differences in strategic use of light and space by emergent species represent one of the mechanisms responsible for the establishment of different plant communities according to water-level conditions.

The drying of deep marshes (+0.5 to 1 m CD) also reduced the biomass of obligatory emergents and led to colonization by various grass (*Phragmites australis*, *Leersia oryzoides*) and annual species (*Impatiens capensis, Polygonum* spp.*, Ranunculus trychophyllum, Sonchus oleraceus, Hypericum* spp.) previously confined to elevations > +1.0 m (Fig. 4). A marked increase in the above- and belowground biomass of emergent species was thus observed at that elevation (Table 3). Obligatory emergent species found under average water levels occurred at roughly the same frequency (2–20% of samples), yet registered a decline in biomass by factors of between 7 (*Sparganium eurycarpum, Sagittaria latifolia*) and more than 20 (*Butomus umbellatus*, *Schoenoplectus lacustris*) (Table 4). Of all the species commonly occurring under average level conditions, only *Lythrum salicaria* increased both in frequency of occurrence and in biomass, with large adult plants interspersed with a multitude of young seedlings. *L. salicaria* seedlings were especially numerous just above the water line (0 to +0.5 m CD elevation range), where open dry ground was available for colonization in between shoots of obligatory emergent wetland species. Submerged plant species, which used to grow among the stems of emergent plants under average level conditions, were mostly absent, except for small (< 2 cm) *Heteranthera dubia* germlings subsisting on waterlogged soil.

Very shallow open water into barren ground (0 to -0.24 m CD). At this elevation, the water was about 1-m deep under average level conditions, resulting in a dense cover of submerged plants; under low water levels, this zone alternated between submerged (up to 30 cm in May and October) and dry (August to mid-September) conditions. This was the stratum at which species composition and biomass were most variable, closely following seasonal water-level variations. Low water levels turned very shallow open-water areas (0 to -0.25 m CD) into barren grounds periodically flooded and dried out (Fig. 4), as water levels fluctuated above and below chart datum during most of the summer of 1999 (Fig. 3a). Under average water-level conditions, this elevation range supported dense submerged vegetation, which disappeared when the water line receded beyond the edge of emergent plants (Fig. 4, Table 3). In fact, this stratum was the most obviously impacted by extreme low water levels as it supported the lowest biomass of all the strata (121 g DM m^{-2} in mid-summer, Table 3) and appeared as a band of dried, barren soil, with a dense layer of filamentous algae (Table 4). This was as a result of its location at an elevation below the threshold of previously established emergent macrophytes yet above the level which was constantly under water. The rapid succession of flooded and dried-out conditions thus effectively prevented the establishment of either aquatic or terrestrial vegetation, since seedlings of both types were killed by the onset of new water-level conditions.

Macroscopic algae (*Chara* 30% of 57 samples, filamentous algae 39%) were commonly encountered in the samples and accounted for most of the biomass; this group showed a very short response time to low water levels and became very abundant during July and August, coinciding with conditions of high illumination and warm water temperatures in very shallow (2–10 cm) waters. Submerged macrophytes (*Vallisneria americana* 39%, *Myriophyllum* spp. 32%, *Potamogeton richardsonii* 18% and *Heteranthera dubia* 11%) also responded relatively quickly, although part of their biomass might have originated from plants carried ashore and beached by cycles of rising and falling water levels. From late June onwards, germlings of obligatory (*Schoenoplectus lacustris, Alisma gramineum, Eleocharis smallii* and *Typha angustifolia*) and facultative (*Polygonum lapathifolium, P. persicaria, Phalaris arundinacea*) emergent macrophytes were also frequently observed (Fig. 6), albeit representing the smallest biomass (Fig. 5c).

On May 6, small fragments of living submerged vegetation were found, suggesting that submerged vegetation (*Elodea canadensis, Lemna trisulca, Ceratophyllum demersum, Vallisneria americana*) initiated seasonal growth when water temperatures > 10°C, around May 1. On May 20, biomass was dominated by *Potamogeton richardsonii* and *Lemna trisulca*, with the common occurrence of other submerged species. The shallowest samples were composed exclusively of dead plant material. On June 1, plants in this elevation range were at the water's edge, with samples rich in *Myriophyllum* spp. and *Vallisneria americana* (8 cm deep) and others covering a bare zone of anoxic mud (< 5 cm). The zone of bare mud was beyond the water on June 17, adjacent to *Vallisneria* and *Chara* in shallow water (20 cm). In late July, the transition zone became dry and showed a thick mat of dead *Chara* sp. and filamentous algae, which overlaid a layer of wet *Vallisneria americana* just above the water's edge. Minute germlings of flowering *Heteranthera dubia* were also observed next to small *Schoenoplectus* spp*., Butomus umbellatus, Sagittaria latifolia, Alisma gramineum,* (mostly small individuals and buds) on waterlogged soil during this period (Fig. 7a).

Two (August 10) and four (August 24) weeks later, the zone was still dry and small *Polygonum* spp. germlings were visible, while a thick mat of dried-up filamentous algae overlaying *Vallisneria americana, P. richardsonii* and *Myriophyllum* spp. was still present at the water's edge. It is likely the algae prevented the submerged macrophytes from desiccating whichever basal parts could remain alive owing to a few short-lived episodes of rising waters during this period, through water percolation and capillary movement through the sediments. The presence of shallow water (< 15 cm) in September and the drop in temperature prompted another change in the assemblage, which became dominated by submerged (Aug. 24–September 7) and emergent macrophytes (subsequent dates). On October 6, dead *Vallisneria* was found above the water's edge, carried up by the previous episode of water rise and fall (Figure 7a).

Shallow water to very shallow open water (-0.25 to -0.50 m CD). This range of elevation shifted from about 1.3 m to 0.3 m deep when water levels dropped from average to low (1999); such a change resulted in a markedly different species composition and biomass (Figure 4b), with extensive colonization by macroscopic algae (*Chara* sp. and filamentous algae, Table 4). This zone was always submerged, although from mid-July to mid-September, water depth was < 0.10 m, with brief periods < 0.02 m. This stratum was dominated by submerged macrophytes (*Elodea canadensis* 96% of 52 samples, *Vallisneria americana* 85%, *Myriophyllum* spp. 96%, *Potamogeton* spp. 58% and *Heteranthera dubia* 58%), with a period of high macroalgal (*Chara* sp. 69%, filamentous algae 46%) biomass during the period of lowest water levels (August), as was observed in the previously described barren zone (Figure 7b).

Dominance by algae most likely resulted from their ability to grow rapidly under conditions of high temperature, high illumination and rapid depth fluctuations, including the occasional, albeit short-lived, dry period. A comparison of individual species biomass for macroscopic algae between water level conditions also points to a shift from *Nitella* to *Chara* sp. and to a much higher frequency (from 2 to 45% of samples, Table 4) and a 30-fold increase in overall algal biomass (Table 3).

When lowest water levels were reached in mid-August, bleached filamentous algae and *Chara* sp. formed a crust on top of vascular macrophytes, which remained alive throughout the mid-summer low-water period. By the end of August and early September, after one month of very low water levels (depth < 0.10 m), numerous germlings of emergent (*Typha angustifolia* and *Alisma gramineum*) species were observed. *Alisma gramineum* formed extensive prairies with emergent flowering structures throughout adjacent shallow-water mudflats. Emergent macrophyte germlings disappeared after water depth rose above 0.25 m after the middle of September.

Deep to shallow open water (-0.51 to -1 m CD). Whereas, under average water levels, this elevation range was under 1 to 2 m of water, water depth in 1999 was reduced < 1 m, with depth being shallowest (30 cm) in August. The lowest elevation range (-0.5 to -1m CD) corresponded to waters > 2 m deep under average level conditions, which were reduced to < 1 m under low levels; this stratum exhibited a high biomass of macroscopic algae in conjunction with a high biomass of submerged macrophytes. The same species assemblage of submerged plants (*Elodea canadensis* 98% of 48 samples, *Vallisneria americana* 88%, *Myriophyllum* spp. *98%*, *Potamogeton richardsonii* and *Stuckenia pectinata* 25% and *Heteranthera dubia* 83%), dominated this stratum, both in frequency of occurrence and in biomass (Figure 7c). A greater water depth than at the previous stratum fostered the formation of a two-layered assemblage, with species forming a sub-surface canopy (*Elodea, Myriophyllum* spp., *Potamogeton)* expanding above those remaining closer to the bottom *(Vallisneria* and *Heteranthera*). Throughout the sampling season, canopy-forming species represented > 50% of total biomass, with maximum canopy development at the time of lowest water levels (August). The biomass of macroscopic algae (*Chara* 85%, filamentous algae

52%) during the period of lowest water depth (July–August) was in the same range (50–100 g DM m^{-2}) as observed in the above stratum.

Although the species composition and structural arrangement of the community under low levels were very similar to conditions under average water levels, aboveground biomass under low levels (0.535 kg DM m^{-2}) was twice as high as under average levels (0.266 kg DM m^{-2}) (Table 3). Reduced depth had a negative effect on the biomass of *Vallisneria americana* (3x decrease) and *Myriophyllum* spp. (2x decrease) and a positive effect on the biomass of *Heteranthera dubia* (3x increase) (Table 4).

Discussion

Comparison of wetland responses to low levels in 1999 and 1931

Water level is the predominant physical force acting to shape wetland community structure and biomass, especially in the wet-dry transition zone, and our study offers the opportunity to quantify the magnitude and speed of response of wetland species. Wetlands and riparian vegetation respond to small changes in water levels between years (Ekzertzev 1979; Keddy and Reznicek 1986). Events of a relatively small amplitude and short duration such as seiches or wind-tides can affect the zonation of plant communities, although they are poorly understood (Batterson et al. 1991). In addition to the low levels of the 1931 season, Marie-Victorin (1943) identifies both the decrease in water levels in the 20 years previous (1910–1930) and the reduction in spring floods (as a result of control of ice jams) as other hydrological mechanisms explaining the changes in vegetation.

The abundance of *Butomus umbellatus* varied markedly since its first introduction near Montreal in 1897. This species showed a strong expansion from 1920 to 1950, especially along the south shore of the Montreal archipelago, where it was the dominant plant on the littoral (Marie-Victorin 1943). A marked decrease of this species' abundance and density was reported since the 1950's, attributed to (unspecified) changes in environmental conditions and competition with *A. gramineum* (Pageau et al. 1971). Nevertheless, *B. umbellatus* remains a common plant along the St. Lawrence River shorelines. It is noteworthy, however, that the biomass of *Butomus umbellatus* and *Myriophyllum* spp. decreased with low water levels, whereas that of *Typha* *angustifolia, Lythrum salicaria* and *Phalaris arundinacea* increased, from 11 to 60% of total emergent plant biomass (Table 4). This strong response to disturbance could be an indication of the major, cumulative, physical perturbations the islands of Boucherville have withstood over the decades. Native and non-native species alike are reported to invade or increase in abundance on river margins following water-level regulation (Johnson 1994; Bush and Smith 1995; Décamps et al. 1995). Colonization by opportunistic annuals (*Polygonum lapathifolium*), perennials (*Cyperus* spp.) and trees (*Populus deltoides*) was also observed in both studies in the newly dried-out zone, as was the establishment of a new zonation based on a new water line.

Both Marie-Victorin's 1931 study and the present one show the increased susceptibility to monospecific dominance by exotic and aggressive species under low water levels: the rapid expansion of *Phalaris arundinacea* was observed both in 1931 and in 1999. *Typha angustifolia, Phragmites australis, Lythrum salicaria* (in 1999 only) and exotic *Butomus umbellatus* (in 1931 only) gained territory under low water-level conditions. In addition, both studies highlight the success of taxa specifically adapted to water level variations: the expansion, massive germination and flowering of *Alisma gramineum* in water-saturated mudflats as well as the increased occurrence of linear-leaved forms of *Butomus umbellatus* were noticed in 1931 and in 1999. Conversely, our results suggest the negative effects of low winter levels on species located at the lower margin of the emergent plant bed, such as *Sagittaria latifolia*, which became much less frequent in 1999, possibly following the exceptional freezing of its roots. Other deep-rooted perennial species growing at higher elevations (such as *Sparganium eurycarpum, Typha angustifolia, Butomus umbellatus*) showed a dramatic biomass reduction (Table 4), but remained in place.

Colonization of opportunistic annuals (*Polygonum lapathifolium*), perennials (*Cyperus* spp.) and trees (*Populus deltoides*) was also observed in both studies in the newly dried-out zone and in the establishment of a new zonation according to a new water line (towards a new steady state). Plants with short generation times are often favoured in human-impacted ecosystems, but such species also benefit from the natural formation of disturbance patches (Grime 1979; Huston 1994), such as those opened by ice scouring (Bélanger and Bédard 1994).

Major species composition also differed in some respects between 1931 and 1999. Marie-Victorin's finding that «*Equisetum* are numerous in species and individuals in this habitat which is eminently favourable for them, in which they form distinct zones» includes *E. fluviatile, E. arvense, E. palustre var. americanum* and *E. littorale*. In addition, Marie-Victorin (1935) indicates that «*E. palustre* covers vast expanses around the low-lying islands of the St. Lawrence». Although *Equisetum* spp. are still observed in more recent plant surveys, they no longer dominate riparian assemblages or form distinct zones; such a reduction in the abundance of Equisetales may be the result of nutrient enrichment in water and in sediments. The hypothesis of a shift in dominant species composition prompted by nutrient enrichment is supported by results of a negative correlation of *Equisetum fluviatile* and of a positive correlation of *Typha angustifolia* with wetland fertility (Auclair et al. 1976).

Nutrient enrichment may also explain the occurrence, in the 1990s, of three species of *Potamogeton* tolerant to high nutrient concentrations (Riis and Sand-Jensen 2001) — something not mentioned in Marie-Victorin's (1943) paper*: P. crispus, P. richardsonii* and *Stuckenia pectinata* (*P. pectinatus).* Eutrophication and a warm water temperature may also account for the massive growth of *Chara* sp. and filamentous algae in 1999 in very shallow (< 10 cm) waters, also not reported by Marie-Victorin in 1931. Under low level conditions, massive algal growth could be sustained by high light intensity, warm temperatures and nutrients released from sediments and decomposing vascular plants in shallow water.

Implications of water-level variations for faunal habitat quality

Under high level conditions, *Typha angustifolia, Schoenoplectus* spp.*, Bolboschoenus fluviatilis* and *Sagittaria latifolia* coexist with *Elodea canadensis* and *Myriophyllum* spp. growing in cool, shaded waters amongst the stems, which provide food, shelter and protection from predators for a wide variety of invertebrates and vertebrates (Giroux and Picard 1993). Narrow-leaved native wetland species (*Typha angustifolia, Schoenoplectus lacustris*) allow a fraction of light to reach the ground/water surface, leading to the growth of some vascular plants and algae between their stems (Table 5). Our measurement of a 68-99.8% reduction of incident light within the canopy of various emergent wetland species are consistent with those reported by

Ondok (1978). Flooded marshes with an optimal ratio of open water to emergent vegetation represent important habitats for aquatic birds and waterfowl (Weller and Spatcher 1965; Kaminsky and Prince 1981), providing a food supply of plants and invertebrates as well as shelter from predators (Lemay 1989). The presence of emergent plants shading the shallow waters from direct sunlight maintains cool water temperatures, prevents the excessive development of filamentous algae, and maintains high O_2 saturation.

Conversely, under low level conditions, the dense monospecific growth of *Phalaris arundinacea, Phragmites australis* and *Lythrum salicaria* on dry ground monopolizes most of the incident light (Table 5) and forms dense strands on dry land, thus preventing the growth of other plant species under its canopy. Although dense grass strands provide optimal nesting habitat for ducks, juvenile survival may be affected by the presence of a dry barren zone at the water's edge; ducklings loafing or sleeping on mudflats and in open, dry areas are vulnerable to predation by mammals, which have easy assess to the area (Keith 1961). Rapid shifts (< 1 month, Figures 5C and 6) from wet to dry conditions generate barren mudflats, because vegetation can never adapt to wet or dry conditions. This shoreline band, completely devoid of vegetation, likely persists after high water levels subside and maintains reduced shallow-water productivity the year following the return to normal. In addition to altered biomass distribution and productivity, the vulnerability of ducklings to disturbance and predation is also enhanced by their visibility, since the shallow open waters they must use for foraging lie outside the belt of emergent plants. Submerged plants growing in open water outside the emergent plant cover are subject to warm and highly illuminated conditions, thus favouring *Chara* sp., filamentous algae and *P. richardsonii* at the expense of native *Vallisneria americana*. Such changes alter the surface area and modify the habitat potential for aquatic micro-invertebrates and vertebrates.

Spring flooding of the tall grass cover that has proliferated during a season of low water levels in the previous summer may provide the optimal ground cover for esocids using the floodplain for egg laying and larval rearing (Casselman and Lewis 1996). *Phalaris arundinacea* and other graminoid plant cover is preferred to *Typha* spp. and *Schoenoplectus* spp., since it provides an elevated area for egg attachment, adequate cover for juveniles but little obstruction to adult movements (Bry 1996; Fortin et al. 1981; Franklin and Smith 1961). The benefits of alternating low summer levels and subsequent high spring flood for pike recruitment should be examined in the future, in conjunction with water levels and temperature effects within and outside the floodplain (Farrell 2000). Sports fish yield was positively correlated to wetland surface area and emergent vegetation in 66 lakes of north eastern North America (Whillans 1989).

Water-level variations also affect the distribution and quality of biomass along the vertical shoreline gradient as well as the overall productivity of the littoral fringe of wetlands, both in terms of primary and secondary production. Disruption of biomass cover and differences in carbon quality further alter the food chain structure supported by the wetland. It could be argued that episodes of low water levels increase the spatial variability of primary production, since such events favour high biomasses of cellulose-rich grasses and sedges at high elevations, and low biomasses of rapidly recycled labile macroscopic and filamentous algae at elevations located in the wet-dry transition zone. Under low water-level conditions, the detrital organic matter resulting from litter and emergents (35% and 45%) is four times as large as the more labile fractions produced by submerged plants (16%) and algae (3%). In contrast, under average and high water-level conditions, terrestrial detrital components of litter and emergent (21% and 42%) plants represent only about twice the amount of organic standing-stock in the adjacent aquatic submerged (36%) macrophytes and algae (1%). In the short term, low levels thus deprive micro-invertebrates and vertebrates of the shelter and proximity of food provided by flooded, dense emergent plants. Water-level changes over a five-year period resulted in an 18-fold difference in the primary productivity of a prairie wetland, as the vegetation went through phases of drying, regenerating, degenerating and extreme flooding (van der Valk and Davis 1978).

Effects of water-level fluctuations on wetland vegetation dynamics

Differences in weather and water-level conditions between years of average and extremely low water levels generated important differences in immersion-emersion regimes at equivalent elevations along the riparian zone (Figure 4). In turn, water availability and the frequency of immersion-emersion cycles had a major effect on aquatic plant species composition and biomass. Their speed of adaptation to strong variations in water levels largely depends on the ecological traits of aquatic plants and the period at which changes in levels occur; changes in the biomass of algae, submerged vascular and emergent vascular plants were recorded in a matter of days, weeks, and months, respectively. Our results show that, during the growth period, germlings of numerous species of facultative and obligatory emergent macrophytes were found in the barren, periodically emergent and submersed zone near the water's edge. This observation suggests that, given recurrent low levels over several years, a dense cover of emergent vegetation could re-establish itself within 2 to 3 years.

Similarly, our observations of marsh vegetation response to dry conditions in 1999 reveal that perennial obligatory wetland vegetation can maintain itself under dry conditions for at least one year, thereby ensuring an intact emergent flora if water levels were to return to their previous values. Inter-annual changes in water level can be accompanied by dramatic changes in vegetation: it often takes 3 to 5 years to re-establish plant communities in a wetland after a significant disturbance (Bush and Lewis 1984; Quinlan and Mulamootil 1987). Plant community displacement models with a constant topographic gradient are useful to assess changes in wetland zonation following inter-annual water-level fluctuations (Harris and Marshall 1981; Herdendorf et al. 1981; 1986; Keddy and Reznicek 1986; Quinlan and Mulamootil 1987). The shift of vegetation to shallow or deep water can only occur if the slope is shallow, in the absence of natural or human-induced barriers, with suitable substrate, and if the rate of water-level change is gradual enough for vegetation to re-establish itself (Bedford et al. 1976).

In the period prior to discharge regulation and control of ice-jams (i.e. pre-1960), repeated physical stresses induced by seasonal variations in water levels and ice kept the wetlands of the St. Lawrence River in a constant state of flux. Subsequent excavation of the Montreal Harbour and shoreline alterations have likely reduced water circulation through the Boucherville archipelago, which is slowly becoming filled in with emergent vegetation (Fig. 2) and invaded by new plant species. Such morphological alterations could explain some of the differences recorded between Marie-Victorin (1943) and the present study.

Since 1960, however, human interventions such as water-level regulation, reduction of ice scouring, control of ice jams and reduction of spring floods have markedly decreased the within-year range of water levels but increased their among-year variability (Figure 1). Whereas exceedingly high supplies were a problem in the 1970s and 1980s, the 2000s may bring extended periods of extremely low water supplies to the Great Lakes. Although managing extremes is always a challenge, managing drought conditions may prove to be the biggest challenge of all, since drought exacerbates human pressures, thus imposing the need to weigh economic interests against other concerns. The strong response of St. Lawrence River wetlands (and associated fauna) to water level changes makes them highly vulnerable to the cumulative impacts of climate change and human interventions.

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Acknowledgments

This study could not have been completed without the help of many staff members of the St. Lawrence Centre (Environment Canada). The author thanks J.-P. Amyot, D. Poulin, C. Lemay, S. Légaré, J. Amaral, J. Tena-Russell and visiting staff for their help with field and laboratory work. Maps and diagrams were drawn by F. Boudreault and D. Seguin; G. Létourneau supplied recent remote sensing data. Hydrographic data and support information were supplied by G. Morin and J. Laroche (Meteorological Service of Canada , Environment Canada), D. Spears and T. Dougherty (Marine Environment Data Service, Fisheries and Oceans Canada). Thanks also to Ms Anne-Marie Bernier-Brière and the staff of the Charles-J. Des Baillets (City of Montreal, LaSalle) water filtration plant for water temperature data. M. Montpetit, A. Julien and R. Dragovici (Meteorological Service of Canada, Environment Canada) kindly gave us access to the National Meteorological Data base. D. Lehoux and A. Armellin helped identify the implications of wetland quality for fauna. J.-P. Amyot, M. Jean, C. Plante and P. Potvin (St. Lawrence Centre, Environment Canada) reviewed earlier versions of the manuscript.

List of Figures

Figure 1. Average monthly (vertical lines), seasonal average during the growing season (bold line), and long-term average (dotted line) water levels recorded between April 1–September 30 in Montreal Harbour (Jetty No. 1), for the period 1913–2002. Vertical arrows indicate the years 1931 and 1999.

Figure 2. Maps of the study area, contrasting the extent of urbanization on Montreal Island (top panels) in 1932 (A, city plan from Divay and Gaudreau 1992) and in 1989 (B, LANDSAT imagery obtained from G. Létourneau, St. Lawrence Centre, Environment Canada, pers.comm.). Alteration of the shoreline and land use patterns in the Boucherville Islands (bottom panels) are shown for 1931 (C, black and white aerial photographs taken on May 6th, 1.14 m above CD) and 1996 (D, multispectral videography taken on October 17th, 0.81 m above CD). Enclosed areas on panels C and D indicate the study sites of Marie-Victorin (1943) and of the present study, respectively.

Figure 3. Seasonal variations in (*a*) water level and (*b*) water temperature in 1931 (dashed line) and 1999 (solid line) compared to the previous ten-year intervals of 1921–1930 (bold dashed line) and 1989–1998 (bold solid line) for the Montreal area. The water level was measured at Montreal Harbour (Jetty No. 1); water temperature was obtained from the Charles-J. Des Baillets water filtration plant (City of Montreal, LaSalle).

Figure 4. Schematic representation of wetland plant zonation under average and low water levels, showing the limits of the elevation strata and corresponding changes in water depth/plant assemblages documented in this study. For each hydrological regime and plant community, the distribution of aboveground biomass (kg DM m^{-2}) into emergent, submerged, algae and litter plant type is shown.

Figure 5. Seasonal variations in aboveground biomass of facultative (full symbols) and obligatory (open symbols) emergent macrophytes, for the three plant assemblages located in the upper littoral zone: A, Dry meadow, +1 to +0.51 m CD; B, Wet meadow, +0.50 to +0.025 m CD; and C, Barren ground, 0 to -0.24 m CD. Note that the scale of biomass (left Y axis) is identical for dry and wet meadows, whereas scale is reduced by a factor of 80 for barren ground. The dotted line on each panel (right Y axis) indicates water-level variations with respect to mean elevation of samples (dashed horizontal line); hatched areas indicate periods under water.

Figure 6. Seasonal variations in the relative frequency of obligatory emergent, facultative emergent, vascular and non-vascular submerged plant species in barren grounds (0 to -0.24 m CD), showing short-term colonization by different plant groups under variable water levels (right Y axis).

Figure 7. Seasonal variations in aboveground biomass of emergent (full triangles) and submerged vascular plants (full circles) and of macroscopic algae (open circles) for the three plant assemblages located in the lower littoral zone: A, Barren ground, 0 to -0.24 m CD; B, Very

shallow open water, -0.25 to -0.50 m CD; and C, Shallow open water, -0.51 to -1 m CD. Note that the scale of biomass (left Y axis) differs on the three graphs. The dotted line on each panel (right Y axis) indicates water-level variations with respect to mean elevation of samples (dashed horizontal line); hatched areas indicate periods under water.

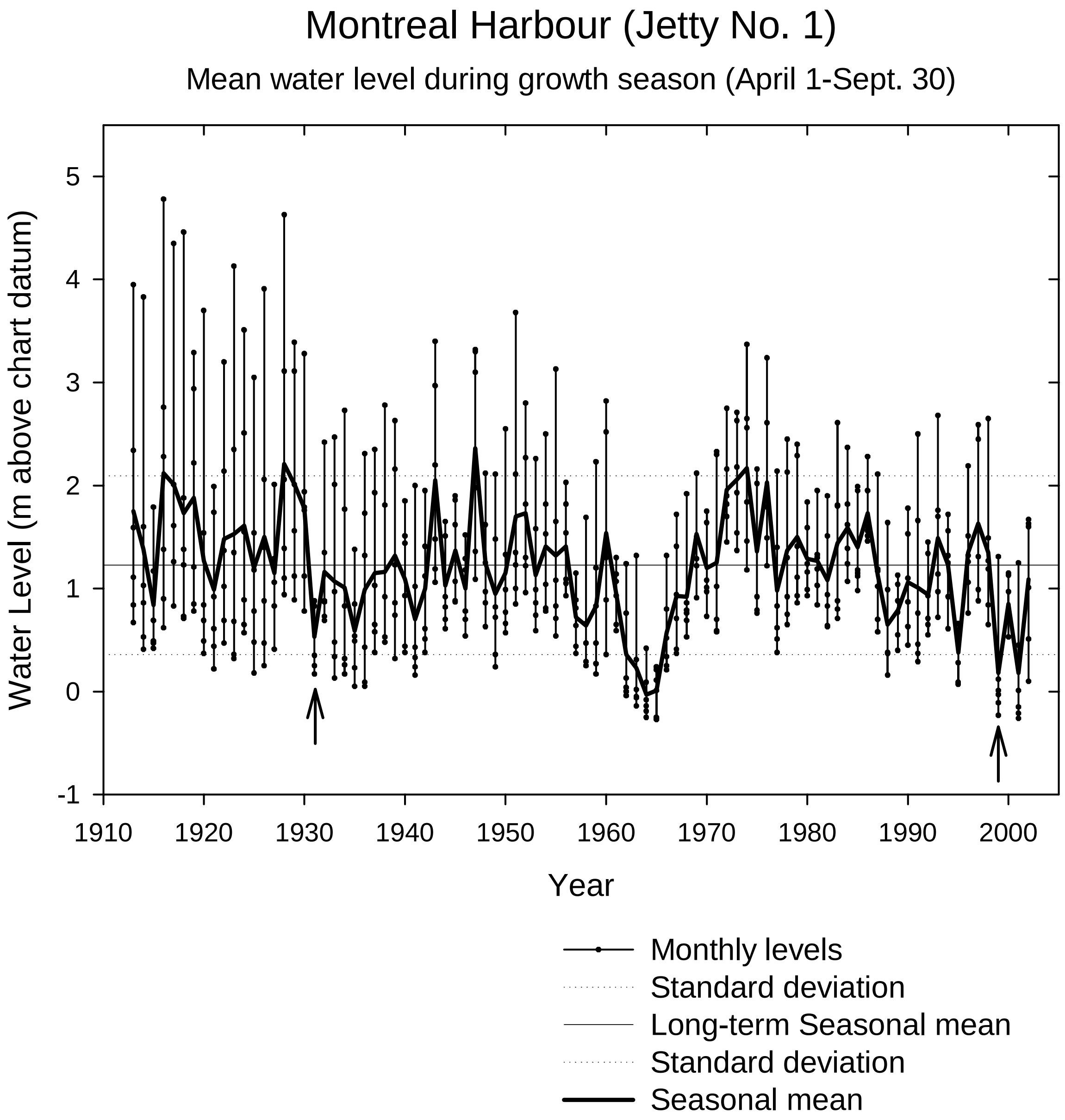
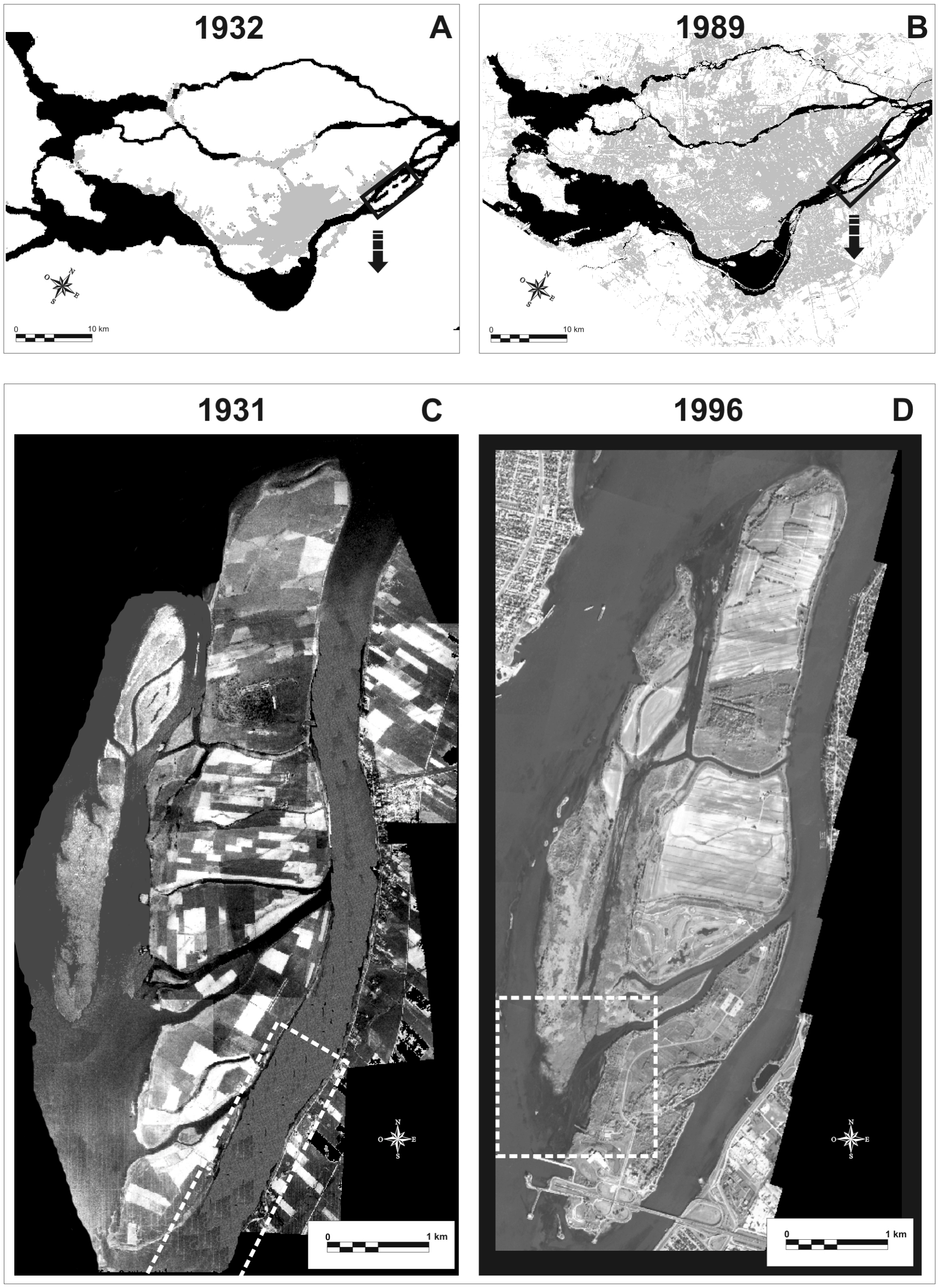

Montreal Harbour (Jetty No. 1)
Mean water level during growth season (April 1-Sept. 30)
Water Level (m above chart datum)
5
4
3
2
1
0
-1
1910
1920
1930
1940
1950
1960
1970
1980
1990
2000
Year
Monthly levels
Standard deviation
Long-term Seasonal mean
Standard deviation
Seasonal mean

Figure 1

Figure 2- Historical and current condition of the study area



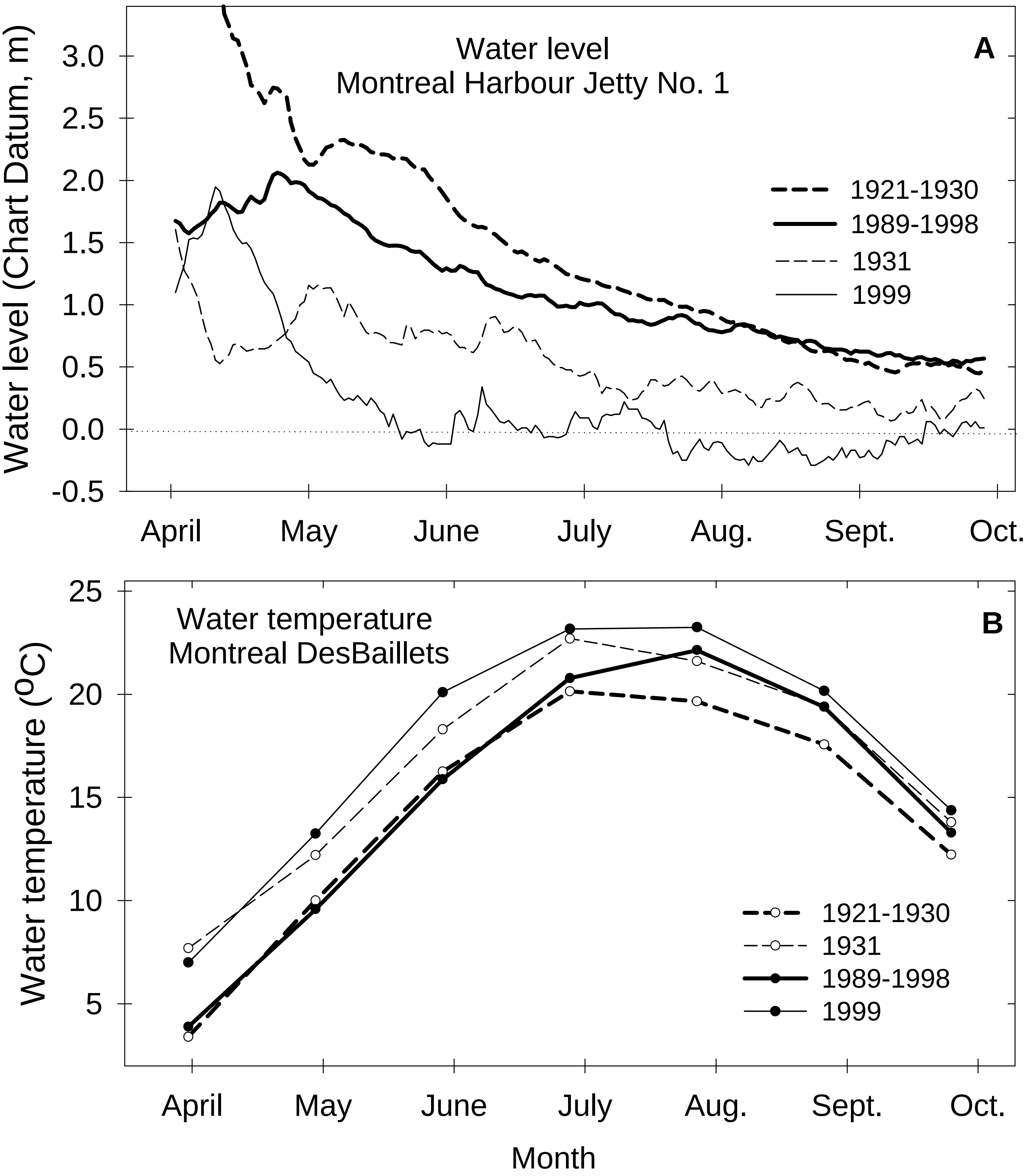

Water level
Montreal Harbour Jetty No. 1
A
Water level (Chart Datum, m)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
1921-1930
1989-1998
1931
1999
April
May
June
July
Aug.
Sept.
Oct.
Water temperature
Montreal DesBaillets
B
Water temperature (^{o}C)
25
20
15
10
5
1921-1930
1931
1989-1998
1999
April
May
June
July
Aug.
Sept.
Oct.
Month

Figure 3

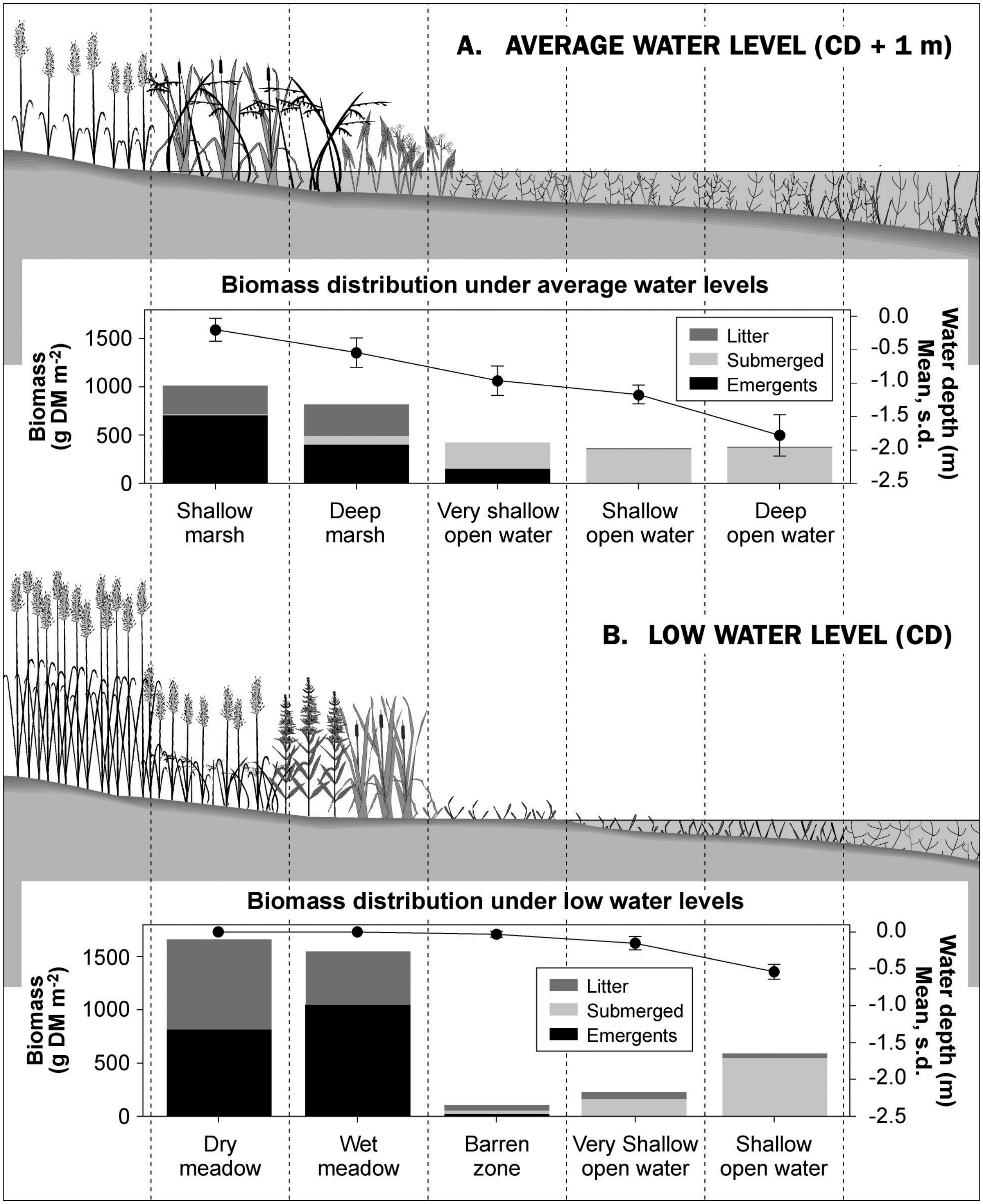

A. AVERAGE WATER LEVEL (CD + 1 m)
Biomass distribution under average water levels
Biomass (g DM m-2)
1500
1000
500
0
Water depth (m) Mean, s.d.
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
Litter
Submerged
Emergents
Shallow marsh
Deep marsh
Very shallow open water
Shallow open water
Deep open water
B. LOW WATER LEVEL (CD)
Biomass distribution under low water levels
Biomass (g DM m-2)
1500
1000
500
0
Water depth (m) Mean, s.d.
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
Litter
Submerged
Emergents
Dry meadow
Wet meadow
Barren zone
Very Shallow open water
Shallow open water

Figure 4

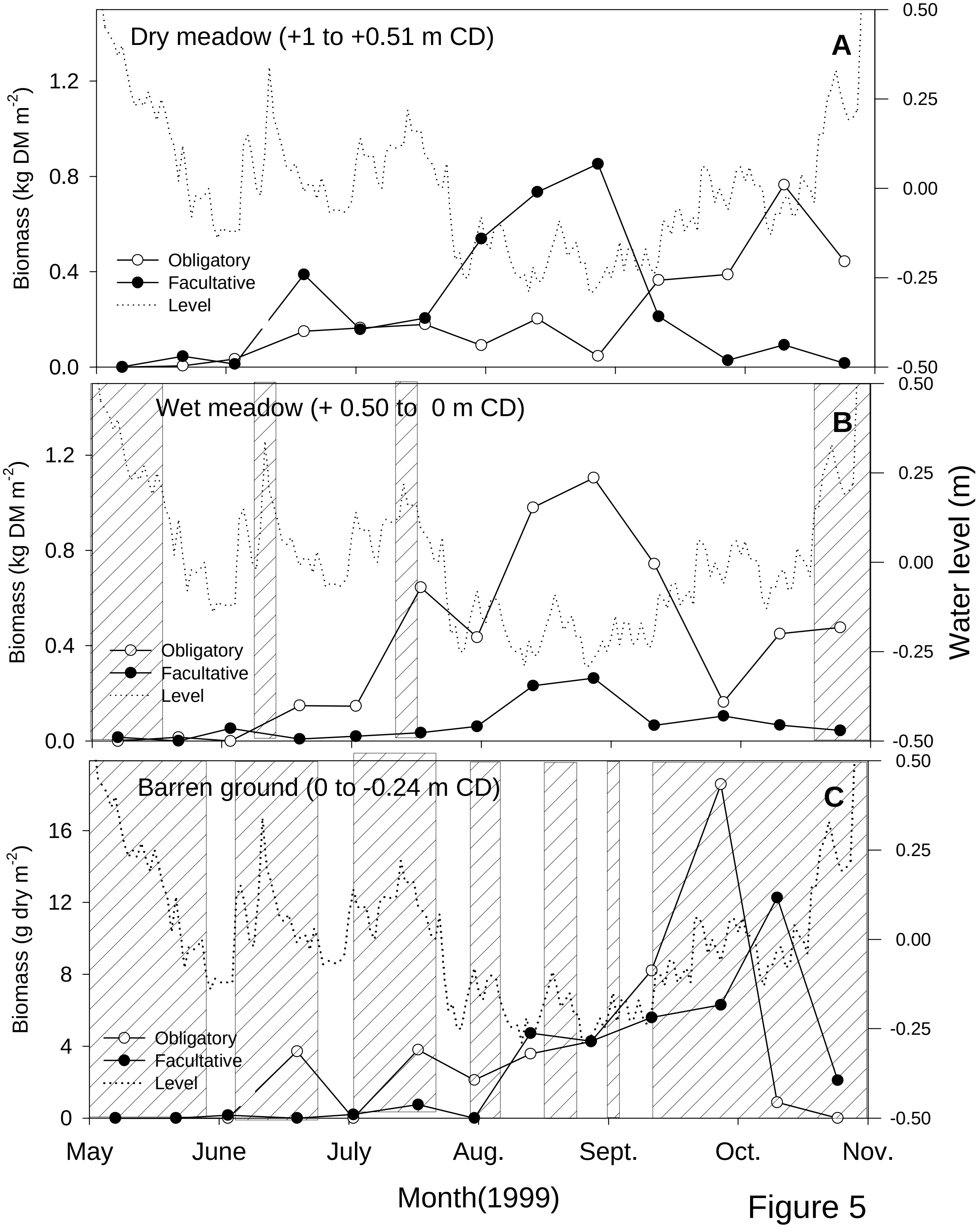

Dry meadow (+1 to +0.51 m CD)
A
Biomass (kg DM m-2)
1.2
0.8
0.4
0.0
0.50
0.25
0.00
-0.25
-0.50
Obligatory
Facultative
Level
Wet meadow (+ 0.50 to 0 m CD)
B
Biomass (kg DM m-2)
Water level (m)
Barren ground (0 to -0.24 m CD)
C
Biomass (g dry m-2)
16
12
8
4
0
May
June
July
Aug.
Sept.
Oct.
Nov.
Month(1999)

Figure 5

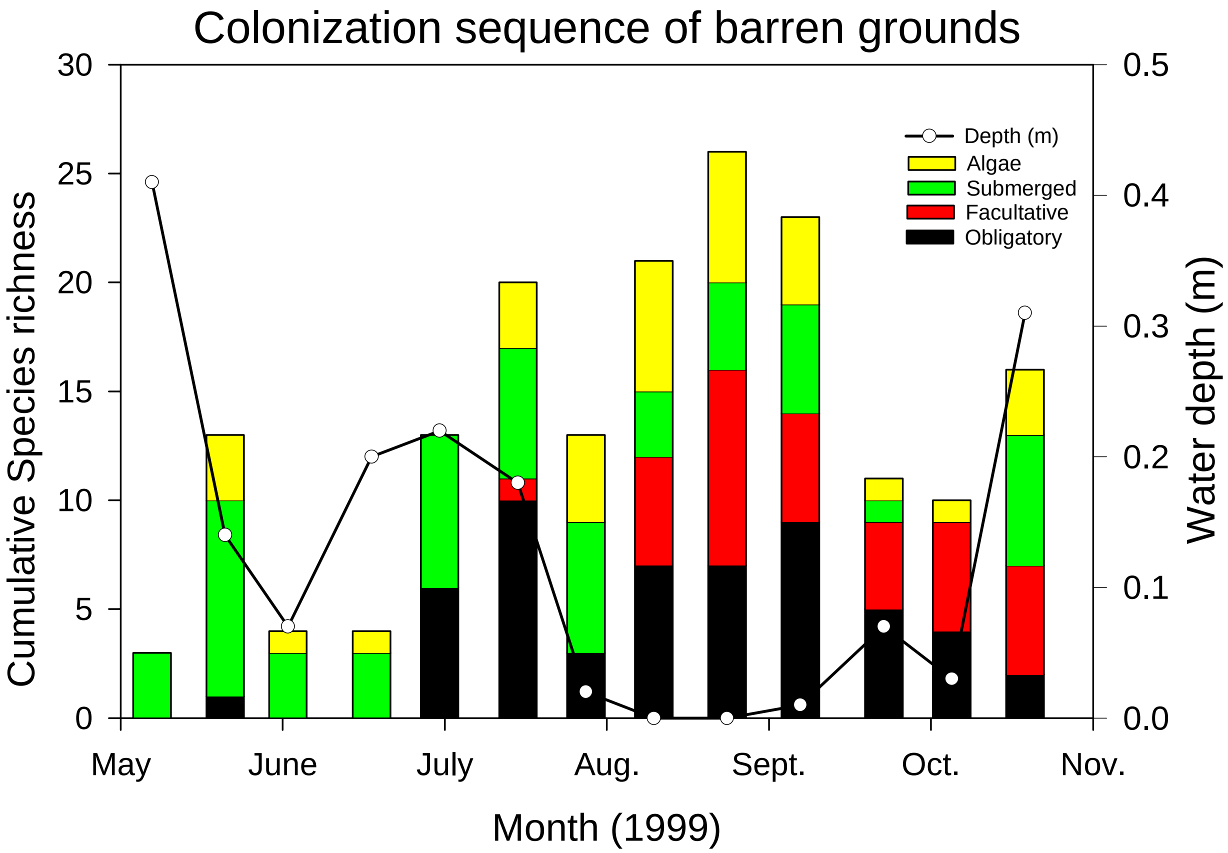

Colonization sequence of barren grounds
Cumulative Species richness
0
5
10
15
20
25
30
Water depth (m)
0.0
0.1
0.2
0.3
0.4
0.5
May
June
July
Aug.
Sept.
Oct.
Nov.
Month (1999)
Depth (m)
Algae
Submerged
Facultative
Obligatory

Figure 6

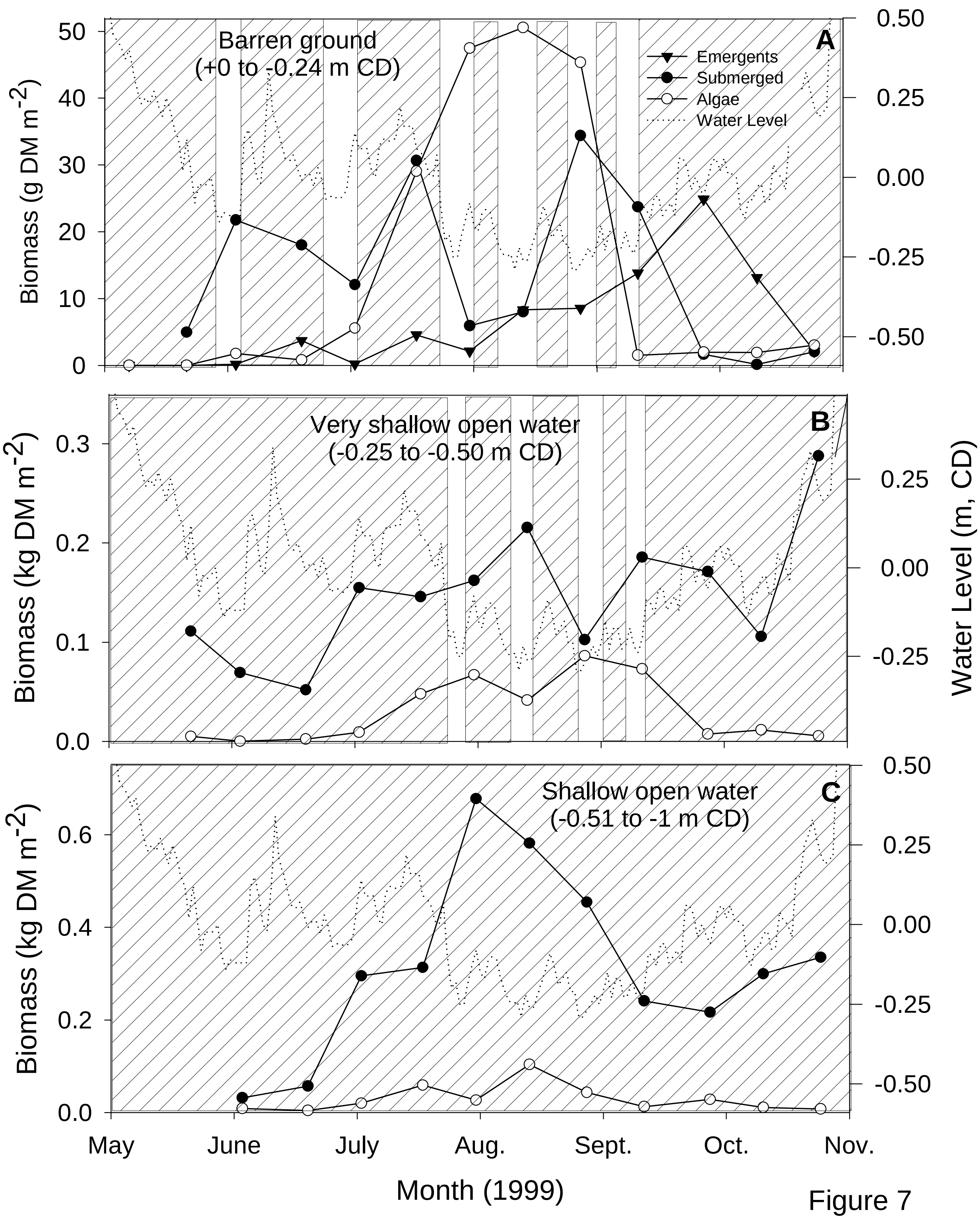

Barren ground
(+0 to -0.24 m CD)
A
Emergents
Submerged
Algae
Water Level
Biomass (g DM m-2)
0
10
20
30
40
50
0.50
0.25
0.00
-0.25
-0.50
Very shallow open water
(-0.25 to -0.50 m CD)
B
Biomass (kg DM m-2)
0.0
0.1
0.2
0.3
0.25
0.00
-0.25
Water Level (m, CD)
Shallow open water
(-0.51 to -1 m CD)
C
Biomass (kg DM m-2)
0.0
0.2
0.4
0.6
0.50
0.25
0.00
-0.25
-0.50
May
June
July
Aug.
Sept.
Oct.
Nov.
Month (1999)

Figure 7

Table 1. Comparison of level and climatic conditions observed during the growing season (April 1–September 30) for sampling years of low water levels (1931 and 1999) and the preceding ten-year period. Water level at Montreal Harbour represents the average of monthly mean values measured at Jetty No. 1. Meteorological data for the Montreal area were obtained from the McGill (1921–1931), Saint-Hubert (sunshine, 1989–1999) and Dorval (1989–1999) weather stations. Historic (1921–1931) data for sunshine was not available (n.a.). Water temperature is the average of monthly mean values at the intake of the Charles-J. Des Baillets water filtration plant (City of Montreal, LaSalle).

	Average levels	Low levels	Average levels	Low levels
	1921–30 Mean (s.d.)	1931 Mean (s.d.)	1989–98 Mean (s.d.)	1999 Mean (s.d.)
Water level (m above Chart Datum)	1.55 (1.05)	0.53 (0.31)	1.03 (0.50)	0.18 (0.57)
Sunshine (Average daily no. of hours)	n.a.	n.a.	7.2 (1.8)	8.3 (1.5)
Air temperature (Average monthly, in ^{o}C)	15.2 (5.6)	17.0 (5.4)	20.8 (5.5)	22.9 (5.5)
Precipitation (Average monthly rain accumulation, in mm)	88.1 (42.4)	96.7 (50.3)	84.5 (30.6)	81.6 (60.4)
Water temperature (Average monthly, in ^{o}C)	14.4 (6.2)	17.0 (5.8)	15.3 (6.7)	17.8 (6.4)

Table 2. Comparison of wetland strata and species composition between average (before 1931 and before 1999) and low water level reported in 1931 (Marie-Victorin 1943) and 1999 (this study, in bold), at the end of the growing season (early September) for Boucherville Islands and Longueuil.

Average water levels before 1931 **Average water levels before 1999**		Low water levels (1931) **Low water levels (1999)**	
Stratum	Plant species composition	Stratum	Plant species composition
Shrubs	*Salix interior* and *S. longifolia* flooded extensively in spring due to ice jams and high water levels. **Before 1999: *Salix* sp. abundant on higher grounds.**	Shrubs	Extensive flowering of *Salix* due to rapid water level drop in early spring. **1999: No observation of flowering conditions.**
Wet meadow	*Plantago major, Xanthium pungens, Ambrosia artemisifolia, Strophostyles helveola, Equisetum arvense.* **Before 1999: *Phragmites australis, Lythrum salicaria, Phalaris arundinacea, Butomus umbellatus, Equisetum fluviatile, Rumex verticillatus.***	Dry meadow	Proliferation of *Phalaris arundinacea* which formed large colonies in subsequent years, and later invaded the entire island. Persistence of *Equisetum arvense.* **1999: Same as 1931.**
Marsh	*Butomus umbellatus, Equisetum palustris* var. *americanum, Equisetum fluviatile, E. littorale.* **Before 1999: *Typha angustifolia, Phragmites australis, Lythrum salicaria, Schoenoplectus lacustris, Bolboschoenus fluviatilis, Sparganium eurycarpum, Sagittaria* sp. with submerged *Elodea canadensis, Myriophyllum* spp.**	Meadow	Proliferation of *Phalaris arundinacea* and disappearance of *Equisetum* spp., Persistence of *Butomus umbellatus.* **1999: Same as 1931. Proliferation of Graminea and facultative wetland (annual) species, various Compositae, *Lyhrum salicaria*; reduction of obligatory wetland species; disappearance of submerged species.**
Very shallow open water	*Myriophyllum exalbescens, Najas flexilis, Callitriche hermaphroditica, Elodea canadensis, Heteranthera dubia* (on mud or gravel bottom). **Before 1999: Same as 1931, with *Potamogeton richardsonii* and *Stuckenia pectinata.***	Dry, barren zone	Dry, barren zone colonized by annuals such as *Polygonum lapathifolium* var. *nodosum, Cyperus inflexus, C. esculentus.* **1999: Same as 1931. *Polygonum* spp., *Cyperus* spp., *Populus deltoides*.**
Shallow open water	*Chara* spp. (on clay or mud bottom). **Before 1999: *Myriophyllum sp., Elodea canadensis, Heteranthera dubia, Vallisneria americana, Ceratophyllum demersum, Potamogeton richardsonii* and *Stuckenia pectinata.***	Water-logged mud	Disappearance of submerged plants (*Chara*). Waterlogged mud extensively colonized by emergent and flowering *Alisma gramineum.* **1999: Same as 1931; presence of *Chara*, dense filamentous algae and submerged plant debris brought in by short-term rises in level.**

Open water (0.3–3 m deep)	Presence of *Butomus umbellatus* var. *vallisneriifolius* – submerged sterile form with ribbon-like leaves. **Before 1999: *Vallisneria americana, Elodea canadensis, Myriophyllum* spp., *Heteranthera dubia, Potamogeton richardsonii.***	Shallow open water	Proliferation of *Butomus umbellatus* var. *vallisneriifolius* with ribbon-like leaves extending to and floating on the surface; presence of the submerged, linear-leaved forms of *Sagittaria heterophylla* and *Alisma gramineum.* **1999: Presence of submerged, linear forms of *Butomus* and *Alisma*. Proliferation of other submerged vascular plants, especially canopy-forming species.**

Table 3. Comparison of elevation, water depth and maximum summer (late July–early September) biomass (Mean, s.d., g DM m^{-2}) of major plant groups between average (1 m above chart datum) and low (chart datum level) water level conditions. Values which differ significantly between level conditions (ANOVA on $\log_{10}$ transformed data + 1) are indicated in bold. The two median strata, which covered only a 25 cm elevation range, were assigned half the weight of the elevation strata covering a 0.5 m range for the calculation of overall weighted mean.

Stratum	Shallow marsh to dry meadow Average level/low level mean (s.d.)/mean (s.d.) biomass (g DM m^{-2})	Deep marsh to wet meadow Average level/low level mean (s.d.)/mean (s.d.) biomass (g DM m^{-2})	Very shallow open water to barren zone Average level/low level mean (s.d.)/mean (s.d.) biomass (g DM m^{-2})	Shallow to very shallow open water Average level/low level mean (s.d.)/mean (s.d.) biomass (g DM m^{-2})	Deep to shallow open water Average level/low level mean (s.d.)/mean (s.d.) biomass (g DM m^{-2})	Overall weighted mean Average level/low level biomass (g DM m^{-2})
N	19 / 20	35 / 13	14 / 21	16 / 18	21 / 20	
Elevation (m)	**0.63 (0.11) / 0.87 (0.11)**	**0.32 (0.14) / 0.14 (0.11)**	-0.08 (0.09) / -0.10 (0.08)	-0.41 (0.08) / -0.36 (0.07)	**-0.97 (0.25) / -0.71 (0.10)**	+1 m to -1 m CD
Water depth (m)	**0.20 (0.17) / 0 (0)**	**0.54 (0.22) / 0 (0)**	**0.96 (0.22) / 0.03 (0.04)**	**1.17 (0.14) / 0.15 (0.09)**	**1.78 (0.31) / 0.54 (0.10)**	
Aboveground emergent plants	707 (510) / 817 (628)	**404 (399) / 1046 (771)**	154 (228) / 9 (12)	0 (0) / 0 (0)	0 (0) / 0 (0)	237.6 / 373.5
Aboveground submerged plants	2 (10) / 0 (0)	**90 (133) / 0 (0)**	**275 (312) / 19 (45)**	**358 (262) / 161 (86)**	371 (248) / 548 (362)	155.9 / 127.6
Algae	11 (33) / 0 (0)	< 1 (1) / 0 (0)	**1 (3) / 32 (36)**	**13 (36) / 67 (58)**	**7 (21) / 43 (54)**	5.1 / 18.5
Litter	**298 (512) / 848 (442)**	**326 (544) / 503 (456)**	**< 1 (0) / 51 (82)**	**7 (16) / 7 (5)**	**6 (18) / 37 (44)**	126.7 / 283.4
Belowground biomass	**1586 (2086) / 2310 (1296)**	**490 (869) / 1507 (1433)**	**103 (143) / 10 (11)**	50 (72) / 25 (16)	43 (45) / 47 (41)	439.1 / 776.3
Sum	**2604 (2229) / 3975 (2048)**	**1310 (1229) / 3056 (2503)**	**533 (360) / 121 (90)**	428 (323) / 260 (81)	**427 (281) / 675 (425)**	964.4 / 1579.3

Table 4. Comparison of maximum summer biomass (g DM m^{-2}, Mean, s.d., N) recorded for various emergent and submerged macrophyte taxa collected in the +1 m to -1 m CD elevation range, under average (1 m above CD, 1993–94) and low (near CD, 1999) water-level conditions in the St. Lawrence River (Montreal area). Taxa were classified into obligatory (OBL) and facultative (FAC) wetland plants (Gauthier 1997; Reed 1988). Differences in biomass between average and low water conditions were tested using ANOVAs on log$_{10}$ transformed biomass data. Significantly different biomass values depending on water-level conditions ($p < 0.05$) are in bold. [1] Includes *Potamogeton richardsonii*, *P. crispus* and *Stuckenia pectinata* (*P. pectinatus*).

Taxon	**Wetland Classification System**	**Average water levels (Aug. 3–Sept. 3, 1993–94) Mean (s.d., N)**	**Low water level (July 27–Sept. 8, 1999) Mean (s.d., N)**	**Ratio of biomass Average: low level**
N		93	92	
Emergent vascular plants				
Populus deltoides	OBL	**0**	**0.6 (0, 1)**	
Polygonum spp.	FAC	**0**	**97.7 (164.3, 19)**	-
Phalaris arundinacea	FAC	189.8 (199.2, 3)	520.7 (597.7, 19)	1:3
Leersia oryzoides	OBL	**0**	**30.6 (37.7, 12)**	-
Other graminea	**-**	**0**	**1.20 (0.71, 4)**	-
Lythrum salicaria	FAC	34.4 (0, 1)	481.8 (228.8, 3)	1:15
Typha angustifolia	OBL	122.7 (0, 1)	434.4 (626.1, 23)	1:3.5
Butomus umbellatus	OBL	**313.9 (267.0, 7)**	**13.6 (14.4, 12)**	23:1
Sparganium eurycarpum	OBL	**865.8 (481.5, 10)**	**124.3 (92.5,3)**	7:1
Bolboschoenus fluviatilis	OBL	376.0 (280.9, 6)	212.8 (211.4, 15)	1.5:1
Schoenoplectus lacustris	OBL	**381.9 (354.8, 16)**	**13.8 (20.0, 13)**	28:1
Eleocharis smallii	OBL	24.4 (27.7, 8)	14.7 (22.9, 11)	2:1
Sagittaria latifolia	OBL	**368.8 (333.3, 26)**	**49.0 (30.4, 4)**	8:1
Alisma gramineum	OBL	43.4 (71.8, 7)	3.5 (3.8, 8)	12:1
Ranunculus spp.	OBL	**4.0 (0, 1)**	**27.5 (37.3, 5)**	1:7
Submerged vascular plants				
Ceratophyllum demersum	OBL	24.0 (57.5, 9)	15.6 (39.3, 8)	1.5:1
Lemna trisulca	OBL	0	0.3 (0.2, 7)	-
Elodea canadensis	OBL	86.2 (143.3, 36)	102.7 (176.3, 43)	1:1
Myriophyllum spp.	**OBL**	**177.5 (239.6, 42)**	**67.5 (96.5, 43)**	3:1
Heteranthera dubia	**OBL**	**29.1 (52.7, 10)**	**78.6 (137.6, 32)**	1:3
Potamogeton spp.[1]	OBL	49.6 (55.2,16)	27.5 (40.1, 20)	2:1
Vallisneria americana	**OBL**	**113.8 (95.3, 35)**	**27.2 (27.6, 40)**	3:1
Macroscopic algae				
Filamentous algae	**OBL**	**70.9 (59.7, 3)**	**32.1 (34.8, 42)**	2:1
Nitella sp.	**OBL**	**23.4 (43.0, 10)**	**0**	-
Chara sp.	**OBL**	**0**	**26.7 (41.3, 41)**	-

Table 5. Comparison of light extinction coefficient and percent light intensity available for plant colonization among the stems of established strands of different emergent wetland species. For each species, the equation allowing a determination of the fraction of incident light intensity (Iz /Io) remaining within strands of different heights (H) is given, with the fraction of total variance explained (r^2), the probability level of the relation (p) and number of measurements (N). All relationships are very highly significant ($p < 0.001$).

Taxon	**Above-ground biomass (kg DM m^{-2})**	**Plant height (H, cm)**	**Light extinction coefficient (K, m^{-1})**	**% incident light at ground level / below the canopy**	**Equation**	**r^2 (p)**	**N**
Phalaris arundinacea	1	140	4.271	0.25	$Iz/Io = 0.0042\ e^{0.0427\ H}$	0.95 $p < 0.001$	15
Phragmites australis	1.5	250	2.607	0.15	$Iz/Io = 0.0031\ e^{0.0261\ H}$	0.95 $p < 0.001$	26
Typha angustifolia	1.5	200	1.326	7	$Iz/Io = -0.0135 + 0.052\ H$	0.94 $p < 0.001$	21
Schoenoplectus lacustris	0.1	120	0.941	32	$Iz/Io = 0.3258 + 0.0061\ H$	0.96 $p < 0.001$	13