

## THE EFFECTS OF WATER-LEVEL FLUCTUATIONS ON VEGETATION IN A LAKE HURON WETLAND

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**Abstract:** The diversity and resultant habitat value of wetland plant communities in the Laurentian Great Lakes are dependent on water-level fluctuations of varying frequency and amplitude. Conceptual models have described the response of vegetation to alternating high and low lake levels, but few quantitative studies have documented the changes that occur. In response to recent concerns over shoreline management activities during an ongoing period of low lake levels in lakes Superior, Michigan, and Huron that began in 1999, we analyzed a quantitative data set from Saginaw Bay of Lake Huron collected from 1988 to 1993 during a previous lake-level decline to provide the needed information on vegetation responses. Transects were established that followed topographic contours with water-level histories that differed across a six-year period, ranging from barely flooded to dewatered for varying numbers of years to never dewatered. Percent cover data from randomly placed quadrats along those transects were analyzed to assess floristic changes over time, document development of distinct plant assemblages, and relate the results to lake-level changes. Ordinations showed that plant assemblages sorted out by transects that reflect differing water-level histories. Distinction of assemblages was maintained for at least three years, although the composition and positioning of those assemblages changed as lake levels changed. We present a model that uses orthogonal axes to plot transects by years out of water against distance above water and sorted those transects in a manner that matched ordination results. The model suggests that vegetation response following dewatering is dependent on both position along the water level/soil moisture gradient and length of time since dewatering. This study provided quantitative evidence that lake-level fluctuations drive vegetative change in Great Lakes wetlands, and it may assist in making decisions regarding shoreline management in areas that historically supported wetlands.

**Key Words:** drawdown, Great Lakes, hydrodynamic model, plant communities, *Schoenoplectus pungens*, *Typha angustifolia*

### INTRODUCTION

Decreases in water levels in lakes Superior, Michigan, and Huron of the Laurentian Great Lakes beginning in 1999 raised public concerns regarding recreational boating, shipping, lakefront property, and natural resources (Figure 1). Docks, marinas, and boating channels in marginally deep water required dredging or suffered from limited use. In sand-rich areas, many beaches greatly increased in width and new shoreline dunes began to form. Reaches of shoreline that historically had been wetlands began to develop new wetland plant communities as germination of the exposed seed bank promoted growth of emergent species that had been eliminated by a period of sustained high lake levels. Some owners of shoreline property did not see this as a positive situation (Wilcox and Krygier 2002). The State of Michigan Legislature subse-

quently passed Public Act 14 of 2003 that exempted property owners in selected regions of lakes Michigan, Huron, and St. Clair from obtaining a permit to conduct maintenance operations such as mowing and removal of washed-up vegetation from exposed lake bottoms. The legislation also created a permitting process to allow mechanical removal of certain types of vegetation in selected areas. The resulting actions by property owners resulted in physical and chemical alterations of wetlands, with concomitant effects on plant, invertebrate, and fish communities (Albert 2005, Uzarski and Burton 2005, MDEQ 2006).

Fluctuations in lake levels are necessary to sustain coastal wetlands of the Great Lakes, as high water levels kill trees, shrubs, and other emergent vegetation, and low water levels following these highs result in seed germination and growth of a multitude of species (Keddy and Reznicek 1986, Wilcox 1995,

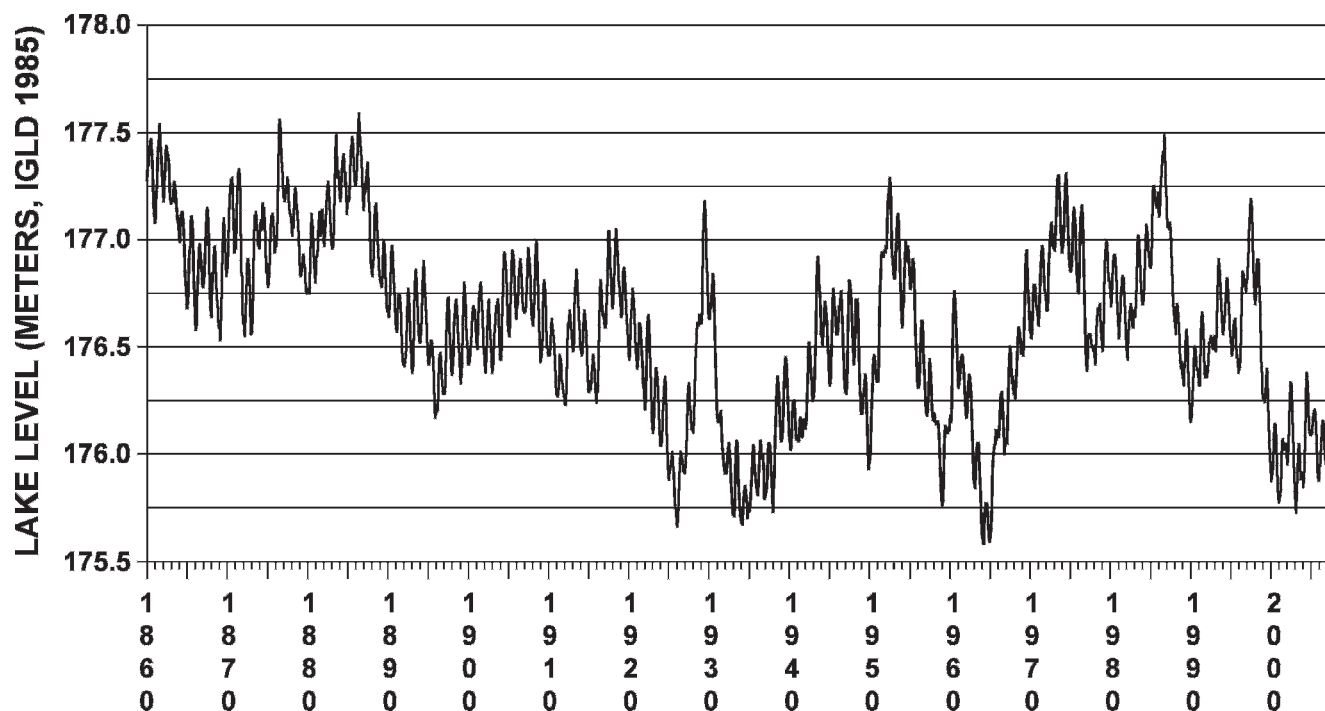


Figure 1. Hydrograph showing recorded water levels in Lake Michigan-Huron (one lake hydrologically) from 1860 to present (referenced to International Great Lakes Datum 1985).

Maynard and Wilcox 1997, Environment Canada 2002). Individual plant species and communities of species have affinities and physiological adaptations for certain water-depth ranges (Sculthorpe 1967, Spence 1982, Kozłowski 1984), and their life forms may show adaptations for different water-level environments (Wooten 1986, Hejny and Hroudova 1987, Keddy 2000). Changes in water level add a dynamic aspect to the species/depth relationship. Water-level dynamics result in shifting mosaics of wetland vegetation types (e.g., Keddy 2000; Figure 4.32).

Some species are particularly well-suited to recolonizing the drawdown zone, like that which began to appear in 1999 following high lake levels in 1997 (Keddy and Reznicek 1982, Wilcox et al. 1985), and several emergents may coexist there because of their diverse responses to natural disturbance (van der Valk and Davis 1980). In the first year following a reduction in water levels, the distribution of new seedlings is due to the distribution of seeds in the sediments. In ensuing years, the distribution of adults is due to seedling survival through competitive interactions across environmental gradients (Welling et al. 1988, Seabloom et al. 1998, 2001, Keddy 2000). If one species is favored in early colonization, its density may be great enough that it can maintain dominance of an area (site preemption) (Grace 1987). In most cases, early colonizing

species or communities are later lost through competitive displacement, but the opportunity to go through a life cycle allowed them to replenish the seed bank (van der Valk and Davis 1978, Keddy and Reznicek 1982).

Although the general conceptual models for wetland plant community response to changing water levels in the Great Lakes (Jaworski et al. 1979, Harris et al. 1981, Keddy and Reznicek 1986, Quinlan and Mulamoottil 1987, Painter and Keddy 1992, Maynard and Wilcox 1997, Environment Canada 2002) conform to those developed by others working elsewhere (e.g., van der Valk and Davis 1978, Poiani and Johnson 1993, van der Valk 2000), they have not been confirmed by field data collections designed to show the relation of plant communities to lake-level history (Keddy 2000). In response to the now-burgeoning public concerns about low lake levels and resulting human activities that affect wetlands, we analyzed a set of previously collected quantitative data taken in Saginaw Bay of Lake Huron from 1988 to 1993 following a similar decline in lake levels after the historic high of 1986. Peak lake levels dropped about 0.8 m within two years following highs in both 1986 and 1997, dropped another 0.2 m over the next two years, and followed the same fluctuation pattern for the next five years in both sequences (Figure 1). The Saginaw Bay data were generated as part of the

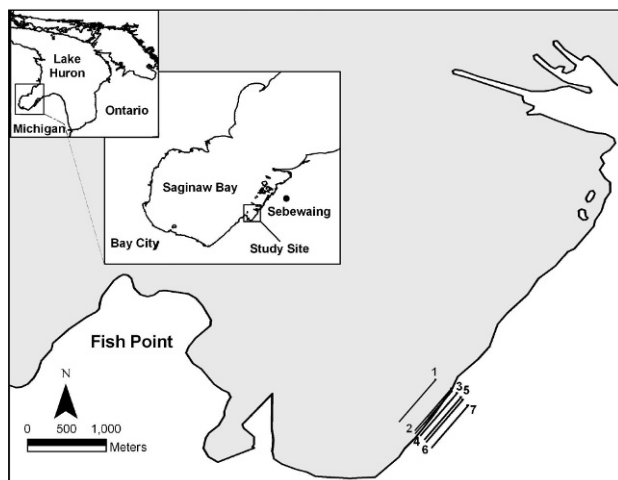


Figure 2. Map of Fish Point wetland study area in Saginaw Bay of Lake Huron, Michigan, USA showing approximate placement of seven sampling transects that follow elevation contours.

International Joint Commission Great Lakes Water Levels Reference Study and were collected in a manner specifically designed to address lake-level questions. We present results of that study here to demonstrate quantitatively that lake levels are a controlling factor in determining composition and potential zonation in wetland plant communities of the Great Lakes following a large decline in water levels, as evidenced by development of different plant assemblages at elevations with different water-level histories. We then place the results in a modeling framework that includes water depth and duration of exposure.

### STUDY SITE

The study site was a coastal wetland of Lake Huron in a small embayment between Fish Point and the town of Sebawaing, Michigan, USA on the east shore of Saginaw Bay (Figure 2). The embayment, 2,000–2,500 m wide and generally less than 1 m deep at average growing season lake levels, has little bottom relief, and seiches of only 20 cm can flood and dewater large areas. Sampling was conducted along the east shore of the embayment, where a low ridge (likely formed as an amalgamation of beach ridges aggraded through time; T. Thompson, Indiana Geological Survey, pers. comm.) parallels the shoreline. When sampling began in 1988, emergent marshes occurred along the shore, submersed plant communities were dominant offshore, and islands of cattails were scattered across the offshore area. The bottom substrate in the embayment was sand, which was

overlain by as much as 20 cm of organic sediments in the offshore area.

Lake Huron water levels (referenced to meters, International Great Lakes Datum (IGLD) 1985) that affect the study site vary at a number of scales of time and amplitude. Since systematic recording of lake levels began in 1860, monthly mean water levels in Saginaw Bay have varied by nearly 2 m, from a low of 175.58 m in March 1964 to a high of 177.50 m in October 1986 (Figure 1) (NOAA 2007a). Sedimentological studies of relict shorelines have identified a range in amplitude in Lake Michigan-Huron (one lake hydrologically) of as much as 2.3 m over the past 3,500 years, with an inferred low of 175.5 m occurring 1050 cal. yr. BP and a high of 177.8 m occurring 1600 cal. yr. BP (Baedke and Thompson 2000). These long-term lake-level studies show a quasi-periodic behavior, with changes in high lake levels ranging from 0.5–0.6 m occurring about every 30–33 years as part of a larger quasi-periodic cycle with changes ranging from 0.8–0.9 m about every 160 years (Baedke and Thompson 2000).

Seasonal low lake levels on Lake Huron typically occur in February and seasonal high levels in July. Seiches provide nearly continuous water-level changes at Fish Point during the open water seasons, with amplitudes typically about 10 cm and not uncommonly 20 cm. Lake-level extremes in Saginaw Bay, including seiches, spanned a range of over 2.2 m in the period before and during this study, from 177.87 m on October 4, 1986 to 175.66 m on January 25, 1990 (NOAA 2007a). Mean lake levels from May 1 to August 31 at Fish Point, and thus relevant to the growing season affecting this study, decreased from 177.35 m in 1986 to 177.04 m in 1987, 176.65 m in 1988, 176.53 m in 1989, and 176.45 m in 1990. They increased to 176.62 m in 1991, decreased to 176.53 m in 1992, and then increased to 176.83 m in 1993 (NOAA 2007a).

### METHODS

In August 1988, we surveyed a line perpendicular to the shoreline at a randomly selected point and produced a representative cross-section of the wetland (Figure 3). The shoreline elevation was referenced to the 10:00 am, August 30, 1988 lake-level reading from the National Oceanographic and Atmospheric Administration gage at Essexville, Michigan (176.55 m) (NOAA 2007b). Seiches occurred throughout sampling and were monitored by periodic reference to a temporary staff gage. Elevations for placement of sampling transects, which were laid out roughly parallel to the shoreline

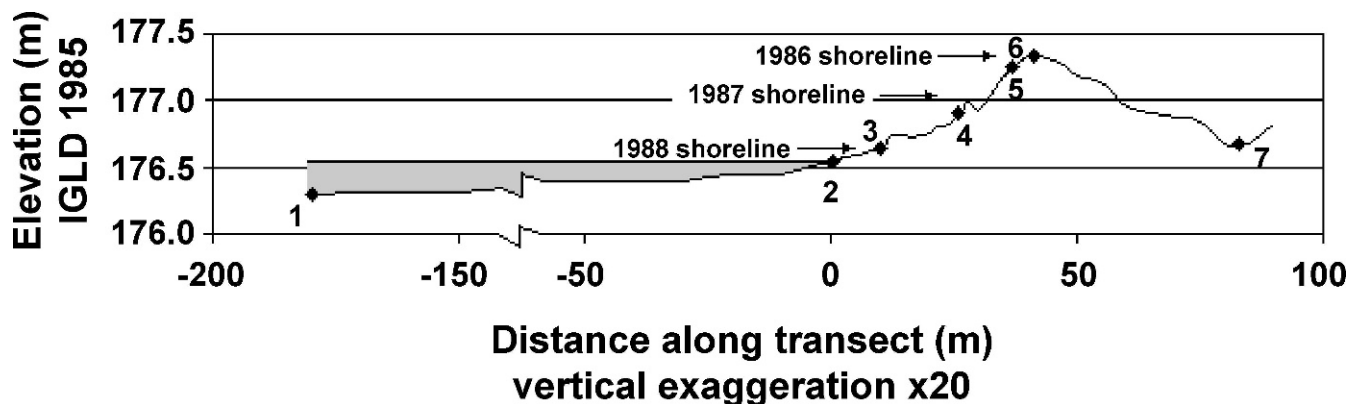


Figure 3. Cross-sectional diagram of Fish Point wetland showing elevations of transects 1–7 that followed topographic contours with specific water-level histories following high lake levels in 1986. Referenced shorelines are May–August means. Water level depicted is from first sampling date (30 August 1988) and referenced to International Great Lakes Datum 1985.

to represent different elevations/water depths (Figures 2, 3), corresponded to important water levels of 1986, 1987, and 1988 (Figure 4). These elevations and relations to lake levels prior to and during sampling years are listed in Table 1.

Following the topographic contour for each of these elevations, transects up to 500 m in length, as permitted by topography at each elevation, were

established. Ten randomly placed 1 m  $\times$  1 m quadrats were sampled along each transect for the presence and optically estimated percent cover of plant species (same observer; 1% increments to 10, then 5% increments). The quadrats extended lake-ward from the transect line. All seven transects were sampled in late August 1988, 1989, and 1990, with different random placement of quadrats each year.

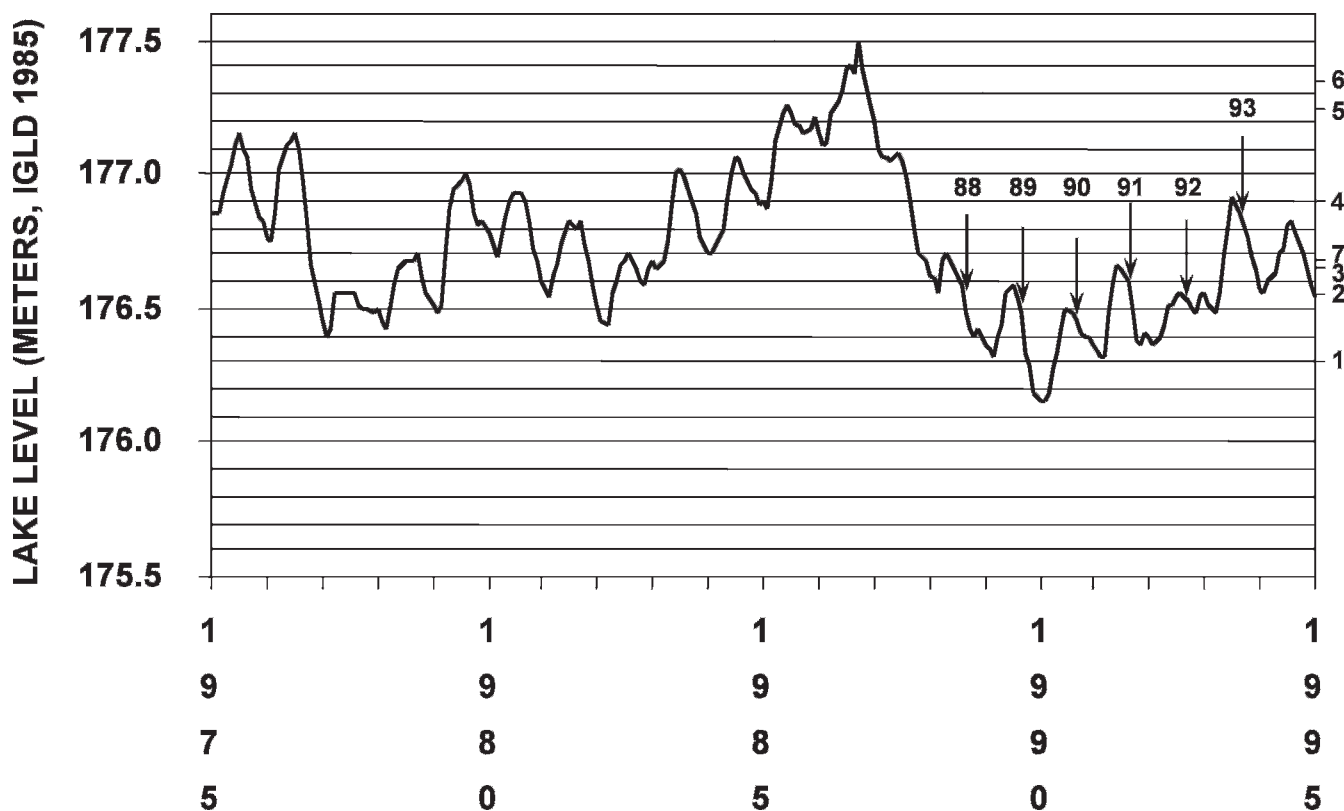


Figure 4. Monthly mean water-level record for Lake Huron from 1975 to 1995 taken from NOAA (2007a) gage at Essexville, Michigan. Elevations of transects 1–7 and sampling periods in 1988–1993 are identified (referenced to International Great Lakes Datum 1985).





Table 2. Continued.

Taxa	1988										1989										1990										1991					1992					1993				
	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7	4	5	4	5	4	5	4	5																
	49.3	73.8	42.8	-	-	-	-	-	-	-	29.7	-	-	-	-	4.1	-	-	-	-	-	-	-	-	-	-	-	-	-																
<i>Najas flexilis</i> (Willdenow) Rostkovius & W. L. E. Schmidt																																													
<i>Najas marina</i> Linnaeus	61.0	28.0	-	-	-	-	-	9.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-																
<i>Nymphaea odorata</i> Aiton	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-																
<i>Panicum capillare</i> Linnaeus	-	-	-	8.9	-	3.1	-	-	-	-	-	3.8	-	-	-	-	-	2.2	2.5	-	0.8	-	1.3	-	1.2	-	3.0	-	-																
<i>Phalaris arundinacea</i> Linnaeus	-	-	-	-	-	-	-	-	-	-	-	-	-	2.6	-	-	-	6.2	-	-	-	-	2.1	2.3	2.2	-	7.3	-	-																
<i>Phragmites australis</i> (Cav.) Trin. ex Steudel	-	-	-	-	-	-	-	-	-	-	-	-	2.0	3.0	-	-	-	-	-	-	-	2.3	-	-	-	4.6	-	-	-																
<i>Pilea pumila</i> (L.) A. Gray	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.1	-	1.8	-	-	-	-	-	-	-	-	-																
<i>Polygonum amphibium</i> Linnaeus	-	-	-	3.6	3.4	-	-	-	-	-	-	6.3	-	1.1	-	-	-	-	1.5	-	-	-	-	-	-	-	-	-	-																
<i>Polygonum lapathifolium</i> Linnaeus	-	-	-	4.4	10.6	5.6	21.4	-	-	-	3.2	3.6	-	1.1	-	-	-	4.4	-	-	5.1	-	-	-	-	-	-	-	-																
<i>Polygonum persicaria</i> Linnaeus	-	-	-	1.6	1.4	-	1.2	-	-	-	-	3.4	-	2.5	-	-	-	4.3	-	2.8	-	-	-	-	-	-	-	-	-																
<i>Polygonum punctatum</i> Buch.- Ham. ex D. Don	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.1	-	-	3.5	2.7	-	-	-	-	-	-	-																
<i>Populus deltoides</i> Marsh.	-	-	-	1.7	-	1.2	-	-	-	-	-	4.1	-	4.5	-	-	-	-	0.8	-	1.6	-	-	-	-	-	-	-	2.5																
<i>Potamogeton granineus</i> Linnaeus	8.4	5.8	-	-	-	-	-	59.9	39.7	41.5	-	-	-	4.0	-	16.0	-	-	-	-	-	-	-	-	-	-	-	-	-																
<i>Potentilla anserina</i> Linnaeus	-	-	-	1.4	3.0	-	-	-	-	-	-	-	-	-	4.1	-	-	-	3.6	-	-	-	6.5	3.1	12.5	-	10.7	-	-																
<i>Rumex maritimus</i> Linnaeus	-	-	-	2.2	1.5	9.8	-	-	-	-	-	1.5	-	-	-	-	5.1	0.7	-	-	0.8	-	-	-	-	1.4	-	-	-																
<i>Sagittaria latifolia</i> Willdenow	-	13.3	11.0	8.8	2.9	1.6	-	-	11.9	-	4.9	-	-	1.3	16.7	-	2.4	-	-	-	0.9	-	-	-	-	3.8	-	-	-																
<i>Salix discolor</i> Muhl.	-	-	-	-	-	-	-	-	-	-	-	1.3	-	-	-	-	-	-	-	-	-	-	3.2	1.2	3.1	2.5	4.9	0.8	-																
<i>Salix exigua</i> Nutt.	-	-	-	7.5	3.6	10.2	-	-	-	-	-	25.3	-	-	-	-	-	9.6	17.3	-	-	-	1.0	19.4	1.7	16.4	2.0	10.5	-																
<i>Schoenoplectus acutus</i> (Muhl. ex Big.) A. Löve & D. Löve	-	-	-	22.5	-	-	-	-	12.1	-	-	-	-	4.0	-	-	-	9.7	0.8	-	-	9.0	-	1.9	-	4.9	0.8	-	-																
<i>Schoenoplectus</i> (dead)	-	-	-	-	63.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-																
<i>Schoenoplectus pungens</i> (Vahl) Palla	-	8.7	8.8	29.8	29.4	4.7	-	-	-	5.4	25.2	22.9	-	-	4.1	27.1	41.3	18.4	9.8	-	-	20.6	15.1	28.8	12.8	20.8	11.1	-	-																
<i>Schoenoplectus tabernaemontani</i> (C. C. Gmelin) Palla	-	-	16.9	9.2	-	-	9.6	-	-	22.0	24.6	-	-	4.9	-	2.4	36.1	-	-	-	2.4	1.5	-	7.1	-	9.6	-	-	-																
<i>Solidago canadensis</i> Linnaeus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.1	1.6	-	-	5.9	1.7	15.3	-	15.9	-	-																
<i>Sonchus arvensis</i> Linnaeus	-	-	-	-	-	-	-	-	-	-	-	1.2	-	-	-	-	-	0.7	14.5	7.3	-	1.2	-	1.5	3.3	-	4.2	-	-																
<i>Spartina pectinata</i> Link	-	-	-	1.5	3.6	-	-	-	-	-	-	5.8	-	-	-	-	-	-	9.2	-	0.8	-	-	-	27.3	-	8.1	-	-																
<i>Symphytotrichum lanceolatum</i> (Willdenow) G. L. Nesom	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.8	13.2	45.2	9.7	18.9	11.7	-	-																
<i>Symphytotrichum puniceum</i> (Linnaeus) A. Löve & D. Löve	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.2	4.8	-	-	-	-	-	-	-	-	-	-																
<i>Symphytotrichum</i> spp.	-	-	-	4.1	1.6	1.2	-	-	-	-	-	5.6	2.0	1.1	-	-	-	11.3	5.9	-	0.8	6.5	-	-	-	-	-	-	-																
<i>Taraxacum officinale</i> F.H. Wiggers	-	-	-	5.6	-	-	-	-	-	-	-	7.8	-	-	-	-	-	2.1	1.5	-	-	-	-	-	3.3	-	0.9	-	-																
<i>Toxicodendron radicans</i> (Linnaeus) O. Kuntze	-	-	-	-	-	-	-	-	-	-	-	5.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-																
<i>Typha angustifolia</i> Linnaeus	-	-	15.0	25.3	19.3	36.9	2.6	-	-	-	12.2	10.9	30.7	4.0	-	21.6	22.6	6.6	5.5	21.1	10.2	14.4	1.5	24.5	2.3	70.5	3.5	-	-																
<i>Typha</i> (dead)	-	-	-	-	-	7.9	-	-	-	-	-	22.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-																
<i>Vallisneria americana</i> Michaux	16.5	10.0	-	-	-	-	46.4	-	-	-	-	-	-	15.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-																
<i>Verbena hastata</i> Linnaeus	-	-	-	-	2.8	5.5	-	-	-	-	-	1.9	9.0	-	-	-	-	-	8.2	10.1	0.8	-	-	-	-	-	-	-	-																



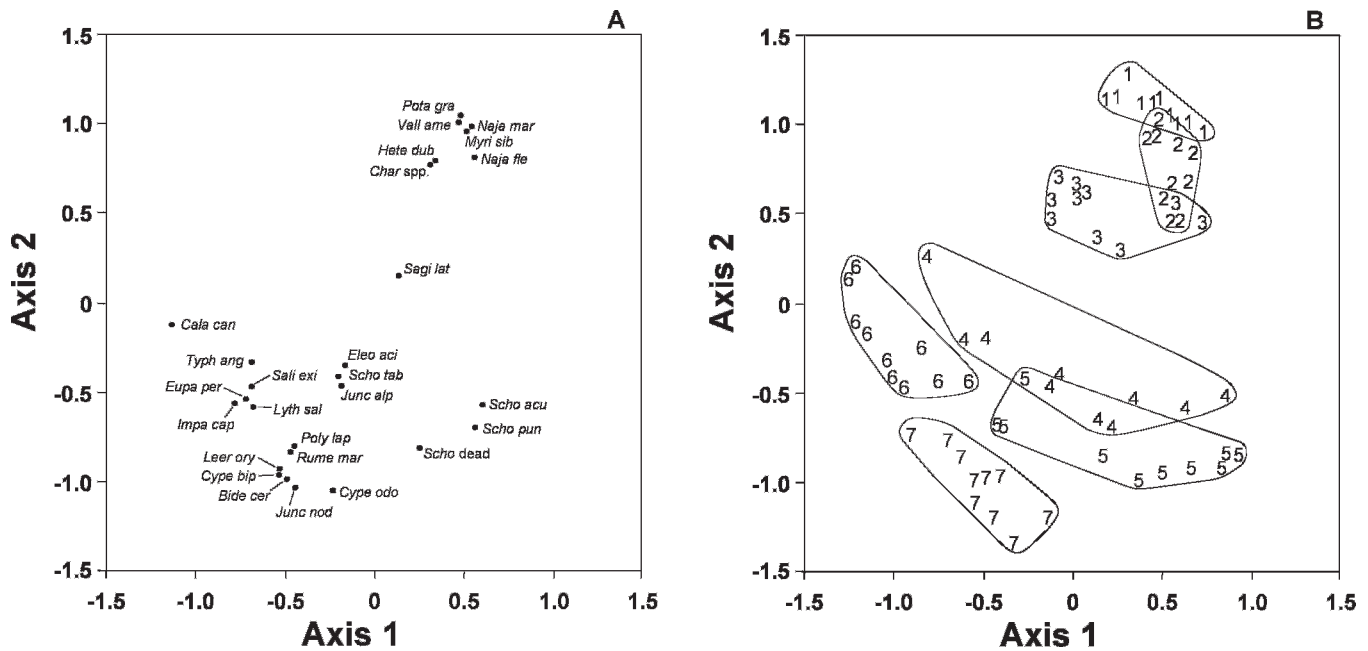


Figure 5. Two-dimensional plot of NMDS ordination of importance value  $\times$  quadrat matrix for 1988 data from Fish Point wetland (autopilot on, Sorensen distance, no species weighting, final stress = 20.40, final stability = 0.00012, number of iterations = 400): A) points plotted are selected taxa; B) points plotted are quadrats along transects 1–7.

to those transects with constant flooding, as the others had more plasticity and were also found on transects that were dewatered in 1988. Quadrats along the seiche-zone transect 3 contained only eight taxa, none of which were unique to that transect. Transect 6 had mostly been dry, with the exception of shallow flooding in 1986; quadrats with this flooding history contained 24 taxa, of which only five were unique. Lake-level changes from 1986 to 1988 caused transects 4, 5, and 7 to pass from flooded to dewatered conditions (Figure 4); these transects supported 43 taxa, of which 21 were unique to that hydrologic history.

**1988 Ordination.** Axis 2 of the NMDS ordination of taxa separated the aquatic taxa of transects 1–3 from the vegetation found along transects at higher elevations (Figure 5A); both Axes 1 and 2 assisted in separating the different taxa at higher elevations. Ordination of individual quadrats showed the obvious effect of water depth (elevation vs. lake level) on development of wetland plant assemblages (Figure 5B). Quadrats along transects 1, 2, and 3 that were in or close to the water in 1986–88 and contained aquatic taxa had higher Axis 2 scores, with some sorting among those transects related to depth. Transects 4 and 5 were under water in 1986, transect 5 was emerged in 1987, and transect 4 became emerged also in 1988. Quadrats along these two transects sorted out by the number of years out of the water. Transect 6 was minimally flooded for

part of 1986 and had its own assemblage. Transect 7 was under water in 1986 and out in 1988, but it is protected from wave action, so it had a different assemblage of species. Because all transects were selected according to distinct water-depth histories, the separation of those transects in Figure 5B demonstrates the role of water-level fluctuations and water-level history in determining wetland plant communities in that year.

#### Continued Response to Lake-Level Change

**1989–1993 Floristics.** In 1989, 63 taxa were sampled, of which 46 appeared in at least three quadrats along one transect (Table 2). Taxa of note (IV > 20) on individual transects included 1) *Potamogeton gramineus*, *M. sibiricum*, *Vallisneria americana*, and *Chara* spp.; 2) *Chara* spp. and *P. gramineus*; 3) *Chara* spp., *P. gramineus*, *N. flexilis*, and *Schoenoplectus tabernaemontani*; 4) *Juncus nodosus*, *S. pungens*, *S. tabernaemontani*, and *Eleocharis erythropoda*; 5) *Salix exigua*, *Impatiens capensis*, and *S. pungens*; 6) *I. capensis*, *T. angustifolia*, and dead *Typha*; and 7) *Lythrum salicaria* and *E. perfoliatum*.

In 1990, 76 taxa were sampled, of which 56 appeared in at least three quadrats along one transect (Table 2). Taxa of note on individual transects included 1) *M. sibiricum*, *H. dubia*, and *Chara* spp.; 2) *Chara* spp., *S. pungens*, and *T. angustifolia*; 3) *Chara* spp., *S. pungens*, *S. tabernaemontani*, and *S. rigida*; 4) *Juncus nodosus*, *S. pungens*, *S. tabernaemontani*, and *Eleocharis erythropoda*; 5) *Salix exigua*, *Impatiens capensis*, and *S. pungens*; 6) *I. capensis*, *T. angustifolia*, and dead *Typha*; and 7) *Lythrum salicaria* and *E. perfoliatum*.



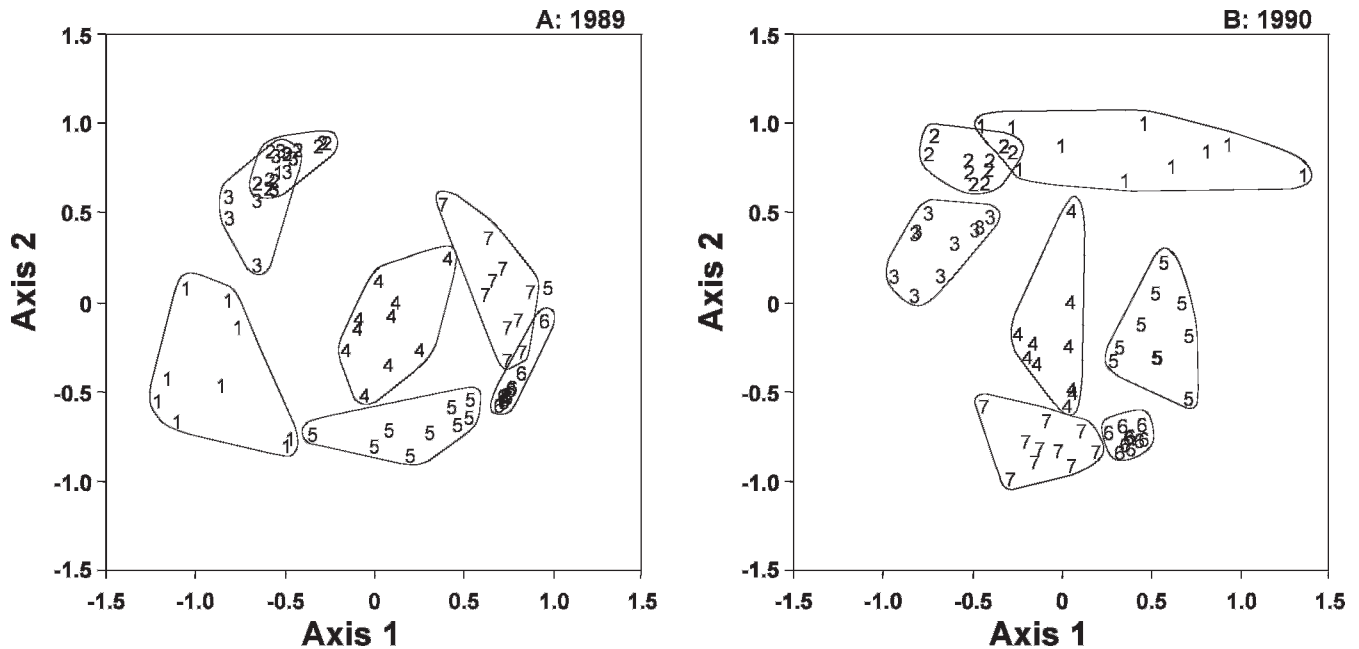


Figure 6. Two-dimensional plot of NMDS ordination of importance value  $\times$  quadrat matrix for data in 1989 and 1990 for Fish Point wetland: A) points plotted are quadrats along transects 1–7 in 1989 (autopilot on, Sorensen distance, no species weighting, final stress = 13.85, final stability = 0.00001, number of iterations = 159); B) points plotted are quadrats along transects 1–7 in 1990 (autopilot on, Sorensen distance, no species weighting, final stress = 13.56, final stability = 0.00057, number of iterations = 400).

*montani*, *T. angustifolia*, and *E. erythropoda*; 4) *Eleocharis olivacea* and *E. perfoliatum*; 5) *Euthamia graminifolia*; 6) *I. capensis* and *T. angustifolia*; and 7) *I. capensis* and *L. salicaria*.

The total number of taxa sampled on transect 4 increased from 19 in 1988 and 18 in 1989 to 36 in 1990. The total then decreased to 30 in 1991, 26 in 1992, and 21 in 1993 (Table 2 plus taxa not shown). The total number of taxa sampled on transect 5 increased from 24 in 1988 to 35 in 1989 to 41 in 1990, then decreased to 36 in 1991 and 31 in 1992, and then increased to 39 in 1993 (Table 2 plus taxa not shown).

**1989 and 1990 Ordinations.** With the exception of one outlier quadrat each on transects 1 and 5, the general distinction of plant assemblages by transect (i.e., water-level history) remained in 1989, with dewatered transects 2 and 3 continuing to show some overlap but now separated from still-flooded transect 1 (Figure 6A). By 1990, virtually complete separation was found among the plant assemblages of the seven transects (Figure 6B).

**1988–1993 Ordination.** Results of the NMDS ordination using all 1988 data and multi-year data from transects 2–6 (Figure 7) suggest that the aquatic plant assemblages along transects 2 and 3 remained similar from 1988 to 1989 when water

levels dropped about 12 cm (Table 1) because seiches were able to keep those elevations wet. However, when water levels dropped an additional 8 cm in 1990, transect 2 and 3 plant assemblages began to resemble more closely those of transect 4, which was first emerged by 25 cm in 1988. The ordinations of transects 2 and 3 (1990) and transect 4 (1988, 1989, 1993) in Figure 7 were influenced similarly by species such as *S. pungens*, *S. tabernaemontani*, *T. angustifolia*, and *E. erythropoda*. However, transect 2 retained more aquatic taxa, such as *Chara*, *P. gramineus*, *H. dubia*, and *M. sibiricum* in 1990 (Table 2). Transect 6 plant assemblages, which were already well out of the water in 1988, shifted in composition in 1989 and 1990, with a decrease in dominance of *C. canadensis* and *E. perfoliatum* (Figure 7, Table 2).

Longer term changes on transects 4 and 5 were more complicated and influenced by both changes in composition and percent cover. Transect 4 plant assemblages were similar in 1988 and 1989, the first two years out of water. However, the vegetation on transect 4 shifted in 1990, 1991, and 1992 to a composition more closely resembling transect 5 in 1988 and 1989 (second and third year out of water) and transect 6 in 1988 (second year out of water) (Figure 7). The ordination of those transects by year was influenced largely by *S. pungens*, *T. angustifolia*,

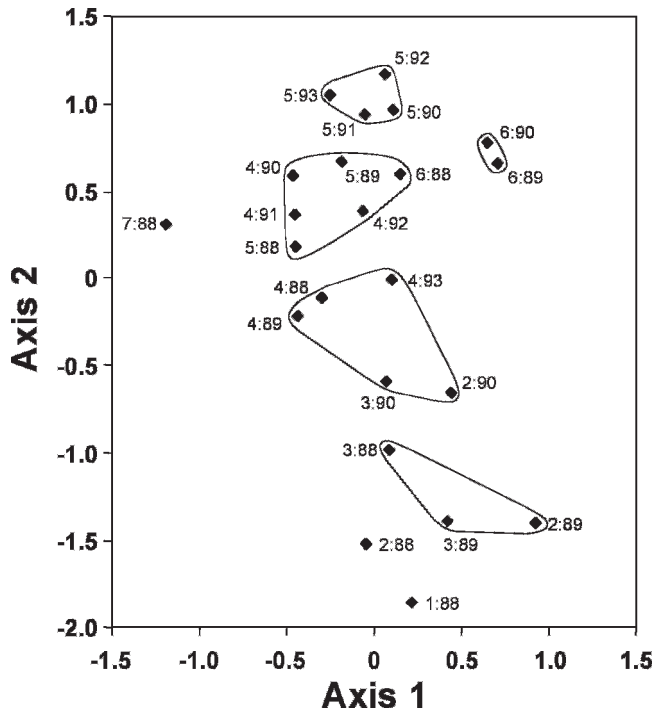


Figure 7. Two-dimensional plot of NMDS ordination of importance value  $\times$  transect matrix for data from Fish Point wetland showing changes in plant communities on transects 4 and 5 between years and relative to adjacent transects. Points plotted (transect:year) are transects 1–7 in 1988, 2–6 in 1989 and 1990, and 4–5 in 1991–1993 (autopilot off, Sorenson distance, no species weighting, final stress = 14.81, final stability = 0.00730, number of iterations = 100).

*E. perfoliatum*, *S. exigua*, and *Juncus alpinoarticulatus* and to a lesser extent by *C. canadensis*, *E. graminifolia*, *J. nodosus*, and several other species (Table 2). When lake levels increased in 1993 (Figure 4), transect 4 returned to the seiche zone, and the plant assemblages again more closely resembled those of 1988 and 1989 (Figure 7), plus the return of aquatic species such as *Lemna minor*, *Nymphaea odorata*, *N. flexilis*, and *N. marina* (Table 2).

As the number of years of emersion increased (1989–1993), transect 5 vegetation shifted (Figure 7). Ordination of these transects by year was influenced by many species. *Calamagrostis canadensis*, *E. graminifolia*, and *S. exigua* were prominent in 1989–1993, with *S. pungens*, *Solidago canadensis*, *Potentilla anserina*, *Phalaris arundinacea*, *E. perfoliatum*, and *T. angustifolia* also appearing in all years. Species such as *Spartina pectinata*, *Sonchus arvensis*, *Cirsium arvense*, and *Symphytotrichum lanceolatum* were shared in most years and also affected the ordination (Figure 7, Table 2).

### Individual Species Response

Tracking of the responses of selected individual species with respect to water depth or elevation above lake level and number of years since emersion provided no clear definition of hydrologic niches for most taxa, with the obvious exception that submersed species such as *M. exalbenscens*, *N. marina*, and *V. americana* did not survive drawdown conditions. On the other hand, *Chara* spp., *H. dubia*, and *P. gramineus* continued to grow along transect 3 in 1990 when it was about 20 cm above lake level but kept wet by periodic seiches (Tables 1 and 2). Mudflat annuals such as *Bidens*, *Cyperus*, and *Polygonum* generally appeared in the first year of emersion (1988) on transects 4 and 7, decreased in importance in the second year, then increased again in the third year (Table 2). In the first year of emersion, mudflat taxa were considerably more prominent on transect 7, where the seed bank has been protected from waves (Figure 3).

Many emergent species became established near the shoreline as water levels receded. *Schoenoplectus pungens* was able to grow in shallow standing water and across the full span of higher elevations, but Importance Values were highest in the middle of that range (Table 2). *Typha angustifolia* became established on transects when sediments were exposed by lower lake levels but also persisted in mature stands along transect 6 at the highest elevation. *Schoenoplectus tabernaemontani* grew mostly at elevations not far above lake level, and *E. erythropoda* was more prevalent at higher elevations. The abundance of all four species decreased on transects 4 and 5 when water levels decreased in 1990 and increased again on transect 4 when lake levels increased in 1993 (Tables 1 and 2). *Typha angustifolia* abundance remained low in 1993 on higher and drier transect 5; it also decreased from 1988 to 1990 on transect 6 at even higher elevation. The distribution of *E. perfoliatum* and *C. canadensis* shifted to lower elevations when water levels receded. However, *Eupatorium* and *Calamagrostis* decreased in importance on transect 4 when lake levels increased in 1993 (Table 2).

## DISCUSSION

### Role of Water-Level Fluctuations

Our study design incorporated transects that followed elevation contours with specific recent water-level/depth histories; our data from 1988 (Table 2, Figure 5) thus demonstrated for this site that water-level fluctuations are an important driving force in development of wetland vegetation

in the Great Lakes, as conceptualized by Keddy and Reznicek (1986) and modeled by Painter and Keddy (1992). Ordinations of 1989 and 1990 data shown in Figure 6 reinforce this conclusion, as they represent a continuation of separation based on water-level/depth histories.

The data from 1988 sampling also demonstrate the importance of alternating flooded/dewatered conditions in generating diversity in the plant community (Keddy 2000, van der Valk 2000), as transects that were flooded and then dewatered (4, 5, 7) contained substantially more taxa than those that were always flooded (1, 2), in the seiche zone (3), or briefly flooded (6). Although transect 7 had the same water-level history as transect 3 when sampled in 1988, the assemblage of plants differed greatly, thus demonstrating the importance of protection from waves in generating plant diversity along lakeshores (Keddy 1984a,b, Keddy and Fraser 2000).

#### Modeling Plant Community Response

Several models have been proposed for predicting the response of wetland and shoreline vegetation to water-level changes. Do they apply to the conditions and responses we observed? Keddy and Reznicek (1986) proposed a conceptual model that seems largely accurate and has been well-accepted in the Great Lakes research community; however, it provides no time scale for vegetation change. In addition, the data from our site suggest that the strand zone may not respond as predicted because seiches keep it too wet for annuals and ruderals to colonize readily from the seed bank. Harris et al. (1981) provided a descriptive model of vegetation change in wetlands of Green Bay in Lake Michigan. However, the scale of time change is short and the non-quantitative, predicted vegetation response is for vegetation types vs. area of wetland rather than changes in plant community composition. Quinlan and Mulamootill (1987) used a series of aerial photographs to develop a quantitative model for percent of various vegetation types in barrier-beach wetlands in Lake Ontario. However, such a model is highly dependent on the basin morphometry of individual wetlands and again provides no time scale or means to assess any time lag in vegetation response. Painter and Keddy (1992) used an exponential model for predicting the relative area of wet meadow and marsh vegetation in Great Lakes wetlands over decade-scale time spans with differing water levels. This model is more widely applicable and also addresses time lags; however, it too lacks the species-level description of vegetation change needed to relate to our data.

The conceptual model proposed by Day et al. (1988) from studies of shoreline vegetation on the Ottawa River in Ontario, Canada provides a time scale and the potential to evaluate sequences and time lags among different plant communities. It plots duration of flooding against a gradient of exposure to wave attack and the resulting gradients of litter removal and soil fertility. According to this model, temporary flooding with less wave attack and more litter would result in domination by *Typha*, equivalent to our Transect 6. Intermediate elevations with more wave exposure, less litter, and less fertility would be dominated by species with deeply buried rhizomes, such as *S. pungens*, equivalent to our Transects 5, 4, and eventually 3. Lower elevations that are flooded would support aquatic species. This model is a more detailed version of Keddy and Reznicek (1986) and Maynard and Wilcox (1997) that adds additional gradients; however, it was presented by the authors with stated need for refinement by field studies and still lacks specificity regarding the time line.

Yet other approaches were recommended by Keddy and Fraser (2000). In one example, they used shoreline wetland data from a lake in Nova Scotia, Canada (Keddy 1984) to demonstrate that species richness was greater in the middle shoreline zone that was subject to year-to-year fluctuations in water levels. Plotting number of taxa identified on shoreline transects 1–6 in our study against the relative elevation above water level provided similar results, as shown in Figure 8A,B. In the years sampled, transects 1–3 were either flooded or wetted by seiche action; the brief flooding of transect 6 in 1986 did little to affect species richness. As expected, transects 4 and 5 that were flooded and then dewatered supported the most taxa.

In another example, Keddy and Fraser (2000) used data from Hill et al. (1998), in which the frequency of flooding was plotted against the depth of flooding or amplitude of water-level change. Limited data suggested that different plant communities with differing species richness would occur along shorelines separated by these axes. After testing many options, we modified this approach by plotting our transects in various years on orthogonal axes of years out of water and distance above water in each specific year, factors also found important by Odland and del Moral (2002) in plant succession following drawdown. The resulting model (Figure 9A) resembled the Keddy and Fraser (2000) illustration (Figure 9B) of data from Hill et al. (1998). It identified four vegetation types that correspond to both elevation above water and duration of drawdown. The grouped transects

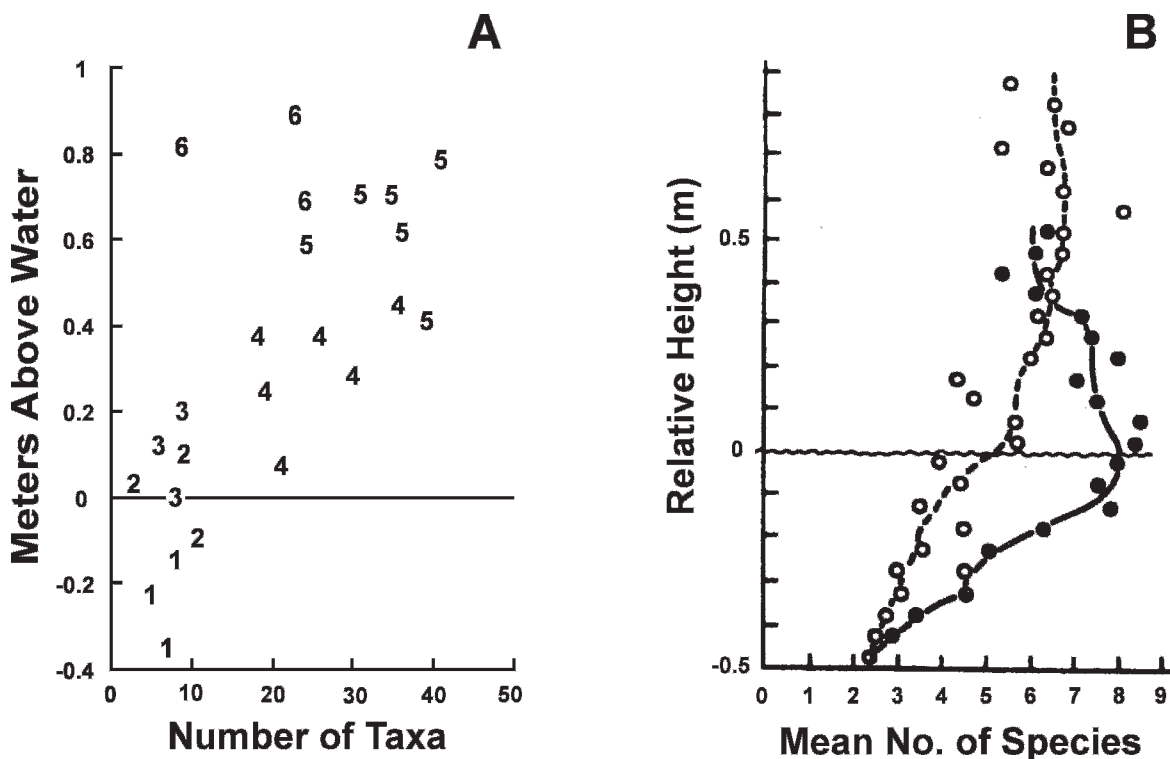


Figure 8. A) Relation between the number of taxa sampled along shoreline transects 1–6 at Fish Point wetland (1988–1993) and relative elevation with respect to lake level (numbers plotted refer to transects; see Table 1 to correlate with years). B) Relation shown by Keddy and Fraser (2000) between mean number of species and August water level in shoreline wetlands of a lake in Nova Scotia, Canada; data from Keddy (1984).

sorted out by communities that can also be grouped in the NMDS ordination (Figure 7). If near lake level ( $< 0.15$  m above), vegetation in the first year out of water will still be dominated by aquatic taxa such as *Chara* spp. and *P. gramineus* (2:89, 3:89). However, in the second year (2:90, 3:90), the vegetation will start gaining emergent species such as *S. pungens*, *S. tabernaemontani*, *T. angustifolia*, *J. alpinoarticulatus*, and *E. erythropoda*, thus more closely resembling transects 0.15–0.4 m above lake level in years 1 and 2 (4:88, 4:89). In ensuing years, vegetation that is 0.4 m out of water (4:90) shifts to resemble that of elevations  $> 0.5$  m above lake level in the first year out of water (5:88, 6:88), dominated by *T. angustifolia*, *S. pungens*, *E. perfoliatum*, *S. exigua*, and *C. canadensis*. This vegetation type may also be maintained for a couple years (e.g., 5:89, 4:91, 4:92) but may change once again as the number of years out of water continues to increase (5:90, 5:91, 5:92, 5:93; 6:89, 6:90), with dominants *I. capensis*, *C. canadensis*, *T. angustifolia*, *E. perfoliatum*, and *Solidago canadensis*. Return of transect 4 to periodic flooding by seiches in 1993 (Figure 4) caused enough vegetation change to affect its position in the ordination (Figure 7) and make it appear as an outlier in the model (Figure 9A).

However, the X-axis placement at six years out of water may not be appropriate given intermittent reflooding of transect 4 by seiches in 1993.

This model demonstrates that the vegetation response following dewatering is due to a combination of elevation above water (how dry it is in the year sampled) and the length of time since dewatering. Resulting vegetation types can develop as an initial response to drawdown at a given elevation or wetness (e.g., 3:89, 4:88, 5:88) or a delayed response in which the time lag achieves the same result as a higher elevation (e.g., 3:90, 4:90, 5:90) (Figure 9). The time lag appears to be two years, which is within the 2–4 year range suggested by others (Keddy and Fraser 2000, Wilcox and Xie 2007, Wilcox et al. 2008), although seiches may influence the outcome. We also recognize that reflooding of transects 2 and 3 in years not sampled would likely have allowed them to support aquatic taxa again. This model provides an example of the type of field data collection suggested by Day et al. (1988) that is necessary to refine models for predicting vegetation response to water-level change. A similar approach might be taken for wetlands elsewhere in the Great Lakes that support a different assemblage of species.



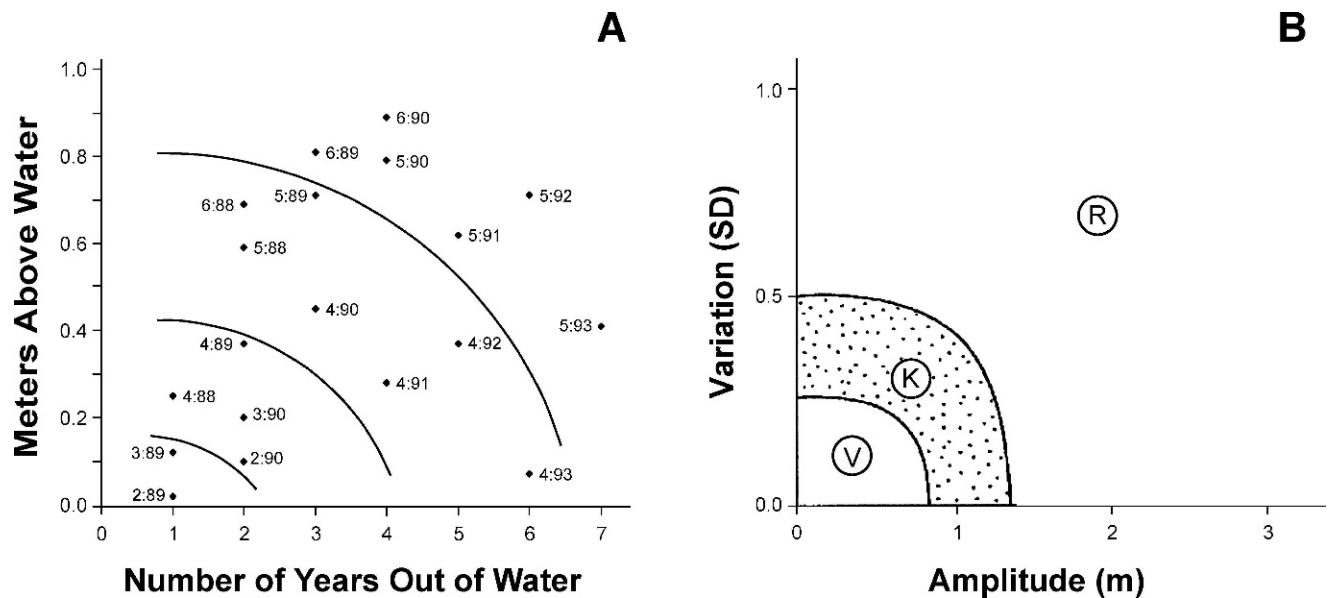


Figure 9. A) Model of response of wetland vegetation at Fish Point wetland to decline in lake level following high levels in 1986. Points plotted are transect:year showing meters above water vs. the number of years out of water at the time of sampling. B) Modeling approach recommended by Keddy and Fraser (2000), as illustrated using data from Hill et al. (1998), where plotting of amplitude of water-level change against standard deviation for three lakes (Vaughn, Kejimikujik, Rossignol) in Nova Scotia, Canada correlates to a corridor of high species richness (K).

#### Relation to Shoreline Management Actions

Our quantitative data and model document the previously reported importance of water-level fluctuations in driving vegetative change and resultant habitat diversity in Lake Huron wetlands (Wilcox 1995); they illustrate the natural response of wetlands to periodic low lake levels. The historic (Figure 1) and paleo lake-level records (Baedke and Thompson 2000, NOAA 2007a) both demonstrate the occurrence of lower lake levels approximately every 30–33 years, which is part of a natural, climate-driven pattern (Fraser et al. 1990, Thompson 1992). Thus, following lows in the 1930s and 1960s, the return of lower lake levels beginning in 1999 was not unexpected. Indeed, it was an important ecological event that restored wetland vegetation without the costs of active management (Wilcox and Krygier 2002). Our work therefore underscores the importance of retaining new vegetation derived from the seed bank during periodic low lake levels, despite perceived conflicts with certain human activities (Wilcox and Krygier 2002). This may become increasingly important if lake levels recede further than in the past in response to global warming. At some locations around the Great Lakes, the role of ground water in maintaining soil moisture along exposed shorelines must also be factored into management actions (Burkett et al. 2005).

One difference between revegetation during the most recent low lake level and prior events is an increase in the prevalence of invasive plant species. In our study, *Typha angustifolia* established from seed along all transects that were dewatered, but it then decreased in abundance at higher elevations, most likely because it was too dry for survival (Wilcox et al. 2008). An extended low lake-level event now or in the future might thus limit cattail invasion at upper elevations. Haplotype M (Salt-onstall 2002) of *Phragmites australis* (common reed) became prominent along the dewatered shoreline of Saginaw Bay following the latest lake-level decline (Albert 2005, Uzarski and Burton 2005, MDEQ 2006), as it can expand rapidly via an extensive system of horizontal rhizomes (Haslam 1972, Amsberry et al. 2000). *Phragmites* was the target of many of the maintenance operations instituted in selected areas of exposed lake bottoms (Wilcox and Krygier 2002). However, many other wetland plant taxa were also affected, as well as faunal communities that use them as habitat. The conflict between human actions and natural processes might be reduced if selective control methods can be developed for *Phragmites*, shoreline property owners are taught the value of restored wetland plant communities to human activities such as fishing and birdwatching, and permits for mechanical removal of plants are restricted to designated invasive species

while retaining native vegetation derived from the seed bank.

### ACKNOWLEDGMENTS

This study was partly funded by the U.S. Corps of Engineers as part of the International Joint Commission Water Level Reference from the U.S. and Canadian governments. Field data in various years were collected with the assistance of the late Barbara Madsen, Donald Schloesser, and Lisa Kensler. Species identifications for difficult taxa were made or confirmed by Tony Reznicek. Ordinations were completed by Martha Carlson, who also produced most of the figures. Paul Keddy, Arnold van der Valk, and Kurt Kowalski provided helpful reviews of an early version of the manuscript. This article is contribution 1473 of the USGS Great Lakes Science Center.

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Manuscript received 18 July 2007; accepted 21 February 2008.