# Vegetation Change in Great Lakes Coastal Wetlands: Deviation from the Historical Cycle

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**ABSTRACT.** Water-level change is integral to the structure and function of Great Lakes coastal wetlands, and many studies document predictable relationships between vegetation and water level. However, anthropogenic stressors, such as invasive species, land-use change, and water-level stabilization, interact to shift the historical cycle (of native vegetation migration up- and down-slope) toward dominance by invasive Typha species. Knowing from earlier studies that water-level stabilization alters the historical vegetation cycle, we asked if similar shifts can occur where water levels are not stabilized. Using historical aerial photographs of three coastal wetlands (in Lake Michigan's Green Bay, Wisconsin), we determined that habitat dominated by Typha species has expanded to eliminate wet meadow habitat. Between 1974 and 1992, linear regressions showed strong, significant relationships of both meadow area ( $R^2 = 0.894$ ; p < 0.02) and marsh area ( $R^2 = 0.784$ ; p < 0.05) to water level in all three wetlands. In 2000, meadow area was below that predicted by the historical pattern due to the landward advance of marsh habitat during a year of decreasing water levels. In the same period, land use in the wetland watersheds converted from agriculture to urban. Urbanization and the replacement of native Typha latifolia by the invasive hybrid Typha xglauca may have overwhelmed the beneficial impact of water-level fluctuation. The documentation of vegetation shifts, as herein, is an essential step in the process of preserving and restoring ecological integrity.

INDEX WORDS: Historical cycle, Typha, Great Lakes, wetlands, aerial photographs.

## **INTRODUCTION**

Coastal wetlands of the Laurentian Great Lakes exemplify the integral role of water-level change in wetland structure and function (Planck 1993, Wilcox et al. 2005). High water levels renew structural complexity, restrict the advance of trees and shrubs, and keep the abundance of aggressive species in check (Keddy and Reznicek 1986, Planck 1993, Wilcox 2004). Low levels maintain patchiness, allow for the expansion of wet meadow areas, and renew the seed bank (Keddy and Reznicek 1986, Gottgens et al. 1998, Wilcox 2004, Wilcox et al. 2005). In fact, relationships between vegetation area and water level are quite predictable (Lyon and Drobney 1984, Williams and Lyon 1997, Chow-Fraser et al. 1998, Gottgens et al. 1998). Four habitat types of Great Lakes coastal wetlands,

shrub-carr, wet meadow, marsh, and aquatic (Harris *et al.* 1981, Kelley *et al.* 1984), also change in amount, kind and proportion (Guntenspergen 1985). In this "shifting mosaic" (Wilcox 2004), species and habitat types die back and reinvade based on their water depth affinities, with each type expanding as it moves lakeward (van der Valk 1981, Keddy and Reznicek 1986).

Water-level stabilization disrupts the historical cycle and is held responsible for promoting aggressive species (Wilcox 1993, Herrick and Wolf 2005). It converts formerly diverse, structurally complex wetlands to large areas of only a few species (Keddy and Reznicek 1986, Minc and Albert 1998) by eliminating the high and low water levels important to wetland regeneration, changing competitive interactions among plant species (Shay *et al.* 1999), and increasing phosphorus availability (Richardson and Vepraskas 2000, Boers 2006). For example, *Typha*-dominated habitat increased, displacing wet meadow habitat, in Lake Ontario coastal wetlands

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following the start of water-level regulation (Wilcox *et al.* 2005).

In addition to water-level stabilization, several other anthropogenic stresses have the potential to transform the historical cycle (Patterson and Whillans 1985, Chow-Fraser *et al.* 1998, Gottgens *et al.* 1998). These include land-use change, the introduction of invasive species, other hydrological alterations, and changes in sediment and nutrient loads, all of which can alter competitive relationships (Galatowitsch *et al.* 1999, Weller *et al.* 2003, Zedler and Kercher 2004).

We observed from Landsat TM imagery (30-m pixel) a vegetative trend similar to what occurs with stabilized water levels in a Green Bay, Lake Michigan wetland with natural water-level fluctuation. That is, wet meadow habitat was smaller relative to Typha-dominated marsh habitat in 2001 under low water levels than it was in 1994 when water levels were higher. In this interval, water level rose, peaking in 1997, then decreased, falling below the 1994 level by 1999. While some lag time between waterlevel change and vegetative response is expected, smaller meadow area at a lower water level was contrary to our expectation and prompted us to undertake a more detailed investigation of three Green Bay wetlands using aerial photographs. We examined the relationship of marsh and wet meadow habitat to water level to determine if the historical vegetation cycle has changed despite naturally fluctuating water levels. We hypothesized that (a) historically, both marsh and wet meadow habitats expanded predictably lakeward as water levels fell and wetland area increased, (b) during the most recent water level decline, marsh habitat area was greater and wet meadow habitat area was less than predicted by the historical trend, and (c) marsh habitat continued to expand landward during the most recent water level decline, contrary to the historical pattern.

## **METHODS**

#### **Study Area**

We chose three wetlands and their associated upland areas along the western shore of Green Bay in Brown County, Wisconsin, to represent anthropogenically stressed, embayment wetlands of the Laurentian Great Lakes (Fig. 1). Atkinson Marsh (44°34′00″N/88°02′30″W), Peter's Marsh (44°35′15″N/88°01′30″W), and Long Tail Marsh (44°37′30″N/88°00′45″W) are all directly influenced by natural water-level changes in Lake

Michigan. Each one contains areas of shrub-carr dominated by Salix and Cornus spp., wet meadow dominated by *Carex* spp. and *Calamagrostis* canadensis (Michx.) Beauv., shallow marsh dominated by Typha spp., and deep marsh dominated by Nymphaea odorata Ait. and Sagittaria spp. or newly exposed sand flats dominated by Juncus spp. and Schoenoplectus spp. All were described by Herdendorf et al. (1981) as having low topography, direct exchange with the waters of Green Bay via seiche activity, important wildlife habitat, and surrounding areas undergoing urbanization. Prior to 1973, a chain of islands known as the Cat Islands stretched along the Green Bay coast offshore from Peter's Marsh and Atkinson Marsh. These islands were destroyed by rising water levels and severe storms in the early 1970s, reducing the area suitable for emergent vegetation and likely allowing greater impacts of waves on wetland shores.



FIG. 1. Location of study sites along the coast of Green Bay, Lake Michigan in Brown County, Wisconsin, USA.



FIG. 2. Monthly average water-level elevation of Lake Michigan-Huron (meters above IGLD 1985) from the United States Army Corps of Engineers and aerial photograph dates.

# **Photo Interpretation**

Historical air photo interpretation provides a quantitative method of examining changes in large areas across decades and has proven useful in other studies of Great Lakes coastal wetlands (Gottgens *et al.* 1998, Kowalski and Wilcox 1999). We selected aerial photographs from nine dates based on availability, distribution across the range of dates and water levels, photo quality, and similarity of photo attributes (Fig. 2, Table 1). Even though the water level was extremely low in 1965 (Fig. 2), no photograph was available for that date, and it was not included in this study.

We scanned photographs obtained as  $9'' \times 9''$  contact prints using a Microtek ScanMaster 9600XL at 600 dpi (pixel size = 42 µm on the print and 0.84 m in the field for 1960 and 1967 and 1.64 m in the field for 1974). We then orthorectified the resulting digital images and those photographs obtained in digital form using OrthoMapper<sup>TM</sup> software (Image Processing Software, Inc.), in order to remove the innate distortion caused by topographic variation and camera angle (Wolf and Dewitt 2000). OrthoMapper<sup>TM</sup> uses algorithms to re-map a digital image pixel by pixel based on user-defined horizontal control points, which represent the same geographic point in the image to be rectified and a previously orthorectified image, and a digital elevation model. Basing photo interpretation on orthophotographs reduces distortions in the shape and area of identified vegetation and land cover types and affords multi-date geographic registration, thereby improving the comparison of the areas across time.

Because the 2000 image was obtained as a digital orthophotograph (UTM zone 16, NAD83), we used it as the base image for orthorectifying images from previous years. Land-use changes due to the construction of Interstate 43 in 1967 made it difficult to identify control points for the 1967 and 1960 images in the 2000 image. Therefore, orthorectification of the 1967 image used the 1974 image as a base and orthorectification of the 1960 image used the 1967 image as a base. Despite a large number of control points (7–20), the positional error associated with the orthorectification, expressed as root mean square error (RMSE), ranged from 0.62 to 3.99 pixels, in many cases higher than the ideal of < 1 pixel. This may have been due to differences in photo shrinkage or expansion, irregularities in the scanner, or "drift" (slight distortion) over time in the road intersections used as control points. Posi-

TABLE 1. Summary of aerial photographs interpreted for analyses. Water level is the peak monthly water-level elevation of Lake Michigan-Huron (meters above IGLD 1985) during the previous growing season (May–September).

Date	Film Type	Scale of Original	Source	Original Format	Ortho Resolution	Water Level (m)
Sept. 1960	B&W	1:20000	Farm Service Agency*, USDA	9"×9" print (N = 7)	0.5-m pixels	176.77
Sept. 1967	B&W	1:20000	Farm Service Agency, USDA	9"×9" print (N = 7)	0.5-m pixels	176.50
Oct. 1974	B&W	1:40000	Farm Service Agency, USDA	9"×9" print (N = 4)	1-m pixels	177.32
May 1979	B&W	1:80000	Survey Photography, USDA	digital file $(N = 1)$	1-m pixels	176.71
April 1982	CIR	1:58200	National High Altitude Photography Program, USGS	digital file $(N = 2)$	1-m pixels	176.82
June 1986	CIR	1:58200	National High Altitude Photography Program, USGS	digital file $(N = 3)$	1-m pixels	177.25
May 1992	B&W	1:40000	National Aerial Photography Program, USGS	9"×9" print (N = 3)	1-m pixels	176.66
April 1998	B&W	1:40000	National Aerial Photography Program, USGS	9"×9" printt (N = 3)	1-m pixels	177.19
April 2000	B&W	1:10080	Brown County Land Information Office	digital orthophoto (N = 1)	0.5-m pixels	176.40

\*Known as the Agricultural Stabilization and Conservation Service (ASCS) at the time of photography.

tional error was taken into account during data analysis.

We held the area interpreted as wetland (as opposed to upland), including open water, constant across time and delimited it by approximately the furthest extent of wetland vegetation in any image on the eastern side, and anthropogenic land use or forest to the north, south, and west. We defined associated upland as the watershed of each wetland within 3 km of its upland boundary, which fully encompassed the watersheds of Peter's Marsh and Long Tail Marsh. Watersheds were based on topography and obtained from Danz *et al.* (2005). In each wetland and the associated upland, the boundaries of wetland vegetation and land-use classes were digitized on-screen to create shapefiles using ESRI software (ArcMap<sup>TM</sup> 9.0).

Wetland vegetation class polygons had a minimum mapping unit of  $100 \text{ m}^2$  and were digitized at a 1:1,200 scale to standardize differences in resolution among images. We assigned the polygons thus delineated to one of eight wetland classes: Tree, Shrub, Meadow, Marsh, Mixed Vegetation, Bare soil/Rushes, or Water (Table 2). Other studies of Great Lakes coastal wetlands have identified similar wetland classes from black and white aerial photographs (Harris *et al.* 1981, Kowalski and Wilcox 1999). Upland land-use classes were digitized at a 1:10,000 scale with a minimum mapping unit of 10,000 m<sup>2</sup> and assigned to the Urban, Agricultural, or Natural class (Table 2).

The shape, tone, and texture of the various wetland classes were determined by comparing the 2000 photo with field data collected in 2001 and 2002. In each wetland, transects were randomly placed perpendicular to the perceived water gradient, i.e., moving from water's edge to the upland. Plots, 1 m<sup>2</sup> in area, were then randomly placed along 20-m segments of these transects with a nonrandom plot at the "wet end" of the each transect. In each plot the species rooted within the plot were visually assigned one of six cover classes (< 1%, 1-5%, 6-25%, 26-50%, 51-75%, and > 75%) modified from Braun-Blanquet (1932). The number of plots sampled in each wetland was roughly proportional to the size of the wetland and 33, 58, and 16 plots were sampled in Atkinson, Peter's, and Long Tail marshes, respectively. In all, 15 plots were

## Frieswyk and Zedler

Class	Description	
Water	Open water. Appears in photo in smooth dark tones, with light toned ripples or bright white.	
Bare soil/Rushes	Total vegetation < 50% cover. <i>Schoenoplectus tabernaemontani</i> (K.C. Gmel.) Palla and/or <i>Junca nodosus</i> L. have highest cover, <i>Eleocharis erythropoda</i> Steud. often present. Appears in photo a ve smooth light tone along or close to water's edge	
Marsh	At least 25% (often > 50%) cover m <sup>-2</sup> cover by <i>Typha</i> spp. forming an obvious canopy; under-story often containing <i>Impatiens capensis</i> Meerb., <i>Urtica dioica</i> L., <i>Calamagrostis canadensis</i> (Michx.) Beauv., and <i>Leersia oryzoides</i> (L.) Sw. Appears in photo as mottled, mid-tone, clonal pattern (circles) often evident, may appear cloud-like.	
Meadow	Grass ( <i>Calamagrostis canadensis</i> ) and/or sedge ( <i>Carex lacustris</i> Willd., <i>Carex stricta</i> Lam.) at leas 50% cover; dicots abundant. Appears a grainy, light tone often near and around shrubs	
Mixed Vegetation	A mixture of <i>Typha</i> (5-50%) and Rush or Meadow vegetation. Appears in photo as mottled mixed tones between Marsh and Rushes or Meadow classes.	
Shrub	<i>Salix</i> and <i>Cornus</i> shrubs making up at least 50% continuous cover, under-story of Meadow vegetation. Appears in photo in dark tones, distinguished from water by position, irregular shape and height.	
Tree	Trees (e.g., <i>Populus</i> ) making up at least 50% continuous cover, under-story of Meadow vegetation. Appears in photo in dark tones, distinguished from water by position, irregular shape and height, taller than shrubs.	
Urban	Buildings, streets, parking lots, etc. and their associated landscaping, including artificial ponds.	
Agricultural	Cropped land; fallow fields not distinguished from Natural.	
Natural	Any area in the upland not included in Urban or Agriculture classes: forests, fallow fields, natural water, and grasslands.	

TABLE 2. Description of wetland vegetation and land-use classes. Descriptions were based on a comparison of black and white images from 2000 and visually estimated species cover in  $1-m^2$  quadrats sampled in the field in July 2001/2002.

characterized as Meadow, 56 as Marsh, 12 as Mixed Vegetation, and 16 as Bare soil/Rushes. This information was then used as a guide to interpret the historical photos.

Viewing stereo pairs of contact prints, vegetation maps of Peter's Marsh created by Harris *et al.* (1981) and a set of large scale, oblique, color photos of Peter's Marsh taken between 1974 and 1999 (obtained from G. Fewless, University of Wisconsin-Green Bay) also aided our interpretation of the historical photos. While *Typha* ×*glauca* Godr. (pro sp.) dominated the Marsh vegetation in our 2001/2002 field data (Table 2), this class may have been dominated by other *Typha* species and/or other emergent species in the past. For example, Harris *et al.* (1981) showed *Scirpus* spp. dominating the marsh habitat of Peter's Marsh in 1978. We were unable to distinguish *Typha* and *Scirpus* in our 1979 photo.

The same interpreter (CBF) did all photo interpretation for consistency. For quality assurance, interpretation was duplicated by Aaron Boers, who had experience delineating *Typha*-dominated areas from air photos, for the wetland area of Long Tail Marsh in a low water (1974) and high water (1982) image.

## **Data Analysis**

Topology, which defines the spatial relationship among the polygons in the map, was created for the digitized wetland vegetation and land-use polygons (i.e., shapefiles were converted to coverages). This process also calculated the area and perimeter of each polygon. We analyzed vegetation change using the "overlay-union" tool in ESRI software (Arc Toolbox<sup>TM</sup> 9.0). This tool combined the land-cover information in two maps of consecutive dates into one "change" map. Each polygon in the change map has two land covers associated with it, one from the first date and one from the second. Thus, areas where vegetation or land use had changed have two different land-cover identities, and areas without change have two identical land-cover identities. To reduce positional errors, all polygons with an area less than the minimum mapping unit were excluded from analysis. This reduced the wetland area analyzed by no more than 1.5% and the upland area by no more than 0.4% in any image pair.

Water levels were obtained as coordinated monthly means for Lake Michigan-Huron (one lake hydrologically) from the United States Army Corp of Engineers. Whole-lake levels are coordinated from several gauging stations to create a complete record. These levels are on average 0.02 m below available levels recorded in Green Bay and are highly correlated with the partial Green Bay record (r = 0.99). Because peak water levels during the growing season drive herbaceous vegetation changes, we used the highest monthly mean of the growing season (May–September) preceding each map date for our analyses. Because longer term water-level history can also be important to vegetation dynamics (Gottgens et al. 1998, Wilcox et al. 2005), we followed the method of Williams and Lyon (1997) to determine the lag time in vegetative response to water-level change. This method uses successive trials of a weighted average of the water level of an increasing number of years preceding each image date.

We used linear regression to examine the relationships among water level, the area of wetland vegetation (hereafter Wetland area), and the area of the Marsh and Meadow classes. Data from the 1960 and 1967 land cover maps were not included in regressions on water level because in Atkinson Marsh and Peter's Marsh the presence of the Cat Islands buffered the wetlands from the open bay and likely affected the relationships under consideration by increasing the area suitable for the growth of vegetation at any given water level. In order to determine if the relationship of Marsh and Meadow areas to water level and Wetland area remained constant in recent years, we performed regressions on water level using data from the 1974–1992 maps and regressions on Wetland area using data from the 1960–1992 maps. Then, we compared Marsh and Meadow areas in 1998 and 2000 against the 95% prediction intervals.

Transition matrices created from the "change" maps were used to determine the direction of Marsh recruitment. Transitions from Meadow, Shrub, and Tree classes to Marsh indicated a landward recruitment, which we expected with water level rise, and transitions from Water or Bare soil/ Rushes to Marsh indicated lakeward recruitment, as we expected with water level fall. Because many factors

besides water-level change affect Marsh recruitment, some recruitment in both directions can be expected in most intervals. The ratio of lakewardto-landward recruitment (lake:land) was used to indicate if recruitment occurred primarily lakeward (lake:land > 1), primarily landward (lake:land < 1), or equally in both directions (lake:land 1). The ratios were then compared to the direction of waterlevel change.

#### RESULTS

# General Trends, 1960–2000

Land-use changes were similar among the three wetland watersheds. Natural area remained steady while Urban area increased and Agricultural area decreased. The Peter's Marsh watershed had the largest proportion of Natural area, mostly due to the Fort Howard Paper Foundation Wildlife Area. In Atkinson and Long Tail Marshes, nearly 50% of the Agriculture area converted to Urban area between 1992 and 2000 (Fig. 3).

Wetland area, the combined area of all wetland vegetation classes, was negatively correlated with peak water level of the previous growing season (r = -0.617, -0.774, -0.787 in Atkinson, Peter's and Long Tail marshes, respectively). Wetland area varied from 9.20 ha to 242.06 ha in Atkinson Marsh, 16.09 ha to 120.11 ha in Peter's Marsh, and 5.35 ha to 47.89 ha in Long Tail Marsh with coefficients of variation (CV) of 68.60, 19.22, and 6.61, respectively (Figs. 4 and 5).

Meadow and Marsh areas were also negatively correlated with water level (for Meadow r = -0.466, -0.554, -0.544; for Marsh  $\rho = -0.622$ , -0.628, -0.745). Meadow area ranged from 2.33 ha to 72.68 ha, 1.38 ha to 62.52 ha, and 0.00 ha to 26.99 ha in Atkinson, Peter's and Long Tail marshes, respectively. The Marsh class occupied a larger portion of the wetland, ranging from 0.64 ha to 163.73 ha, 0.39 ha to 53.20 ha, and 0.53 ha to 17.13 ha, respectively. Both classes had high CVs (for Meadow CV = 30.56, 14.46 and 6.80; for Marsh CV = 47.08, 12.41, and 3.21).

In a blind test, separate image interpretations by Frieswyk and Boers showed high concurrence on the wetland and habitat areas of Long Tail Marsh in the 1974 and 1982 images. Neither interpreter had consistently higher or lower habitat areas than the other. Coefficients of variation (CV) between interpreters ranged from 0.02 to 0.47 and were below the CVs for each vegetation class among images. Habitat areas of Boers' interpretation were within



FIG. 3. Area of upland land-use classes in wetland watersheds as determined by air photo interpretation.

the 99% confidence intervals of regression analysis based on Frieswyk's interpretation.

#### **Historical Patterns, pre 1992**

Peak water level of the previous growing season was the best predictor of Wetland area using the weighted average method of Williams and Lyon (1997) to determine the lag time in vegetative response over the period 1974–1992. The regression fit ( $\mathbb{R}^2$ ) decreased for each additional year included in the weighted average of peak growing season water levels up to 10 years in each of the three wetlands. Peak water level of the previous growing season was also the best predictor of Meadow area in Peter's and Long Tail marshes and of Marsh area in all three marshes. A weighted average of 6 yearly water levels was the best predictor of Meadow area in Atkinson Marsh.

As expected, we found predictable relationships among peak water level, Wetland area, Meadow area, and Marsh area during the historical period. Linear regressions over the period 1974–1992 showed the previous growing season's peak water level to be a strong and significant predictor of Wetland (p < 0.02 and  $R^2$ 0.883), Meadow (p < 0.03 and  $R^2$ (0.845), and Marsh areas (p < 0.05and R<sup>2</sup> 0.784). Wetland area was a stronger predictor than water level of Meadow (p 0.001) and Marsh (p 0.001) areas with similar regression fits for Meadow areas (R<sup>2</sup> 0.908) and higher regression fits for Marsh areas  $(R^2 \quad 0.900)$  (Table 3).

Marsh recruitment, defined as the area that converted to Marsh from other habitat types between each sequential pair of images, followed a predictable pattern during the historical period. While at least some Marsh recruitment occurred in both the lakeward and landward direction between most images, recruitment ratios comparing lakeward to landward recruitment (lake:land) showed an overall pattern (Fig. 6). In the time intervals ending in 1967, 1979, and 1992, water levels experienced a net decrease and lake: land ratios were > 1, indicating lakeward recruitment of Marsh. In intervals ending in 1974 and 1986, water levels rose and lake: land ratios were < 1, indicating landward recruitment of Marsh. Variable Marsh recruitment between 1979 and 1982, a period with little net change in water level (Fig. 2), was reflected by lake: land ratios of approximately 1 in Atkinson and Long Tail marshes. In Peter's Marsh, Marsh recruited primarily landward in this interval (Fig. 6).

#### **Deviation from Pattern, Post 1992**

In examining how Meadow and Marsh areas deviated from historical patterns, we considered 95% prediction intervals around the regression line of Marsh and Meadow areas on either water level or Wetland area. Both predictors led to similar results, but we focus on those using Wetland areas as a predictor. Because this study focuses on the relationship between habitat types within the wetland area, we considered Wetland area preferable to water level for the prediction of Meadow and Marsh



FIG. 4. Image interpretation maps showing changes in habitat areas between 1960 and 2000 in Peter's Marsh. Similar patterns occurred in Atkinson and Long Tail marshes.



FIG. 5. Changes in habitat area with peak water level of the previous growing season (May - September).

areas. Wetland area also accounted for geomorphological changes resulting from the loss of the Cat Islands, so data from the 1960 and 1967 images were included in the regression model, which strengthened the model. In addition, wetland area was a better predictor of Meadow and Marsh area (Table 3), and lag time, which is not incorporated in Wetland area, was not a factor in this data set.

As expected, both Meadow and Marsh areas deviated from the historical pattern. When regressed against Wetland area, the Marsh area of Long Tail Marsh was above the prediction interval in 2000

TABLE 3. Historical relationships among peak water level of the previous growing season, wetland area, and habitat area. Regressions on water level based on interpretation of 1974–1992 images (N = 5); regressions on wetland area based on interpretation of 1960–1992 images (N = 7).

Regression	Coefficient	<b>R</b> <sup>2</sup>	p-value				
Wetland area (ha) on water level (m)							
Atkinson Marsh	-116.98	0.883	0.018				
Peter's Marsh	-69.31	0.897	0.015				
Long Tail Marsh	-36.40	0.902	0.013				
Meadow area (ha)	on water level	(m)					
Atkinson Marsh	-15.85	0.861	0.023				
Peter's Marsh	-39.26	0.900	0.014				
Long Tail Marsh	-22.21	0.845	0.027				
Meadow area (ha)	on Wetland ar	ea (ha)					
Atkinson Marsh	0.29	0.937	< 0.001				
Peter's Marsh	0.53	0.977	< 0.001				
Long Tail Marsh	0.60	0.908	0.001				
Marsh area (ha) on	water-level (1	m)					
Atkinson Marsh	-102.06	0.859	0.024				
Peter's Marsh	-24.48	0.784	0.046				
Long Tail Marsh	-14.75	0.991	< 0.001				
Marsh area (ha) on	Wetland area	(ha)					
Atkinson Marsh	0.70	0.987	< 0.001				
Peter's Marsh	0.46	0.900	0.001				
Long Tail Marsh	0.28	0.901	0.001				

and Meadow area was below the prediction interval in 2000 for Peter's and Long Tail marshes. However, Marsh area in 1998 fell within the 95% prediction interval for all three marshes and within the prediction interval for Atkinson and Peter's marshes in 2000, and Meadow area fell within the 95% prediction interval in 1998 for all three marshes and in 2000 for Atkinson Marsh (Fig. 7). Results based on water level rather than Wetland area differed only in that, for Long Tail Marsh, Marsh area was above the prediction interval in 1998.

While the historical pattern of Marsh recruitment continued with a net rise in water level between 1992 and 1998, the pattern of Marsh recruitment changed during the most recent water level decline, as we hypothesized. Variable water levels with a net rise between 1992 and 1998 were associated with lake:land ratios > 1, indicating landward recruitment, as predicted by the historical pattern. During this time period, Marsh patches conglomerated and



FIG. 6. Area of Marsh recruitment in the lakeward and landward directions. Lakeward recruitment is represented by negative areas and landward recruitment is represented by positive areas. The number displayed with each bar is the ratio of lakeward to landward recruitment (lake:land) and \* indicates direction of Marsh recruitment expected based on water-level change. Note the different y-axis scales.

Meadow patches disappeared, although some areas of Marsh converted to Meadow. Despite a 0.8-m drop in water levels between 1998 and 2000, Marsh continued to recruit primarily landward or nearly equal in both directions, with lake:land ranging from 0.2 (Peter's) to 1.5 (Atkinson) as Marsh replaced Meadow, filled Meadow patches, and expanded along its landward border (Fig. 6).

## DISCUSSION

Strong, linear relationships between area and water level supported our first hypothesis that wetland area, marsh, and wet meadow expanded historically as water levels fell and contracted as they rose (Table 3). This pattern is consistent with the contraction and expansion of emergent and wet meadow habitats seen in Pentwater Marsh, Lake Michigan, by Kelley *et al.* (1984) and the strong relationship found between wetland area and water level in other Great Lakes coastal wetlands (Lyon and Drobney 1984, Gottgens *et al.* 1998).

Supporting our second hypothesis, we found evidence that change in Marsh and Meadow area during the most recent water-level decline does not fit the historical pattern in Peter's and Long Tail marshes. In Long Tail Marsh, Marsh area exceeded the 95% prediction interval about the regression line in 2000. This overabundance of Marsh was balanced by lower than predicted Meadow area. In 2000, Meadow area was also lower than predicted in Peter's Marsh (Fig. 7). While we did not find deviation from the historical pattern in Atkinson Marsh, very little Meadow was present in 1998 and 2000. Even though Wetland area recovered after the high water level of 1974, the Meadow area remained small in Atkinson Marsh, which experienced the smallest changes in Meadow area of the three wetlands despite having the largest changes in Wetland area (Fig. 5).

Evidence also supports our third hypothesis that marsh habitat continued to expand landward during the most recent water level decline. The Marsh expansion helps explain the small Meadow areas observed in 2000. In the historical pattern, Marsh recruited primarily landward during rising water levels and primarily lakeward during falling water levels. While water levels began falling after 1997, landward recruitment of Marsh was greater between 1998 and 2000 than in any other interval of declining water levels, and lakeward:landward recruitment was less than or close to 1.

Our third hypothesis is further supported by field



FIG. 7. Ninety-five percent prediction intervals based on linear regressions of habitat area on wetland area. Stars represent areas used in the regression, two-digit years represent areas from the most recent period of water-level decline that were tested against the regression. Note the different y-axis scales.

data collected after several years of sustained low water levels. In June 2003, we mapped the boundary between wet meadow habitat and *Typha*  $\times$ *glauca* Godr. (pro sp.)-dominated (marsh) habitat in each of the study marshes using a hand-held Garmin GPS unit (Frieswyk and Zedler in press). When this boundary was overlain on the 2000 map, we measured both landward and lakeward changes in the boundary position within each wetland. The boundary moved primarily landward, up to 30 m in some places; lakeward movement was never more than 15 m.

We recognize, however, that lag effects could be influencing our results. The decline in water level preceding the 2000 map, while large, occurred over a period of only two growing seasons, while water level declines preceding the 1967, 1979, and 1992 maps occurred over longer periods, giving the vegetation more time to respond. Data on the lag time between water level and vegetation change in Great Lakes coastal wetlands are inconsistent. Williams and Lyon (1997) found a lag time of 14 years for emergent wetlands along the St. Mary's River. Using the same method, our data showed a 6-year lag time in the Meadow area of Atkinson Marsh, but no lag time for Meadow in the other two marshes or for Marsh in all three marshes. Hudon *et al.* (2005) found that broad classes of wetland vegetation (Meadows and mudflats, Marshes, and Shallow submerged) responded quickly to the water level of the current and previous growing seasons in Lake Saint-Pierre. In addition, while few data are available on the drought tolerance of marsh vegetation, Harris and Marshall (1963) found reduced *Typha* spp. density after only 1 year of drawdown in a Minnesota marsh.

Historically, the marsh zone of Green Bay coastal wetlands was dominated by the native *Typha latifolia* L. Today, *Typha* ×*glauca* and *Typha angustifolia* L. are expanding throughout the Great Lakes (Chow-Fraser et al. 1998), and these aggressive invaders are widely dominant (Frieswyk 2005). While *Typha* ×*glauca* has likely been present in Green Bay coastal marshes for the last 50 years, it became ecologically important in the late 1980s (Smith 1987). Our field data found *T.* ×*glauca* to dominate

the marsh habitat in Green Bay coastal wetlands, while sparse T. angustifolia occurred in the bare sand/mud flat areas. T. ×glauca is more competitive and more tolerant of water level fluctuation (Galatowitsch et al. 1999), and it tolerates a wider range of water depths than T. latifolia (Waters and Shay 1990). Its wide tolerance range may be due to the production of both shallow and deep rhizomes (S.G. Smith, University of Wisconsin - Madison, pers. comm.). Its growth form is a dense canopy, due to short intervals between rhizome branches (Woo and Zedler 2002). As a hybrid of T. latifolia and T. angustifolia, T. ×glauca produces very few seeds and therefore reproduces primarily vegetatively (Smith 1987). Sexual reproduction occurs only in the presences of both parents (Chow-Fraser et al. 1998), but unlike most emergent species, seeds are able to germinate under water (Shay et al. 1999). T. angustifolia, on the other hand, is better able to disperse its seeds and colonize disturbed wetlands (Smith 1986) and tolerates deeper water (Grace and Wetzel 1982) than T. latifolia.

When water levels are low, the vegetation that develops on bare soil depends on germination from the seed bank (Keddy and Reznicek 1986), and the subsequent flooding regime influences establishment (Hudon et al. 2005). At the upslope edge, expansion of intact vegetation is limited by drying that shifts competitive advantage (Wilcox et al. 2005). Neither process operates when water levels are stabilized, so Typha spp. expand (as in Lake Ontario coastal wetlands; Wilcox et al. 2005) and wet meadow shrinks. Low water levels can reduce wet meadow habitat if T. ×glauca fails to migrate downslope by tolerating drier conditions. Resilience of wet meadow would then depend on the seed bank or dispersal from other wet meadows. Three factors reduce chances that wet meadow will persist unaided. First, the dense growth and thick litter of T.  $\times$  glauca inhibit germination from the seed bank (Frieswyk and Zedler 2006). Second, bare patches might be swamped by the abundant and widely dispersed seeds of T. angustifolia. Third, floating mats of Typha spp. could arrive on bare sand/mud flats as high waters recede, although we did not find such mats in our study wetlands. The potential for wet meadow vegetation to recover is far from certain, especially where invaders are able to become more aggressive.

While not a prerequisite for the expansion of T. ×*glauca*, the growth and spread of invasive species, including T. ×*glauca*, can be enhanced by an increase of urban and agricultural land use in watersheds (Galatowitsch et al. 1999, Boers 2006). Our results show that increased urbanization in the watersheds of the Green Bay coastal wetlands (Fig. 3) coincided with the loss of wet meadow habitat (Fig. 7). Similarly, Thibault and Zipperer (1994) found that as agricultural land was urbanized near Syracuse, New York, wet meadows converted to scrubshrub or emergent cover in wetlands. The indirect effects of urbanization on Great Lakes coastal wetlands is poorly studied, but the changes in hydrology and sediment quality normally associated with urbanization (Lougheed et al. 2001, Paul and Meyer 2001, Choi and Bury 2003) could affect habitat dynamics and promote invasive species like *Typha*  $\times$  *glauca*, especially when lake levels are low. For example, Harris and Marshall (1963) found that during drawdown in Agassiz Refuge, Minnesota, the expansion and survival of emergents, including Typha  $\times$  glauca, depended in part on the sediment type, which is linked to the rate of drainage and soil chemistry.

In addition to undergoing changes in habitat area, the three study wetlands decreased in total area over time, not regaining their full extent following extreme high water levels (Fig. 5). A similar trend has been recognized in other Great Lakes coastal wetlands where recovery from high water levels has been incomplete in response to anthropogenic stresses such as shoreline armament, land-use change in the watershed, the introduction of common carp (Cyprinus carpio) and altered food webs (Chow-Fraser et al. 1998, Gottgens et al. 1998, Kowalski and Wilcox 1999). In lower Green Bay, long-term loss of wetland area was initiated by the loss of the Cat Islands, which occurred after severe spring storms and extreme high water levels in the spring of 1973. Plans to restore wetland area and provide wildlife habitat by restoring the Cat Island chain are already underway (V. Harris, Wisconsin Sea Grant, pers. comm.).

After we completed our field work, another invasive species, *Phragmites australis* (Cav.) Trin. ex Steud., began expanding in Green Bay. During the 2000 growing season, *Phragmites* formed substantial stands in Green Bay wetlands (G. Fewless, University of Wisconsin - Green Bay, pers. comm.). An ongoing study documented an increase in *Phragmites cover* of more than 100-fold between 2001 and 2004 in one Green Bay coastal wetland (M. Tulbure and C. Johnston, South Dakota State University, pers. comm.). Earlier, Wilcox *et al.* (2003) found that *Phragmites* was increasingly dominant in a Lake Erie wetland between 1995 and 1999, primarily replacing wet meadow and marsh habitat. The long-term relative distributions of *Typha* spp. and *Phragmites* in Great Lakes coastal wetlands are uncertain, because each species can show competitive superiority depending on environmental conditions (Grosshans and Kenkel 1997, van der Putten *et al.* 1997, Shay *et al.* 1999). Grosshans and Kenkel (1997) found *Phragmites* to be less competitive while Shay *et al.* (1999) found *Phragmites* to be more competitive than *Typha* spp. under fluctuating water levels. However, the increasing invasion of Great Lakes coastal wetlands by *Phragmites* will further change habitat dynamics and contribute to the loss of wet meadow and biodiversity.

Because wet meadows are the most species-rich habitat type in Great Lakes coastal wetlands (Keddy and Reznicek 1986, Wilcox *et al.* 2005), their replacement by *Typha*-dominated (marsh) habitat threatens the ecological integrity of regional wetlands. Wet meadows contribute to wetland structural complexity (Wilcox *et al.* 2005) and support a wide range of wildlife, particularly birds (Riffell *et al.* 2001), while marshes dominated by *Typha*, and particularly *T.* ×*glauca*, are known to be structurally uniform and monotypic (Smith 1986, Frieswyk 2005).

Our evidence indicates that Typha-dominated habitat can expand to eliminate wet meadow habitat during periods of low water levels. Although waterlevel variation sustains the structure and function of Great Lakes coastal wetlands (Planck 1993, Wilcox et al. 2005), ecological integrity remains at risk. The dual stresses of invasive species and land-use change could overwhelm the beneficial effects of water level fluctuation (Patterson and Whillans 1985) and allow wet meadow to be displaced by *Typha* spp. Fluctuating water levels are necessary but not sufficient to preserve and restore ecological integrity. Documenting shifts in vegetation before wet meadow is entirely eliminated gives managers cause for action, and we urge more widespread monitoring of vegetation change via historical air photo interpretation.

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