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Douglas A. Wilcox

The College at Brockport, dwilcox@brockport.edu

Kurt P. Kowalski

U.S. Geological Survey

Holly L. Hoare

U.S. Geological Survey

Martha L. Carlson

U.S. Geological Survey, macarlson@usgs.gov

Heather N. Morgan

University of Michigan - Ann Arbor

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Cattail Invasion of Sedge/Grass Meadows in Lake Ontario: Photointerpretation Analysis of Sixteen Wetlands over Five Decades

Douglas A. Wilcox^{1,*}, Kurt P. Kowalski¹, Holly L. Hoare^{1,†},
Martha L. Carlson¹, and Heather N. Morgan²

¹U.S. Geological Survey–Great Lakes Science Center
1451 Green Road
Ann Arbor, Michigan 48105

²University of Michigan
School of Natural Resources and Environment
Ann Arbor, Michigan 48109

ABSTRACT. Photointerpretation studies were conducted to evaluate vegetation changes in wetlands of Lake Ontario and the upper St. Lawrence River associated with regulation of water levels since about 1960. The studies used photographs from 16 sites (four each from drowned river mouth, barrier beach, open embayment, and protected embayment wetlands) and spanned a period from the 1950s to 2001 at roughly decadal intervals. Meadow marsh was the most prominent vegetation type in most wetlands in the late 1950s when water levels had declined following high lake levels in the early 1950s. Meadow marsh increased at some sites in the mid-1960s in response to low lake levels and decreased at all sites in the late 1970s following a period of high lake levels. *Typha* increased at nearly all sites, except wave-exposed open embayments, in the 1970s. Meadow marsh continued to decrease and *Typha* to increase at most sites during sustained higher lake levels through the 1980s, 1990s, and into 2001. Most vegetation changes could be correlated with lake-level changes and with life-history strategies and physiological tolerances to water depth of prominent taxa. Analyses of GIS coverages demonstrated that much of the *Typha* invasion was landward into meadow marsh, largely by *Typha* × *glauca*. Lesser expansion toward open water included both *T. × glauca* and *T. angustifolia*. Although many models focus on the seed bank as a key component of vegetative change in wetlands, our results suggest that canopy-dominating, moisture-requiring *Typha* was able to invade meadow marsh at higher elevations because sustained higher lake levels allowed it to survive and overtake sedges and grasses that can tolerate periods of drier soil conditions.

INDEX WORDS: Lake-level regulation plans, Lake Ontario, meadow marsh, photointerpretation, *Typha*, wetlands.

INTRODUCTION

The Laurentian Great Lakes experience water-level fluctuations at several frequencies, ranging from wind-driven seiches that can occur several times daily to seasonal summer high levels and winter lows that reflect the various components of annual water budgets to climate-driven fluctuations that occur at scales of decades to centuries (Baedke and Thompson 2000, Johnston *et al.* 2004, Wilcox

et al. 2007). Each frequency has its characteristic range in amplitude, timing, and duration. Wetland plant communities of the lakes are affected primarily by the quasi-periodic lake-level cycles related to climate (Wilcox 2004, Wilcox *et al.* 2007). High lake levels periodically eliminate dense-canopy emergent plants, and low lake levels allow less competitive understory species to grow from seed or propagules; the cycle then repeats itself (Keddy and Reznicek 1986, Maynard and Wilcox 1997). Over long periods of time, these wetland plant communities developed in a hydrologic environment with great variability, which now maintains their diversity.

*Corresponding author. E-mail: dwilcox@usgs.gov

†Present address: Grand Rapids Community College, Department of Biological Sciences, Grand Rapids, Michigan 49405

and waterbirds; evaluation of qualitative and quantitative changes in wetland plant communities resulting from past regulation; characterization of patterns of extant vegetation related to water-level history and associated with faunal habitat diversity; and development of predictive models and performance indicators to evaluate proposed new regulation plans for the lake (Hudon *et al.* 2006, Wilcox and Xie 2007). This paper describes the results of photointerpretation studies that evaluated changes in wetland plant communities resulting from past regulation.

Similar studies making use of historic aerial photographs and maps to track wetland vegetation changes in relation to water-level changes through time have been conducted in the Great Lakes (Jaworski *et al.* 1979, Harris *et al.* 1981, Whillans 1982, Wilcox *et al.* 1984, Quinlan and Mulamoottil 1987, Chow-Fraser *et al.* 1998, Kowalski and Wilcox 1999, Wei and Chow-Fraser 2005). None of those studies, however, focused on changes in wetland vegetation associated with regulation of lake levels, although various field studies have shown that regulation can result in major shifts in plant communities (e.g., Nilsson 1981, Nilsson and Keddy 1988, Renman 1989, Rorslett 1989, Wilcox and Meeker 1991).

Photointerpretation studies have also been conducted on the large Canadian prairie lakes. Shay *et al.* (1999) concluded that regulation of lake levels on Lake Manitoba induced expansion of *Typha* up-gradient into *Phragmites* and down-gradient into open, shallow water at Delta Marsh. Grosshans *et al.* (2004) concluded that lack of periodic low water levels on regulated Lake Winnipeg were partly responsible for alterations of vegetation at Netley-Libau Marsh. As part of the Marsh Ecology Research Program at Delta Marsh, in which water levels were controlled to mimic various patterns of lake-level change, van der Valk *et al.* (1994) tracked changes in *Typha*, *Phragmites*, *Scolochloa*, and other cover classes using photointerpretation studies in diked wetland cells.

The photointerpretation studies at the prairie lakes and the Great Lakes had one unifying theme—they all described dynamics of *Typha* invasion into graminoid wetland vegetation and related it to water levels. Studies conducted in the field and in controlled study plots (e.g., Wilcox *et al.* 1984, van der Valk 2000, Kercher and Zedler 2004, Boers *et al.* 2007) have demonstrated the importance of hydrology in controlling competitive interactions between these vegetation types. Previous field stud-

ies in Lake Ontario wetlands also demonstrated that *Typha* invasion was linked to lake-level regulation (Wilcox *et al.* 1992, Wilcox and Meeker 1995). Our research completed during the LOSLR study allowed us to link field studies (Wilcox *et al.* 2005) with photointerpretation studies to evaluate changes in wetland plant communities associated with regulation of Lake Ontario water levels, with an emphasis on the two major extant vegetation types—*Typha* and graminoid meadow marsh.

STUDY SITES

Sixteen sites in the U.S. were selected for study within the section of shoreline for which remote sensing information would be collected for the overall LOSLR study. Sites with minimal human disturbance were selected when possible to allow the study to focus on changes in wetland vegetation driven primarily by water-level changes. Twelve of the sites are located along the Lake Ontario shoreline—four on the southern shore and eight on the eastern shore (Fig. 2). These sites are in rural settings, with the exception of Round Pond and Braddock Bay, which are adjacent to urban areas near Rochester, New York. The remaining four sites are in the impounded upper St. Lawrence River and also in rural settings.

Site selection included four wetlands in each of four wetland types, based on the hydrogeomorphic classification system that is now described by Albert *et al.* (2005). Open embayments and protected embayments fall within the Lacustrine System; open drowned-river-mouth wetlands are in the Riverine System; and barrier-beach lagoons are in the Barrier-Enclosed System). Although more than one wetland type can occur within a site (e.g., small drowned river discharging into a barrier-beach lagoon), the most prominent hydrogeomorphic type was chosen.

Coastal wetland vegetation can be affected greatly by exposure to wave attack, which differed among geomorphic types. Barrier-beach wetlands are protected by the presence of a beach, but a channel through the beach provides hydrologic connection to the lake. Drowned-river-mouth wetlands are located in the protected mouth of a tributary flowing into Lake Ontario or the St. Lawrence River and are influenced by both the hydrology of the lake and the tributary. With no shielding geomorphic feature, open embayments are not protected from erosive wave action unless oriented away from prevailing storm winds. Conversely,

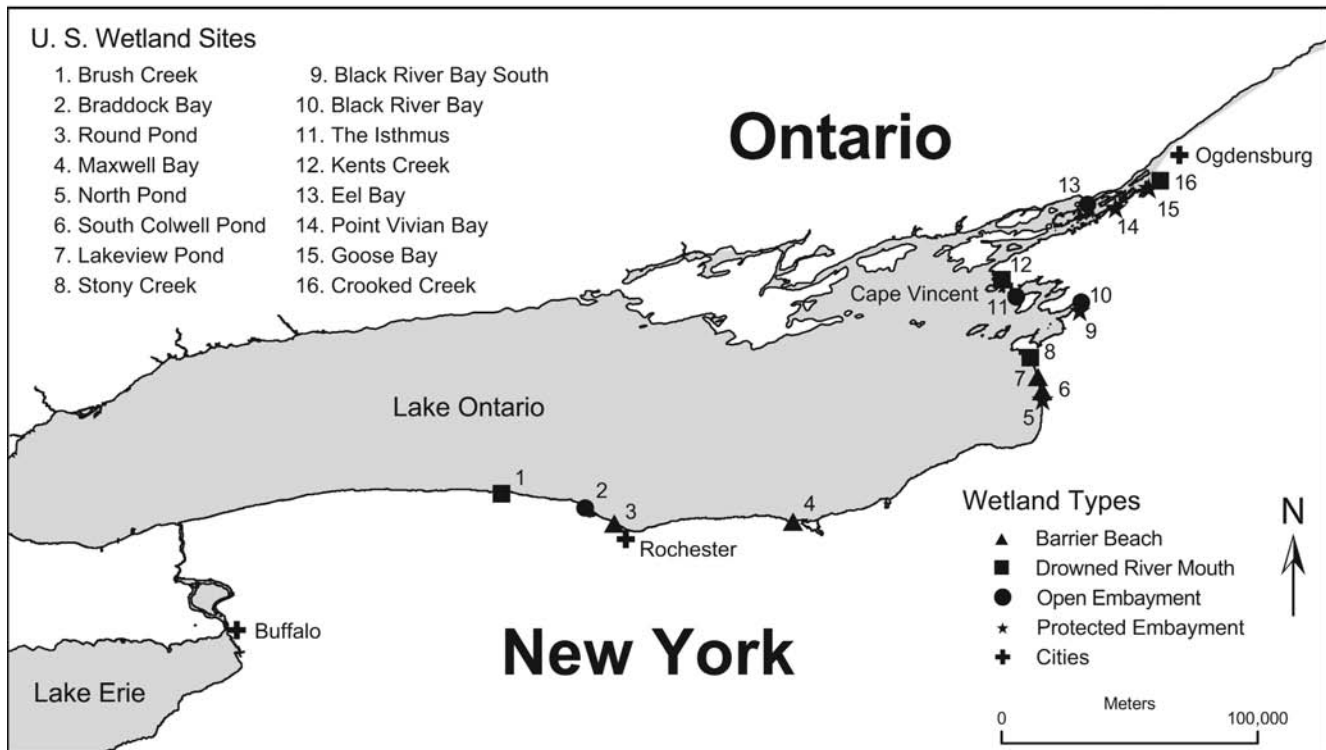


FIG. 2. Map of wetland study sites along the shore of Lake Ontario and the Upper St. Lawrence River.

protected embayments are generally shielded from wave attack by features such as orientation away from the lake.

METHODS

Photointerpretation

Vertical color-infrared aerial photographs (1:10,000 scale) were taken at each of the sixteen sites under leaf-on conditions 22 August 2001. Stereo coverage was achieved by ensuring 60% overlap among frames and 30% sidelap among flight lines. Aerial photographs were interpreted using a magnified mirror stereoscope and a draft quality pen with a drawing width of 0.25 mm to delineate vegetation boundaries on acetate overlays. Delineations were made on a site-by-site basis and supplemented by ground-truth information obtained during July 2002. The minimum map unit for the interpretation was set at 1 mm², which equated to 10 m² on the ground for the 1:10,000 scale photos. Areas smaller than 1 mm² were not delineated separately. Resulting polygons were assigned a label using a modified form of the Ecological Land Classification (ELC) system for Southern Ontario (Lee

et al. 1998), which was selected because similar studies were being conducted along the Canadian shore of Lake Ontario. This layered classification system contains six nested levels that are organized by spatial scale (e.g., from large regions down to specific vegetation types). Specific class rules were developed to standardize the classification process and ensure consistency. Polygons were classified to the Vegetation Type level, as defined by the ELC, or to the most detailed classification possible. When two or more vegetation types occurred in the same polygon, the following rules applied: 1) if one vegetation type composed 90% or more of the stand, it was considered to be purely that type, and 2) if both vegetation types composed more than 10% of the stand, then the polygon was labeled as a mix. During field ground-truthing in July 2002, additions or modifications to polygons of Vegetation Types occurred only if the Vegetation Type and its boundaries were visible in the aerial photos. Similarly, new Vegetation Types were added only if they met the minimum map unit requirement and contained wetland vegetation types.

Historical air photos dating back to 1954 were acquired from numerous sources, including Map-

Mart, Monroe Environmental Council, Monroe Soil Conservation District, New York State Department of Transportation, U.S. Department of Agriculture, and U.S. Geological Survey EROS Data Center. Stereo pairs were acquired whenever possible. The photos were delivered as either contact prints or transparencies and included some images of poor quality (e.g., out of focus, over exposed, excessive sun glint). From the photos received, one set with adequate quality for roughly each decade from the 1950s through 2001 was selected for photointerpretation according to the procedure outlined above to examine vegetation change occurring under different water levels through time. The photos used in the study were black and white panchromatic, color, or color infrared and ranged in scale from 1:4800 to 1:40000 (see Appendix A). Since the 2001 color infrared photos had associated ground-truth information, the known spectral signatures of vegetation types were traced back in time in the older photos until the links between the known vegetation types and spectral signatures were lost.

Georeferenced digital orthoquads were used to calculate x and y coordinates for ground-control points needed to georeference the wetland vegetation coverages. All vegetation boundaries and ground-control points delineated on acetate overlays were digitized into ESRI's pcARC/INFO v 4.0 using an Altek backlit digitizer. The completed coverages were converted from PC Arc/Info coverages to Arc/Info coverages and transformed into the universal transverse mercator projection (zone 18) using the georeferenced ground-control points. A root-mean-square error (RMSE) tolerance of ≤ 5.0 meters was established to ensure ground accuracy within 5 meters and was achieved by removing ground-control points one at a time until the error was less than 5 meters and distortion was minimized. There were four study sites that RMSE values larger than 5 meters were accepted (Point Vivian Bay, RMSE = 5.335; Lakeview Pond, RMSE = 16.994; Braddock Bay, RMSE = 15.899; and Crooked Creek, RMSE = 26.026), as smaller RMSE values at these sites produced unacceptably high distortion in the GIS coverages. Positional errors may have occurred despite taking the appropriate precautions to minimize them; however, they would be minor when viewed at the scale in which our trend analyses were made.

To standardize the manner in which total delineated area was determined, historic high lake-level data obtained from the National Oceanic and Atmospheric Administration were used to identify the

wetland basin boundaries for each site. Mean monthly high water levels were used to determine the extent of the basins because they indicate the highest extent of lake-influenced areas that may be considered wetland. Contours equal to the historic high water level at each site were created using USGS Digital Elevation Models (DEM), which we used as the outer boundary for the wetland basins. Five-meter buffers were created around each of the contours to account for the 10-meter horizontal resolution of the DEM. Each of those coverages at each site was clipped to create a polygon representing the largest extent of wetland vegetation identified through photointerpretation. Finally, the wetland-extent coverage was clipped by the buffered DEM contours to eliminate any areas above the historic high lake level. The one exception to this procedure was Braddock Bay 1978, where a portion of the site did not have aerial photo coverage. This area was included in all the other coverages so that potentially critical data were not lost.

Transformed coverages next went through an attribute selection to eliminate non-wetland areas and were clipped to the new wetland-basin boundary. The selection included all wetland vegetation types and other types (such as deciduous tree or shrub) that could be wetland if below historic high water level or upland if above that level. This method allowed for comparison of wetland vegetation areas only, minimizing risk of over- or under-representation. For analysis purposes, vegetation types were then grouped into four categories: floating-leaf vegetation, meadow marsh (sedges and grasses), mixed-emergent vegetation, and *Typha*. Vegetation types that were mixed with *Typha* were grouped in *Typha*; although some areas with as little as 10% *Typha* were thus characterized as *Typha*, other areas with slightly less than 10% were not recognized as that vegetation type. Area and percent-vegetated cover were calculated for each vegetation category, and the data were summarized for analysis by site and wetland type. To make generalizations about vegetation responses through time by wetland type, the ratio of the sum cover divided by the sum of all basin areas was used instead of simple averaging across basins, as it gives greater influence to sites with a larger proportion of a vegetation type and thus better reflects the responses within a wetland type, rather than individual sites.

Comparisons among Years

Initial evaluation of changes in wetland vegetation types through time suggested that expansion of *Typha*-dominated communities oftentimes was largely landward into areas previously occupied by meadow marsh. To assess the invasion front of *Typha* into meadow marsh, the historic areal coverage of meadow marsh was determined for each site across the sequence of photographs analyzed, resulting in delineation and calculation of the area of "potential meadow marsh." For each year of the sequence within a single site, wetland coverages clipped to the basins went through an attribute selection for meadow marsh. Selected polygons were exported, thus generating a meadow marsh coverage for each year in the sequence. These historical meadow marsh coverages were merged in ArcMap 9.1, and interior polygons were dissolved, creating a coverage of potential meadow marsh. Wetland coverages were clipped to this potential meadow marsh coverage. To determine the percent of the potential meadow marsh area that was mapped as *Typha* or meadow marsh in any given year in the sequence, an attribute selection was performed for vegetation types in the *Typha* or meadow marsh category, respectively. The selected *Typha* or meadow marsh polygons were then exported as new coverages, and the total area of each coverage was determined by summarizing areas in the attribute table. The percent of potential meadow marsh area that was mapped as *Typha* or meadow marsh for each year in the sequence was then calculated.

Expansion of *Typha* into open water also occurred. To determine the relative extent of expansion into meadow marsh vs. open water, the existing *Typha* coverages from the first and last year in the sequence of photographs were compared. A coverage representing total *Typha* expansion into wetland areas was generated by spatially subtracting *Typha* extent in the first year from the last. The resulting coverage of total *Typha* expansion was either clipped to or erased from potential meadow marsh mapped as meadow marsh to determine extent of *Typha* expansion into meadow marsh or into open water, respectively. Percentages by area of total *Typha* expansion were calculated for both directions.

RESULTS

Photointerpretation of color infrared photographs from 2001 produced 16 vegetation maps in GIS format. They included upland classifications, as well

as sub-classifications of wetland vegetation. The data presented are restricted to the delineated wetland areas and the four main vegetation types after collapsing of sub-classifications where suitable. Brief descriptions of changes in vegetation types by decade for each geomorphic type focus on meadow marsh and *Typha*, with figures depicting the changes for one site of each geomorphic type.

Drowned-river-mouth Wetlands

With the exception of Brush Creek, meadow marsh was the dominant vegetation type mapped in 1958-1959, often situated on the floodplain between upland and *Typha* (Table 1, Fig. 3A). Meadow marsh increased in cover at Crooked Creek and Stony Creek in 1966 following low lake levels in 1964-1965. This expansion extended both landward and toward the water, but landward expansion was limited by elevation at the edges of the wetlands. Mapped area of meadow marsh decreased at Kents Creek, but photographs showed evidence that it had been mowed at upper elevations. *Typha* also increased at all sites except Crooked Creek, with expansion largely adjacent to the stream channels. In 1978-1979, *Typha* was the dominant vegetation type at all sites except Crooked Creek, while meadow marsh decreased. The expansion of *Typha* was largely up-slope into areas previously in meadow marsh. By 1988-1990, meadow marsh was reduced to a minor component of the wetland vegetation at all sites except Kents Creek, where the broad basin provided extensive areas of unflooded wetland conducive to growth of sedges and grasses. *Typha* coverage increased by more than 17% at Crooked Creek and remained the major vegetation type at all sites except Kents Creek. Meadow marsh and *Typha* coverage changed little from the late 1980s to 2001 at most sites, although more meadow marsh was converted to *Typha* at Kents Creek.

Barrier Beach Wetlands

The dominant vegetation type in barrier beach wetlands differed on a site-by-site basis in the 1950s (Table 1, Fig. 3B). In the case of Maxwell Bay, the available photographs were taken in 1954, when lake levels were high and shortly after the extreme high lake levels of 1952; floating-leaf vegetation was dominant and very little meadow marsh was mapped (Table 1). *Typha* was already dominant at Round Pond and Lakeview Pond, but little was present at Maxwell Bay. Percent meadow marsh

TABLE 1. Percent of wetland in floating-leaf, mixed emergent, Typha, and meadow marsh vegetation types from the 1950s to 2001 in individual drowned river mouth, barrier beach, open embayment, and protected embayment wetlands of Lake Ontario derived from photointerpretation. The areas of meadow marsh that had been mowed are not included (Kents Creek 1966, The Isthmus 1959, 1966).

Drowned River Mouth	Year	Percent Cover				Barrier Beach	Year	Percent Cover			
		Floating	Mixed Emergent	Typha	Meadow Marsh			Floating	Mixed Emergent	Typha	Meadow Marsh
Brush Creek	1958	—	—	28.9	19.7	Lakeview Pond	1959	0.9	—	31.8	22.1
	1966	4.5	—	39.4	9.3		1966	5.8	—	29.5	20.2
	1979	—	—	6.2	1.6		1979	0.1	0.0	43.3	4.2
	1988	—	—	7.9	—		1988	6.1	0.7	42.4	6.0
Crooked Creek	2001	3.5	—	8.4	—		2001	10.7	0.2	45.1	4.6
	1959	1.3	—	1.4	38.3	Maxwell Bay	1954	36.0	—	3.5	0.4
	1966	0.1	—	4.5	43.5		1963	0.5	—	9.3	14.4
	1978	1.6	—	7.4	29.1		1978	34.4	—	16.5	0.7
Kents Creek	1990	—	—	4.9	8.9		1988	17.8	—	14.5	—
	2001	10.3	1.2	8.1	5.1		2001	30.0	—	26.6	2.2
	1959	—	—	4.0	37.9	Round Pond	1958	4.1	—	57.3	0.9
	1966	0.8	0.2	0.8	24.0		1966	6.2	—	45.9	—
Stony Creek	1978	—	—	2.3	19.7		1980	2.2	—	57.3	—
	1988	6.6	—	2.0	26.7		1988	11.0	—	57.1	—
	2001	9.2	—	7.5	22.5		2001	3.9	—	63.1	0.1
	1959	0.3	2.8	0.7	25.1	South Colwell Pond	1959	1.4	1.9	13.2	28.7
Open Embayment	1966	0.1	—	1.8	35.0		1966	16.6	4.3	9.0	28.3
	1979	—	—	6.7	12.8		1978	5.1	—	33.5	4.5
	1988	8.0	—	9.7	6.8		1988	9.5	1.1	32.0	3.6
	2001	11.0	—	3.5	5.9		2001	10.1	—	29.4	5.7
Black River Bay	1959	—	—	32.1	1.1	Protected Embayment	1959	5.0	—	14.5	5.0
	1966	8.2	—	37.9	2.8	Black River Bay South	1966	6.4	—	7.6	13.4
	1979	0.1	—	25.6	1.5		1979	—	—	14.8	2.5
	1988	20.9	—	0.1	—		1988	29.4	—	25.3	2.7
Braddock Bay	2001	7.4	—	27.4	—		2001	44.6	0.2	19.5	1.6
	1958	1.2	—	32.8	—	Goose Bay	1959	7.3	—	11.4	41.6
	1966	3.9	—	38.4	3.7		1966	1.0	—	19.9	33.3
	1978	5.9	0.1	28.7	0.6		1978	2.2	—	36.6	12.9
Eel Bay	1988	4.0	0.3	27.0	0.6		1990	1.2	1.0	47.2	—
	2001	13.8	—	30.8	0.0		2001	5.6	—	47.1	3.1
	1959	2.0	—	18.0	39.5	North Pond	1959	21.0	—	6.7	10.4
	1966	10.7	—	36.6	23.8		1965	15.8	18.2	6.3	13.5
The Isthmus	1978	5.1	—	55.1	—		1978	37.6	8.8	11.3	4.2
	1990	—	0.5	53.0	—		1988	32.6	4.8	23.7	10.2
	2001	9.2	—	52.6	4.1	Point Vivian Bay	2001	25.2	7.2	21.9	9.8
	1959	—	—	22.6	5.7		1959	0.5	—	23.8	53.3
The Isthmus	1966	0.7	—	23.8	11.5		1966	3.2	—	39.0	32.4
	1978	2.0	0.1	20.3	5.8		1978	4.6	—	59.0	11.7
	1988	1.1	6.2	18.4	4.5		1990	—	—	50.7	17.7
	2001	3.1	2.4	19.1	6.3		2001	13.9	—	55.4	13.1

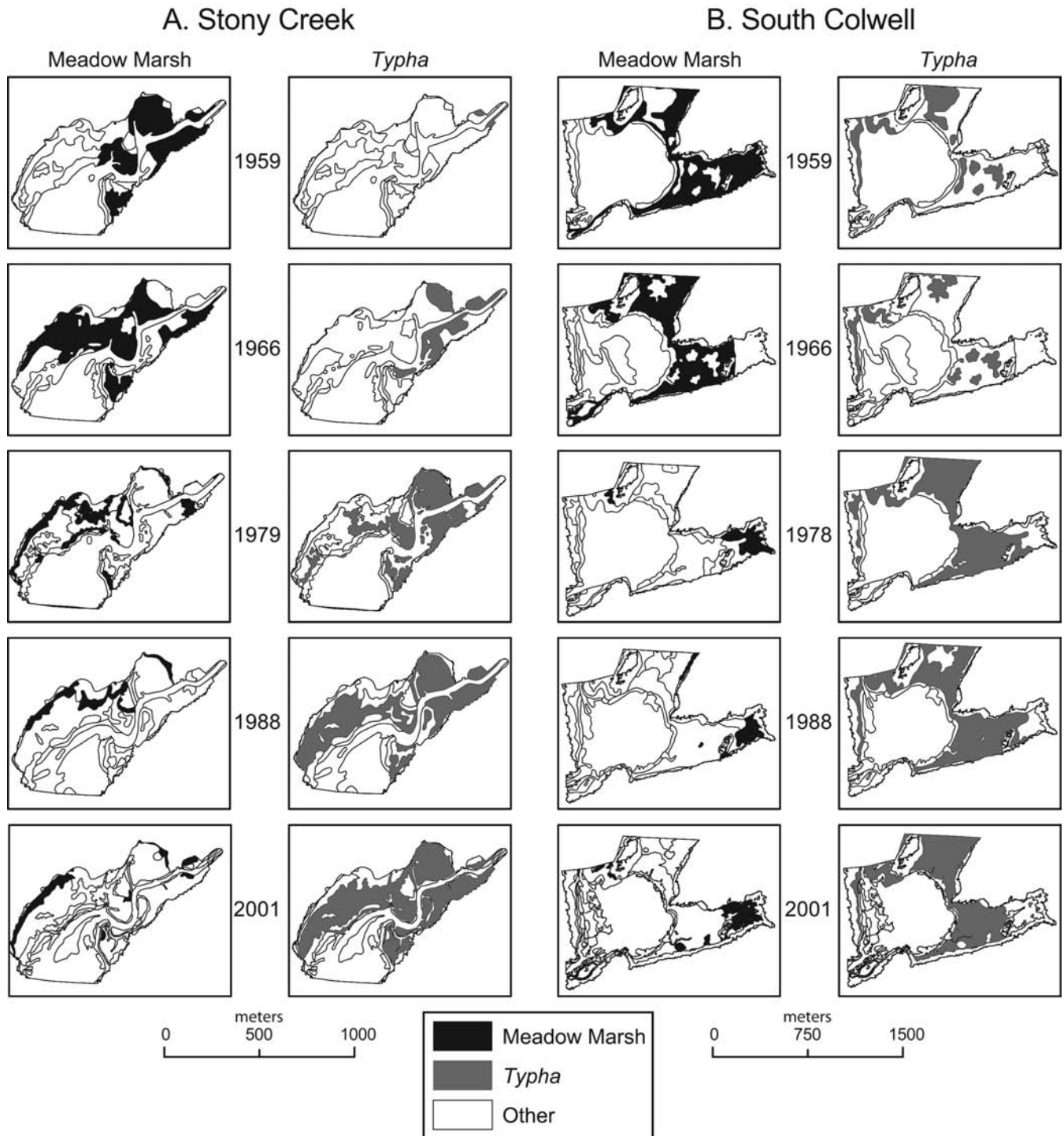


FIG. 3. GIS maps of meadow marsh and *Typha* vegetation types at Lake Ontario drowned river mouth wetland Stony Creek (A) and barrier beach wetland South Colwell Pond (B) derived from photointerpretation of aerial photographs taken in 1959, 1966, 1978, 1979, 1988, and 2001. See Appendix A for details on photographs.

was nearly unchanged in South Colwell Pond in 1966, decreased slightly in Lakeview Pond, and dropped to zero in Round Pond. With lower lake levels, meadow marsh returned to Maxwell Bay in 1963 photos. *Typha* cover decreased at all sites except Maxwell Bay. Meadow marsh decreased substantially in the late 1970s at the three sites where it had been present in the 1960s, and *Typha* expanded at all sites, largely displacing meadow marsh at Lakeview Pond, Maxwell Bay, and South Colwell Pond. Meadow marsh remained a small component of the wetland vegetation in 1988 at all sites, and *Typha* cover changed very little from the late 1970s. Despite minor increases in meadow marsh at three sites in 2001, it remained a minor vegetation type at those sites. More meadow marsh was lost to *Typha* in Lakeview Pond, while *Typha* also increased at Maxwell Bay and Round Pond but decreased slightly in South Colwell Pond.

Open Embayment Wetlands

With the exception of Eel Bay, which has less exposure to wave attack, meadow marsh was not prominent in open embayment wetlands in 1958-1959 (Table 1, Fig. 4A). However, portions of easterly exposed The Isthmus adjacent to meadow marsh had been mowed and classified as agricultural land; those areas likely were meadow marsh and would double the percent meadow marsh at that site. Wave-exposed Black River Bay and Braddock Bay were mostly dominated by *Typha*. Following low lake levels in 1964-1965, meadow marsh increased at all sites except Eel Bay in 1966 but without loss of *Typha*. At Eel Bay, nearly half of the meadow marsh was converted to *Typha* between 1959 and 1966. Mowing of meadow marsh at The Isthmus resulted in the percent value for meadow marsh being about 6% lower (Table 1) than perhaps it should have been. Meadow marsh decreased in cover at all open embayment sites in 1978-1979. Following a high lake-level period, *Typha* likewise decreased at sites other than Eel Bay, where it continued to replace meadow marsh and became the dominant vegetation type. By the late 1980s, meadow marsh had decreased in cover at all sites except Braddock Bay, where it remained constant in very small areas. *Typha* remained the dominant vegetation type at all sites and increased in cover at Black River Bay. A minor increase in meadow marsh appeared in 2001 at Eel Bay and The Isthmus, but it was absent at the other open embayments, as *Typha* continued to dominate all sites.

Protected Embayment Wetlands

Meadow marsh was the dominant vegetation type in Goose Bay and Point Vivian Bay in 1959 (Table 1, Fig. 4B). Although meadow marsh was more prevalent than *Typha* in North Pond, the geomorphic configuration of the site allowed an even greater coverage by floating-leaf vegetation. *Typha* covered greater area than meadow marsh at Black River Bay South (which had the most wave exposure of the protected embayments). Area of meadow marsh increased at Black River Bay South and North Pond in 1966 during a low lake-level period, with small to moderate increases in *Typha*, which also increased at Goose Bay and Point Vivian Bay. In these latter two cases, it seems that *Typha* intermixed with meadow marsh vegetation became dominant enough to change the classification from meadow marsh to *Typha*. Area of meadow marsh decreased and area of *Typha* increased at all sites in 1978-1979 following a high lake-level period, mostly advancing into meadow marsh. Meadow marsh showed modest gains in North Pond and Point Vivian Bay in 1988-1990 photographs and changed very little in Black River Bay South (Table 1). Failure to detect meadow marsh at Goose Bay was tied to a greater dominance by *Typha* in mixed stands that resulted in classification as *Typha* rather than meadow marsh (see Fig. 4B). *Typha* increased at all sites except Point Vivian Bay. Meadow marsh covered a small area of Goose Bay in 2001 but decreased slightly at all other sites. Area of *Typha* rebounded in Point Vivian Bay, showed little change in Goose Bay and North Pond, but decreased in Black River Bay South while floating-leaf vegetation increased substantially.

Correlations between Vegetation Types and Lake-level Changes

Lake Ontario water levels were slightly above 74.5 m (International Great Lakes Datum 1985) during the growing season in 1958 and still near 74.75 m in 1959 (Fig. 1), years in which most of the earliest photographs in this study were taken. This lower lake-level period followed high water levels in the early 1950s that exceeded 75.75 m in 1952. Despite exceptions such as Maxwell Bay (for which photographs were from high water year 1954), Round Pond (adjacent to urban development and already colonized by *Typha*), The Isthmus (mowed), and sites with more wave exposure (Black River Bay, Braddock Bay, Black River Bay South), meadow marsh was generally a prominent

TABLE 2. Area-weighted mean percent (std. dev.) of wetland in floating-leaf, mixed emergent, *Typha*, and meadow marsh vegetation types from the 1950s to 2001 in drowned river mouth, barrier beach, open embayment, and protected embayment wetland types in Lake Ontario derived from photointerpretation.

Wetland Type	Years	Weighted Mean Percent Cover (SD)							
		Floating		Mixed Emergent		<i>Typha</i>		Meadow Marsh	
Drowned River Mouth	1958–1959	0.7	(0.1)	0.5	(0.2)	17.1	(1.3)	33.6	(1.1)
	1966	0.8	(0.2)	0.1	(0.0)	20.9	(1.6)	33.3	(2.0)
	1978–1979	0.7	(0.2)	–	–	29.5	(0.5)	20.7	(1.6)
	1988–90	2.9	(0.6)	–	–	37.8	(1.7)	11.5	(1.4)
	2001	9.3	(0.3)	0.6	(0.1)	41.4	(1.5)	8.6	(1.3)
Barrier Beach	1954–1959	2.9	(0.5)	0.4	(0.1)	33.5	(2.7)	17.3	(1.9)
	1963–1966	8.3	(0.8)	1.0	(0.3)	28.6	(2.2)	16.5	(1.8)
	1978–1980	2.8	(0.6)	–	–	44.0	(1.5)	3.1	(0.4)
	1988	8.6	(0.5)	0.6	(0.1)	43.1	(1.6)	3.7	(0.5)
	2001	9.3	(0.6)	0.1	(0.0)	45.7	(2.0)	3.6	(0.4)
Open Embayment	1958–1959	0.7	(0.1)	–	–	30.7	(0.5)	3.3	(0.9)
	1966	5.6	(0.5)	–	–	36.8	(0.5)	5.3	(0.6)
	1978–1979	3.3	(0.6)	0.1	(0.0)	28.4	(0.7)	1.4	(0.2)
	1988–1990	9.9	(1.7)	0.7	(0.2)	28.9	(0.7)	0.7	(0.1)
	2001	10.2	(0.7)	0.2	(0.1)	29.8	(0.6)	0.8	(0.2)
Protected Embayment	1959	7.4	(0.9)	–	–	13.8	(0.6)	16.4	(2.9)
	1965–1966	6.8	(0.6)	2.9	(1.0)	12.6	(1.5)	18.3	(1.3)
	1978–1979	6.9	(2.1)	1.4	(0.5)	22.2	(2.2)	5.3	(0.7)
	1988–1990	22.7	(1.9)	0.9	(0.3)	30.9	(1.6)	5.2	(0.8)
	2001	32.6	(2.8)	1.3	(0.4)	27.8	(2.1)	4.4	(0.7)

vegetation type during this period when averaged on an area-weighted basis across all sites, especially in drowned river mouth wetlands (Table 2). *Typha* was already present and covered more area than meadow marsh in barrier beach and open embayment wetlands.

Moderate lake levels in the early 1960s were followed by low levels in 1964 and 1965, with growing season levels never exceeding 74.75 m (Fig. 1). Again, despite exceptions, such as a meadow marsh-to-*Typha* classification switch for intermixed vegetation at Goose Bay and Point Vivian Bay and mowing of meadow marsh at Kents Creek and The Isthmus, the average cover of meadow marsh remained relatively stable across all sites in photographs mostly taken in 1966, while *Typha* increased in drowned river mouth and open embayment wetlands (Table 2). Meadow marsh increased at half of the sites (Crooked Creek, Stony Creek, Maxwell Bay, Black River Bay, Braddock Bay, The Isthmus, Black River Bay South, North Pond) but was accompanied by a loss of *Typha* only at Crooked Creek, Black River Bay South, and North Pond (Table 1).

Lake levels were high from 1973 to 1976, ex-

ceeding 75.7 m in 1973 (Fig. 1). When most photographs were taken in 1978 and 1979, growing season levels had dropped into the 75.0 m to 75.2 m range. Average areal cover of meadow marsh decreased substantially in all geomorphic types and at all individual sites (Tables 1, 2). Average cover of *Typha* increased in all geomorphic types except open embayments (Table 2), where decreases were substantial in wave-exposed Black River Bay and Braddock Bay (Table 1).

Water levels remained well above 75.5 m during the growing season in most years from 1980 until 1988, when the next set of photographs was taken (Fig. 1). Average areal cover of meadow marsh and *Typha* changed little in barrier beach and open embayment wetlands, but meadow marsh decreased in drowned river mouth wetlands and *Typha* increased in both drowned river mouth and protected embayment wetlands (Table 2). Crooked Creek had the greatest decrease in meadow marsh and increase in *Typha* (Table 1).

Although lake levels exceeded 75.5 m in 1993 and growing season peaks were below 75.0 m in 1995 and 1999, sustained growing season levels remained well above 75.0 m in the years preceding

the 2001 set of photographs (Fig. 1). Only minor changes occurred in average percent meadow marsh or *Typha* from the late 1980s to 2001 (Table 2), although there was some variability among sites (Table 1).

Directional Expansion of *Typha*

Although *Typha* increased and meadow marsh decreased in areal coverage from the 1950s to 2001 at nearly all sites, the data in Table 1 cannot be used to determine if the loss of meadow marsh was due to invasion by *Typha*. Delineation of potential meadow marsh (maximum extent of meadow marsh mapped across all years at each site) with overlays of mapped meadow marsh vs. mapped *Typha* can address that question. Overlays of *Typha* mapped in 2001 on that mapped in the 1950s photographs can also address the question when the increases are sorted by direction of expansion—into water or meadow marsh. With several exceptions that can be explained by human actions such as mowing of meadow marsh or urbanization that resulted in very little meadow marsh being present in the earliest years mapped, the results showed that most of the *Typha* expansion was into meadow marsh.

In the drowned river mouth wetlands, most potential meadow marsh was mapped as meadow marsh and little was mapped as *Typha* in the late 1950s at all sites (Fig. 5A). Meadow marsh increased in Crooked Creek and Stony Creek in 1966 following low lake levels, then generally decreased at all sites in succeeding years (Fig. 5A) as the potential meadow marsh was invaded by *Typha* (Fig. 5A). Although *Typha* did expand into the previously aquatic zone at all sites, a far greater percentage expanded into meadow marsh from the 1950s to 2001 (Fig. 6A).

With the exception of Maxwell Bay, which was mapped from 1954 photographs following extreme high lake levels in 1952, a high percentage of potential meadow marsh in barrier beach wetlands was mapped as meadow marsh in the 1950s, and less than 20% was mapped as *Typha* (Fig. 5B). Meadow marsh then decreased in succeeding years at all sites (Fig. 5B) as potential meadow marsh mapped as *Typha* increased (Fig. 5B). Expansion of *Typha* from the 1950s to 2001 was mostly into meadow marsh rather than toward water at Lakeview Pond and South Colwell Pond (Fig. 6B). Maxwell Bay and Round Pond had little area in meadow marsh in the 1950s, so there was little opportunity for *Typha* invasion in that direction. In ad-

dition, the small amount of meadow marsh in any year at Round Pond resulted in a very small area of potential meadow marsh from which to make calculations; therefore, changes in data across years for Round Pond in Figure 5B may be less meaningful than they seem.

Of the open embayment wetlands, only Eel Bay had a high percentage of potential meadow marsh mapped as meadow marsh in the late 1950s (Fig. 5C). The Isthmus likely would have shown a higher percentage if mowing had not reduced mappable meadow marsh area. Wave-exposed Black River Bay and Braddock Bay did not reach maximum percentages until 1966 following low lake levels. Percent potential meadow marsh mapped as meadow marsh decreased and percent mapped as *Typha* increased at all sites after 1966 (Fig. 5C). Most of the expansion of *Typha* from the late 1950s to 2001 was into meadow marsh rather than water at Eel Bay (Fig. 6C). Although invasion into meadow marsh was also greatest at The Isthmus, the percentage calculated would likely have been higher if the site had not been mowed in 1959. Expansion of *Typha* at Black River Bay and Braddock Bay was necessarily into water because there was little or no meadow marsh present in the late 1950s (Fig. 6C, Table 1).

Although percent potential meadow marsh mapped as meadow marsh was relatively low in moderately exposed Black River Bay South in 1959 (Fig. 5C), there was an increase in 1966 after low water years (Fig. 5C). An increase occurred at North Pond in 1965 also, but the overall trend for protected embayment wetlands was a decrease in percent potential meadow marsh mapped as meadow marsh accompanying a decrease in mapped *Typha* across the time span of the study (Fig. 5C). Most of the *Typha* invasion at Point Vivian and Goose Bay from the late 1950s to 2001 was into meadow marsh (Fig. 6D), and it extended in both directions at Black River Bay South. At North Pond, much of the *Typha* invasion was into open water and floating-leaf vegetation along a low ridge that had previously been colonized by mixed emergent vegetation, rather than into meadow marsh along the shore.

DISCUSSION

Responses of wetland vegetation to changes in water levels analogous to those in our Lake Ontario studies have been described many times, and a general model applicable to the Great Lakes was pro-

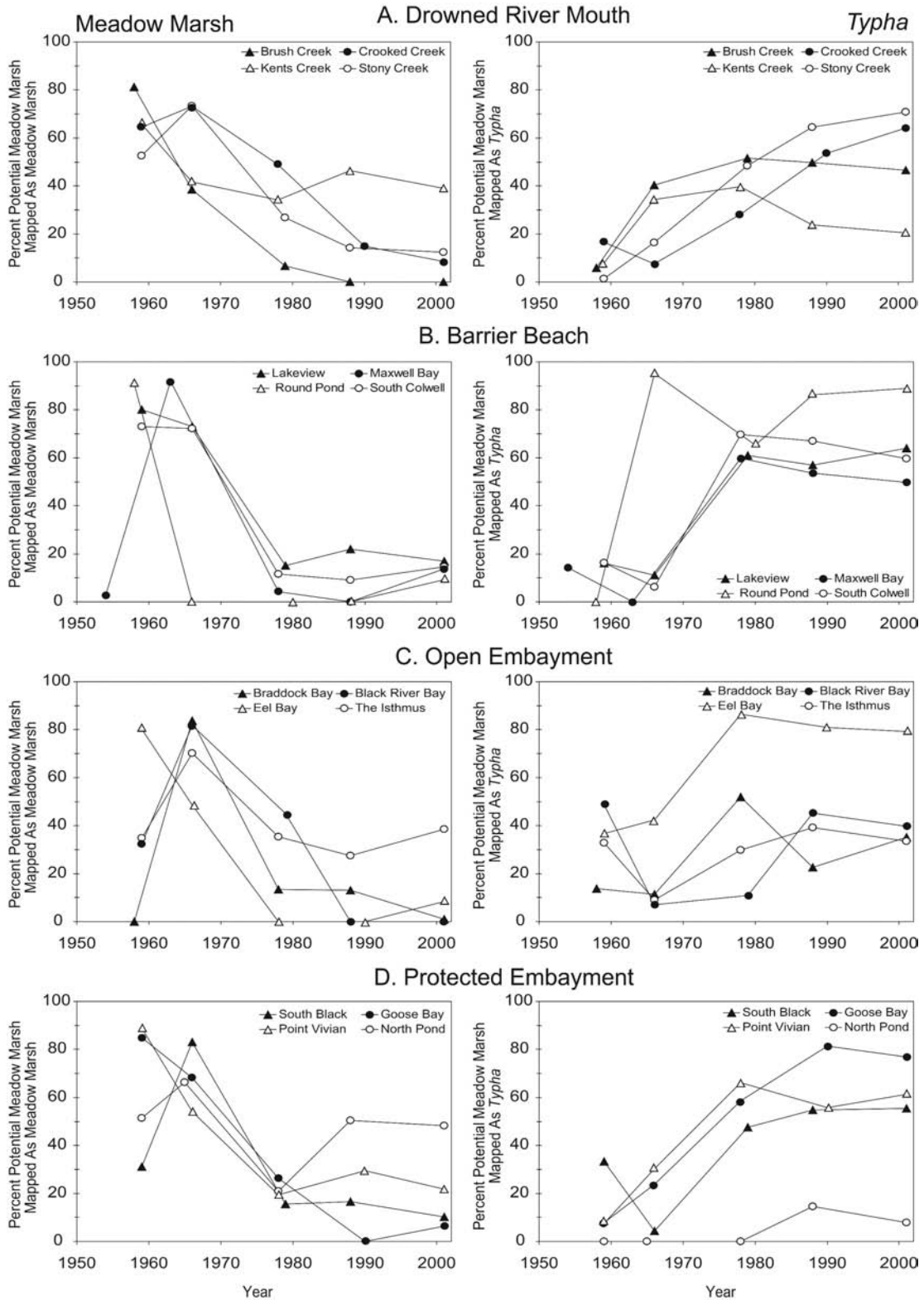


FIG. 5. Percent of potential meadow marsh (derived from maximum areal coverage across all years) mapped as meadow marsh and *Typha* in (A) drowned river mouth, (B) barrier beach, (C) open embayment, and (D) protected embayment wetlands of Lake Ontario from the late 1950s to 2001. Note that areas of meadow marsh that had been mowed at Kents Creek in 1966 and The Isthmus in 1959 and 1966 are not included.

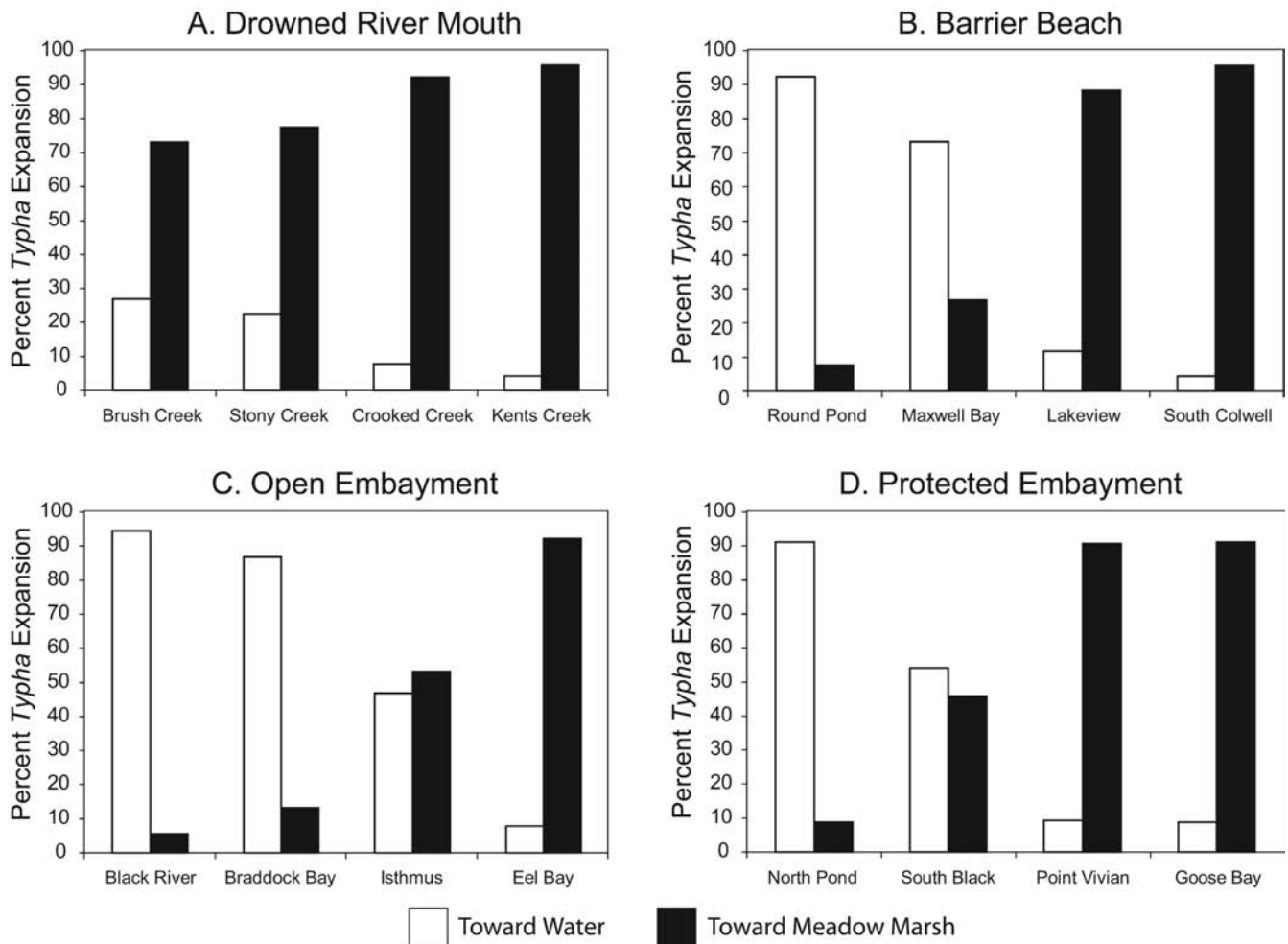


FIG. 6. Percent of *Typha* expansion into open water and meadow marsh in A) drowned river mouth, B) barrier beach, C) open embayment, and D) protected embayment wetlands of Lake Ontario based on a comparison of 1950s and 2001 photographs. Note that Round Pond, Maxwell Bay, Black River Bay, and Braddock Bay had very little meadow marsh in the 1950s to be invaded.

posed by Keddy and Reznicek (1986) that illustrates the relations between aquatic, emergent marsh, wet meadow, strand, and tree/shrub communities and fluctuations in lake level. High water levels generally eliminate many emergent species, while low water levels result in regeneration of emergents from the seed bank. That model is consistent with those conceived by others working elsewhere (e.g., van der Valk and Davis 1978, Poiani and Johnson 1993, van der Valk 2000). Given the changes in vegetation we found in Lake Ontario, we will address the *Typha*-dominated emergent marsh and wet meadow (meadow marsh) components and focus on the dynamics that led to *Typha* invasion of meadow marsh.

Die-back of *Typha*

Published results of field studies on the effects of water-level changes on wetlands have placed a considerable focus on *Typha*. Water-depth tolerance by *Typha* differs by species (Grace and Wetzel 1982, Grace and Harrison 1986, Grace 1987, Grace 1989), but all species likely can be killed by prolonged, excessive flooding (e.g., McDonald 1955, Harris and Marshall 1963, Farney and Bookhout 1982, deSwart *et al.* 1994). Our analyses of Lake Ontario photographs taken in 1978-1980 showed no overall trend toward decreased areal coverage of *Typha* following the high lake levels that occurred during our study period from 1973 to 1976 (Table

1, Fig. 1). However, decreases did occur in open embayments Black River Bay and Braddock Bay, where wave exposure could have been a compounding factor (Keddy 1984a,b).

Three scenarios might explain the general lack of decreased *Typha* in 1978–1980 photographs: lake levels were not high enough in 1973 to cause substantial die-back, *Typha* did die back but recovered by 1978, or floating mats of *Typha* had developed at many sites by 1973 that were immune to increases in lake level. Despite lack of photographic evidence, we suspect that high lake levels in 1973 substantially reduced coverage of *Typha* at our study sites, as was reported for most “emergent vegetation” by Quinlan and Mulamootil (1987) at three wetlands along the Canadian shore of Lake Ontario. Loss of *Typha* during high lake levels in 1973 was also documented in wetlands of Lake Erie, Lake Huron, Lake Michigan, and Lake St. Clair (Jaworski *et al.* 1979, Farney and Bookhout 1982, Kelley *et al.* 1985, Kowalski and Wilcox 1999). A response or lag time for recovery of *Typha* in Lake Ontario wetlands of two to four years (1976 to 1978–1980) would be deemed possible but borderline based on work at Delta Marsh on Lake Manitoba in Canada (van der Valk 2000). However, the results from controlled studies by Boers *et al.* (2007) suggest that recovery likely could have occurred in that time frame, and Quinlan and Mulamootil (1987) did note moderate recovery of emergents (not *Typha* specifically) in Lake Ontario wetlands in 1978. In addition, floating *Typha* mats are prominent along the waterward edge of many of our Lake Ontario study sites (Wilcox *et al.* 2005). *Typha* mats have been shown to be resilient (Krusi and Wein 1988) and would likely remain floating, thereby surviving high lake levels in the mid-1970s if they were present at that time (we have no evidence).

Expansion of *Typha*

In general, *Typha* expanded in areal coverage at our study sites from the 1950s to 2001. Given the increase in lake levels and lack of low levels over the past 40 years, this might be expected. Compared to many sedge and grass species common to wetlands of temperate/sub-boreal North America, *Typha* is more flood-tolerant and is often favored by moderate flooding (e.g., Bedish 1967, Harris and Marshall 1963, Ellison and Bedford 1995, Kercher and Zedler 2004, Boers *et al.* 2007). Extensive studies at Delta Marsh showed that hybrid *Typha* ×

glauca Godr. expanded in response to increasing and stable water levels (Waters and Shay 1990, 1992, Shay *et al.* 1999, Seabloom *et al.* 2001) and did so by vegetative growth from small colonies found in openings created by past extreme flooding (deSwart *et al.* 1994, Seabloom *et al.* 2001). Although *T. × glauca* was present in wetlands of the Lake Ontario region long before regulation (Hotchkiss and Dozier 1945, Marsh 1962), favorable conditions related to stable water levels may have released it for expansion. Invasion by *Typha angustifolia* L. has not been studied as extensively as hybrid cattail, but this species is water-tolerant (Grace and Wetzel 1982, Grace and Harrison 1986) and would be expected to be favored by moderate flooding also.

Quadrat sampling in our Lake Ontario sites in 2003 found *T. angustifolia* to have its greatest mean percent cover in water deeper than for *T. × glauca* in all four wetland geomorphic types (Wilcox *et al.* 2005). Based on those quadrat data, cattail expansion waterward in open and protected embayments that we observed in aerial photographs clearly seems to have been driven by *T. angustifolia*, and expansion into meadow marsh was driven by *T. × glauca*. Likewise, in barrier beach wetlands, where *T. angustifolia* was far less prominent, its invasion front was waterward, while *T. × glauca* expanded in both directions. Both taxa expanded waterward in drowned river mouth wetlands, but only *T. × glauca* showed much invasion into meadow marsh (Wilcox *et al.* 2005). These results are supported by the findings of McDonald (1955) that *T. × glauca* expanded faster than *T. angustifolia* in shallow waters of Lake Erie wetlands when lake levels receded following an extreme high. The plasticity of *T. × glauca* to water-level change reported by Waters and Shay (1990) may also be evident in its invasion of Lake Ontario wetlands.

Growth of *Typha* from the seed bank is also dependent on water depth or soil moisture level. Although Keddy and Ellis (1985) found no effect of water levels from 5 cm below the soil surface to 10 cm deep on germination of *T. angustifolia*, van der Valk and Davis (1978) noted lower germination rates with 10 cm of flooding. Seabloom *et al.* (1998) found increased germination of *T. × glauca* with increasing water depth to 7 cm. These results may help explain the ability of *T. × glauca* to expand landward at our Lake Ontario sites when lake levels were stabilized at a higher elevation following regulation, while waterward expansion of *T. angustifolia* was not as prevalent. However, survival

of seedlings of both taxa is dependent on environmental conditions, especially water depth (Seabloom *et al.* 1998, 2001; Kercher and Zedler 2004; Boers *et al.* 2007). Vegetative reproduction likely played a major role in expansion of both taxa (Bedish 1967, Grace and Harrison 1986, Galatowitsch *et al.* 1999, Boers *et al.* 2007), and apparent clonal growth was observed at many of our sites during ground-truthing and field studies.

Loss of Meadow Marsh

Calamagrostis canadensis (Michx) P. Beauv and *Carex stricta* Lam. are prominent components of the meadow marsh community in Great Lakes wetlands (Jaworski *et al.* 1979; Kelley *et al.* 1985; Stanley *et al.* 2000, 2005; Gathman *et al.* 2005). At our Lake Ontario sites, *Calamagrostis* provided 6-12% mean cover in 2003 quadrat sampling in meadow marsh and was distributed rather evenly across the elevation gradient of the meadow marsh (Wilcox *et al.* 2005). *Carex stricta* was not sampled in barrier beach wetlands but provided 3-4% mean cover in the other wetland types, where it was most abundant at lower, wetter parts of the meadow marsh (Wilcox *et al.* 2005). Twenty other species of *Carex* were identified in our sampling, but none were found consistently (Wilcox *et al.* 2003).

Calamagrostis is a common associate on *C. stricta* tussocks (Costello 1936, Peach and Zedler 2006); however, it favors a moist soil habitat and is seemingly more sensitive to flooding and often found in slightly higher and drier parts of wetlands than *C. stricta* (Costello 1936; Keddy and Reznicek 1982; Keddy 1984a,b; Wilcox and Meeker 1991; Kercher and Zedler 2004; Boers *et al.* 2007). As also noted by Quinlan and Mulamootil (1987) in three Canadian wetlands, sustained higher water levels beginning in the early 1970s (Fig. 1) likely account for the loss of meadow marsh observed in aerial photographs of our Lake Ontario sites. However, *C. stricta* may have fared better than *Calamagrostis*, as established plants can tolerate considerable flooding (Budelsky and Galatowitsch 2004). Wetzal and van der Valk (2005) concluded that pathogenic fungi may reduce above- and below-ground biomass of *C. canadensis* under wet hydrologic regimes but do not affect *C. stricta*. Boers *et al.* (2007) found that both *C. canadensis* and *C. stricta* declined in competition with *T. × glauca* under extended hydroperiods, also consistent with our results.

Many species of *Carex* are less tolerant of flood-

ing than *Typha* (e.g., Sjoberg and Danell 1983, Squires and van der Valk 1992, van der Valk 1994, Seabloom *et al.* 2001, Kercher and Zedler 2004), although tussocks provide *C. stricta* (and co-occurring species) the ability to withstand moderate flooding (Costello 1936, Peach and Zedler 2006). There is evidence that some *Carex* species are resilient to water-level changes (Ewing 1996, Ashworth 1997), but sustained high water levels beginning in the early 1970s (Fig. 1) likely resulted in a decline of most sedges at our Lake Ontario sites.

Area of meadow marsh increased at some of our Lake Ontario sites during the low water-level period in the mid-1960s, suggesting a seed-bank response (Table 1). *Calamagrostis canadensis*, *C. stricta*, and other *Carex* species have been grown readily from seed as part of experimental studies (Kercher and Zedler 2004, Wetzal and van der Valk 2005, Boers *et al.* 2007), and environmental conditions suitable for germination (Baskin *et al.* 1996, Welling *et al.* 1998, Budelsky and Galatowitsch 1999, van der Valk *et al.* 1999) likely existed at our sites during that period. However, both species also grow vegetatively by tillering and can readily expand into open areas, especially when water levels are lower (Costello 1936, Budelsky and Galatowitsch 2004, Stanley *et al.* 2005). Thus, increases in meadow marsh would be expected; they were also observed by Quinlan and Mulamootil (1987) in photographs from their Canadian sites on Lake Ontario.

Typha-Meadow Marsh Dynamics

Most general models of wetland vegetation dynamics on the Great Lakes (Jaworski *et al.* 1979, Harris *et al.* 1981, Keddy and Reznicek 1986, Quinlan and Mulamootil 1987, Painter and Keddy 1992, Maynard and Wilcox 1997) suggest that high lake levels periodically eliminate emergent plants, and ensuing low lake levels allow seed-bank-driven recovery, including *Typha* expansion to lower elevations. In contrast, we found that when the range and amplitude of water-level fluctuations on Lake Ontario remained relatively stable and no low lake levels occurred, *Typha* invasion was mostly landward into meadow marsh, except at sites that had little meadow marsh in the earliest photographs (Figs. 5, 6). Factors that may affect the vegetation dynamics at the boundary between meadow marsh and *Typha* include competition for light, nutrient

availability, sedimentation, and water depth/soil moisture.

Competition

Carex stricta has been shown to be constrained by competition for light at both drier and wetter extremes (Wetzel and van der Valk 1998, Budelsky and Galatowitsch 2004). At our sites, *Calamagrostis* may grow taller and out-compete *C. stricta* in drier areas, but not wetter areas, as suggested by Costello (1936). In our wetter areas at slightly lower elevations, *Typha* with intermixed *Phalaris arundinacea* L. (Wilcox *et al.* 2005) provides the competition (Wetzel and van der Valk 1998, Budelsky and Galatowitsch 2004, Kercher and Zedler 2004, Boers *et al.* 2007). Litter from growth of *Typha* in previous years may also restrict light availability and reduce recruitment of other taxa from the seed bank (van der Valk 1986).

Nutrient Availability

Watershed land-use changes have been shown to result in vegetation changes in downslope wetlands, including reduction in wet meadow species and perennial emergents such as *Typha* (Galatowitsch *et al.* 2000). Increased nutrient availability, which is a potential response to land-use conversion to agriculture and urban areas, has also been linked to invasion of *Typha* in wetlands (Neill 1990, Urban *et al.* 1993, Miao and Sklar 1998, Newman *et al.* 1998, Woo and Zedler 2002). Despite our efforts to select study sites with minimal human disturbance, increased nutrient availability could influence conversion of meadow marsh to *Typha* at drowned river mouth wetlands with agriculture in their watersheds, as well as the two sites near urban Rochester. However, we do not consider it to be a major factor, as invasion of meadow marsh by *Typha* occurred similarly at other sites. In addition, if driven by nutrient availability, we expect that *Typha* invasion would have occurred much earlier than shown by our analysis of aerial photographs, as agriculture and urban land uses were already present in the 1950s photographs (Wilcox *et al.* 2005). Indeed, Wolter *et al.* (2006) found that agricultural land use in the Great Lakes basin actually decreased by 2.3% from 1992 to 2001.

Sedimentation

Increased sedimentation is an additional factor associated with land-use changes that could influ-

ence vegetation changes in Lake Ontario wetlands (Chow-Fraser *et al.* 1998, Chow-Fraser 2005, Wei and Chow-Fraser 2005). Werner and Zedler (2002) quantified a loss of plant species in sedge meadows in Wisconsin when microtopographic variability was reduced around *Carex stricta* tussocks due to sediment deposition, with concomitant increases in *Typha*. Boers *et al.* (2007) found that sediment deposition could weight down leaves of *Carex* spp. and *C. canadensis* in early growth phases and restrict their ability to emerge from standing water. Ewing (1996) also found that sediment deposition reduced biomass of two *Carex* species exposed to different flooding treatments. While sedimentation may have influenced meadow marsh-*Typha* dynamics at our Lake Ontario sites, we do not consider it to be a major factor for reasons similar to those noted for nutrient availability.

Water Depth/Soil Moisture

Reviews of work done by others described above and evidence from our photointerpretation study (coupled with lake-level records, Fig. 1) lead us to conclude that water depth/soil moisture is the primary control influencing *Typha*-meadow marsh dynamics at their interface. However, unlike the focus of other studies on the ability of *Typha* to grow in both moist soil and standing water or on water depths that it can tolerate or on its ability to grow from seed under drawdown conditions, we address the relative abilities of mature *Typha* plants and meadow marsh species to withstand drought or dry soil conditions.

Water-level peaks in Lake Ontario during the summer growing season reached 75.0 m or higher in all but four temporally spaced years from 1967 to the present (Fig. 1). They have not been lower than 74.75 m in successive years since the mid-1960s. Successive years of low lake levels also occurred in the mid-1930s and the late 1890s, bearing resemblance to the long-term, quasi-periodic behavior of Lakes Michigan-Huron and Superior (Baedke and Thompson 2000, Johnston *et al.* 2004, 2007); however, unlike the upper lakes, water levels in Lake Ontario did not enter an extended low phase in 1999. The high lake-level component of the Keddy and Reznicek (1986) model that can reduce the cover of canopy-dominating emergent species occurred in the mid-1970s, but the low lake-level component has been replaced by relatively stable, elevated water levels for about 40 years (Fig. 1). How does this affect vegetation dynamics?

Many wetland models focus on the seed bank as a key component of vegetative change, but our Lake Ontario studies suggest that competition driven by survival of mature plants, with moisture requirements that differ by species, is the primary factor controlling *Typha*-meadow marsh dynamics. Although grasses and sedges have some tolerance of flooding and drier soils (see above discussion), *Typha* has large, fleshy rhizomes and less tolerance of low soil moisture (Weaver and Himmel 1930, Linde *et al.* 1976, van der Valk and Davis 1980). Studies of *Typha domingensis* Pers. in the Everglades of Florida found die-back in Water Conservation Area 2A during droughts (Urban *et al.* 1993) and invasion of Holey Land Wildlife Management Area (which had been rain-fed with substantial dry periods prior to human actions) only after impoundment raised water levels almost continuously (Newman *et al.* 1998).

Wilcox *et al.* (1984) concluded that *Typha* invasion of a *Carex stricta*/*Calamagrostis canadensis* wetland near the south shore of Lake Michigan was initiated by construction of a large diked pond up-gradient from the site. Sedges and grasses persisted during periodic droughts, including the mid-1930s. *Typha* cover remained low until the early 1970s, when constant seepage from the pond increased soil moisture even during dry summers, thus eliminating the hydrology-dependent competitive advantage of the sedges and grasses. Elevated, stable water levels on Lake Ontario seem to have accomplished the same result—*Calamagrostis* and *Carex* are not necessarily enhanced by lower lake levels and reduced soil moisture at upper elevations, but they can survive those conditions. When soil moisture increases at upper elevations, *Typha* can also survive and invasion occurs because *Typha* is a better competitor under those conditions (Newman *et al.* 1998, Kercher and Zedler 2004, Boers *et al.* 2007).

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APPENDIX A. Photograph type, date, and scale of aerial photographs from drowned river mouth, barrier beach, open embayment, and protected embayment wetlands on Lake Ontario used in photointerpretation studies, with lake level (IGLD1985) on date each photograph was taken. BW = black and white, C = color, CIR = color infrared.

Drowned River Mouth	Photo Type	Photo Date	Scale	Lake Level (m)	Barrier Beach	Photo Type	Photo Date	Scale	Lake Level (m)
Brush Creek	BW	07/21/58	1:20,000	74.55	Lakeview Pond	BW	06/04/59	1:20,000	74.87
	BW	07/01/66	1:20,000	74.93		BW	07/02/66	1:20,000	74.93
	BW	06/26/79	1:40,000	75.10		C	04/19/79	1:12,000	75.10
	CIR	08/22/88	1:24,000	74.73		CIR	08/22/88	1:24,000	74.73
	CIR	08/22/01	1:10,000	74.80		CIR	08/22/01	1:10,000	74.80
Crooked Creek	BW	06/03/59	1:20,000	74.86	Maxwell Bay	BW	07/27/54	1:20,000	75.12
	BW	07/02/66	1:20,000	74.93		BW	06/26/63	1:20,000	75.06
	BW	09/23/78	1:38,000	74.68		BW	09/13/78	1:4,800	74.67
	CIR	06/01/90	1:24,000	75.16		CIR	08/22/88	1:24,000	74.73
	CIR	08/22/01	1:10,000	74.80		CIR	08/22/01	1:10,000	74.80
Kents Creek	BW	05/31/59	1:20,000	74.85	Round Pond	BW	07/20/58	1:20,000	74.60
	BW	07/02/66	1:20,000	74.93		BW	07/01/66	1:20,000	74.93
	BW	09/23/78	1:38,000	74.68		BW	06/17/80	1:40,000	75.12
	CIR	08/22/88	1:24,000	74.73		CIR	08/22/88	1:24,000	74.73
	CIR	08/22/01	1:10,000	74.80		CIR	08/22/01	1:10,000	74.80
Stony Creek	BW	06/04/59	1:20,000	74.87	South Colwell Pond	BW	06/04/59	1:20,000	74.87
	BW	07/02/66	1:20,000	74.93		BW	07/02/66	1:20,000	74.93
	C	04/19/79	1:12,000	75.10		BW	09/23/78	1:38,000	74.68
	CIR	08/22/88	1:24,000	74.73		CIR	08/22/88	1:24,000	74.73
	CIR	08/22/01	1:10,000	74.80		CIR	08/22/01	1:10,000	74.80

Open Embayment	Photo Type	Photo Date	Scale	Lake Level (m)	Protected Embayment	Photo Type	Photo Date	Scale	Lake Level (m)
Black River Bay	BW	06/04/59	1:20,000	74.89	Black River Bay South	BW	06/04/59	1:20,000	74.87
	BW	07/02/66	1:20,000	74.93		BW	07/02/66	1:20,000	74.93
	C	04/20/79	1:12,000	75.10		C	04/20/79	1:12,000	75.10
	CIR	08/22/88	1:24,000	74.73		CIR	08/22/88	1:24,000	74.73
	CIR	08/22/01	1:10,000	74.80		CIR	08/22/01	1:10,000	74.80
Braddock Bay	BW	07/20/58	1:20,000	74.60	Goose Bay	BW	06/03/59	1:20,000	74.86
	BW	07/01/66	1:20,000	74.93		BW	07/13/59	1:20,000	74.74
	BW	09/13/78	1:4,800	74.67		BW	07/02/66	1:20,000	74.93
	CIR	08/22/88	1:24,000	74.73		BW	07/06/78	1:4,800	75.09
	CIR	08/22/01	1:10,000	74.80		CIR	06/01/90	1:24,000	75.16
Eel Bay	BW	05/31/59	1:20,000	74.85	North Pond	CIR	08/22/01	1:10,000	74.80
	BW	08/27/66	1:20,000	74.81		BW	06/04/59	1:20,000	74.87
	BW	07/06/78	1:4,800	75.09		BW	07/02/65	1:20,000	74.71
	CIR	06/01/90	1:24,000	75.16		BW	07/05/78	1:4,800	75.11
	CIR	08/22/01	1:10,000	74.80		CIR	08/22/88	1:24,000	74.73
The Isthmus	BW	05/31/59	1:20,000	74.85	Point Vivian Bay	CIR	08/22/01	1:10,000	74.80
	BW	07/02/66	1:20,000	74.93		BW	06/04/59	1:20,000	74.87
	BW	07/05/78	1:4,800	75.11		BW	07/02/66	1:20,000	74.93
	CIR	08/22/88	1:24,000	74.73		BW	07/06/78	1:4,800	75.09
	CIR	08/22/01	1:10,000	74.80		CIR	05/31/90	1:24,000	75.17
						CIR	08/22/01	1:10,000	74.80